TREATISE ON INVERTEBRATE PALEONTOLOGY

Part O
TRILOBITA
Revised

Volume 1: Introduction

H. B. WHITTINGTON, B. D. E. CHATTERTON, S. E. SPEYER, R. A. FORTEY,
R. M. OWENS, W. T. CHANG, W. T. DEAN, P. A. JELL, J. R. LAURIE,
A. R. PALMER, L. N. REPINA, A. W. A. RUSHTON, J. H. SHERGOLD,
E. N. K. CLARKSON, N. V. WILMOT, AND S. R. A. KELLY

Prepared under Sponsorship of
The Geological Society of America, Inc.

PART O, Revised

TRILOBITA

Introduction, Order Agnostina, Order Redlichiida

VOLUME 1

H. B. Whittington, B. D. E. Chatterton, S. E. Speyer, R. A. Fortey,
R. M. Owens, W. T. Chang, W. T. Dean, P. A. Jell, J. R. Laurie,
A. R. Palmer, L. N. Repina, A. W. A. Rushton, J. H. Shergold,
E. N. K. Clarkson, N. V. Wilmot, and S. R. A. Kelly

CONTENTS

INFORMATION ON TREATISE VOLUMES

Parts of the *Treatise* are distinguished by assigned letters with a view to indicating their systematic sequence while allowing publication of units in whatever order each is made ready for the press. Copies can be obtained from the Publication Sales Department, The Geological Society of America, 3300 Penrose Place, P.O. Box 9140, Boulder, Colorado 80301.

VOLUMES ALREADY PUBLISHED

Part A. INTRODUCTION, xxiii + 569 p., 371 fig., 1979.

Part C. PROTISTA 2 (Sarcodina, Chiefly "Thecamoebians" and Foraminiferida), xxxi + 900 p., 5,311 fig., 1964.

Part D. PROTISTA 3 (Chiefly Radiolaria, Tintinnina), xii + 195 p., 1,050 fig., 1954.

Part E. ARCHAEOCYATHA, PORIFERA, xviii + 122 p., 728 fig., 1955.

Part E, Revised. ARCHAEOCYATHA, Volume 1, xxx + 158 p., 871 fig., 1972.

Part F. COELENTERATA, xvii + 498 p., 2,700 fig., 1956.

Part F. COELENTERATA, Supplement 1 (Rugosa and Tabulata), xl + 762 p., 3,317 fig., 1981.

Part G. BRYOZOA, xii + 253 p., 2,000 fig., 1953.

Part G, Revised. BRYOZOA, Volume 1 (Introduction, Order Cystoporata, Order Cryptostomata), xxvi + 626 p., 1,595 fig., 1983.

Part H. BRACHIOPODA, xxxii + 927 p., 5,198 fig., 1965.

Part H, Revised. BRACHIOPODA (Introduction), xx + 539 p., 417 fig., 40 tables, 1997.

Part I. MOLLUSCA 1 (Mollusca General Features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda General Features, Archaeogastropoda, Mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii + 351 p., 1,732 fig., 1960.

Part K. MOLLUSCA 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii + 519 p., 2,382 fig., 1964.

Part L. MOLLUSCA 4 (Ammonoidea), xxii + 490 p., 3,800 fig., 1957.

Part L, Revised. MOLLUSCA 4, Volume 4 (Cretaceous Ammonoidea), xx + 362 p., 2,070 illus. on 216 fig., 1996.

Part N. MOLLUSCA 6 (Bivalvia), Volumes 1 and 2 (of 3), xxxvii + 952 p., 6,198 fig., 1969; Volume 3, iv + 272 p., 742 fig., 1971.

Part O. ARTHROPODA 1 (Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha), xix + 560 p., 2,880 fig., 1959.

Part P. ARTHROPODA 2 (Chelicerata, Pycnogonida, Palaeoisopus), xvii + 181 p., 565 fig., 1955.

Part Q. ARTHROPODA 3 (Crustacea, Ostracoda), xxiii + 442 p., 3,476 fig., 1961.

Part R. ARTHROPODA 4, Volumes 1 and 2 (Crustacea Exclusive of Ostracoda, Myriapoda, Hexapoda), xxxvi + 651 p., 1,762 fig., 1969.

Part R. ARTHROPODA 4, Volumes 3 and 4 (Hexapoda), xxii + 655 p., 1,489 fig., 1992.

Part S. ECHINODERMATA 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), xxx + 650 p., 2,868 fig., 1967 [1968].

Part T. ECHINODERMATA 2 (Crinoidea), Volumes 1–3, xxxviii + 1,027 p., 4,833 fig., 1978.

Part U. ECHINODERMATA 3 (Asterozoans, Echinozoans), xxx + 695 p., 3,485 fig., 1966.

Part V. GRAPTOLITHINA, xvii + 101 p., 358 fig., 1955.

Part V, Revised. GRAPTOLITHINA, xxxii + 163 p., 507 fig., 1970.

Part W. MISCELLANEA (Conodonts, Conoidal Shells of Uncertain Affinities, Worms, Trace Fossils, Problematica), xxv + 259 p., 1,058 fig., 1962.

Part W, Revised. Miscellanea, Supplement 1 (Trace Fossils and Problematica), xxi + 269 p., 912 fig., 1975.

Part W, Revised. Miscellanea, Supplement 2 (Conodonta), xxviii + 202 p., frontis., 858 fig., 1981.

THIS VOLUME

Part O, Revised. Trilobita (Introduction, Order Agnostida, Order Redlichiida), xxiv + 530 p., 309 fig., 1997.

VOLUMES IN PREPARATION

Part B. Protista 1 (Chrysomonadida, Coccolithophorida, Charophyta, Diatomacea, etc.).

Part E, Revised. Porifera. Volume 2.

Part G, Revised. Bryozoa (additional volumes).

Part H, Revised. Brachiopoda (additional volumes).

Part I. Introduction to Mollusca (part).

Part J. Mollusca 2 (Caenogastropoda, Streptoneura exclusive of Archaeogastropoda, Euthyneura).

Part L, Revised. Mollusca 4 (Ammonoidea) (additional volumes).

Part M. Mollusca 5 (Coleoidea).

Part O, Revised. Arthropoda 1 (Trilobita) (additional volumes).

Part Q, Revised. Arthropoda 3 (Ostracoda).

EDITORIAL PREFACE

From the outset the aim of the *Treatise on Invertebrate Paleontology* has been to present a comprehensive and authoritative yet compact statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early *Treatise* volumes was undertaken by a small group with a synoptic view of the taxa being monographed. Two or perhaps three specialists worked together, sometimes co-opting others for coverage of highly specialized taxa. Recently, however, both new *Treatise* volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. This volume, Part O, Arthropoda 1, Revised, the first of a series of volumes on the trilobites, has been prepared by such a team of specialists whose work was coordinated by Professor H. B. Whittington. Editorial matters specific to this volume are

discussed near the end of this editorial preface.

ZOOLOGICAL NAMES

Questions about the proper use of zoological names arise continually, especially questions regarding both the acceptability of names and alterations of names that are allowed or even required. Regulations prepared by the International Commission on Zoological Nomenclature (ICZN) and published in 1985 in the *International Code of Zoological Nomenclature,* hereinafter referred to as the *Code,* provide procedures for answering such questions. The prime objective of the *Code* is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding

unwarranted restrictions on freedom of thought and action of systematists. Priority of names is a basic principle of the *Code,* but under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Commission, ever aware of the changing needs of systematists, is undertaking a revision of the *Code* that will further enhance nomenclatorial stability. Nevertheless, the nomenclatorial tasks that confront zoological taxonomists are formidable and have often justified the complaint that the study of zoology and paleontology is too often merely the study of names rather than the study of animals. It is incumbent upon all systematists, therefore, at the outset of their work to pay careful attention to the *Code* to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise,* especially in this volume. Terminology is explained, and examples are given of the style employed in the nomenclatorial parts of the systematic descriptions.

GROUPS OF TAXONOMIC CATEGORIES

Each taxon belongs to a category in the Linnaean, hierarchical classification. The *Code* recognizes three groups of categories, a species-group, a genus-group, and a family-group. Taxa of lower rank than subspecies are excluded from the rules of zoological nomenclature, and those of higher rank than superfamily are not regulated by the *Code.* It is both natural and convenient to discuss nomenclatorial matters in general terms first

and then to consider each of these three, recognized groups separately. Especially important is the provision that within each group the categories are coordinate, that is, equal in rank, whereas categories of different groups are not coordinate.

FORMS OF NAMES

All zoological names can be considered on the basis of their spelling. The first form of a name to be published is defined as the original spelling (*Code,* Article 32), and any form of the same name that is published later and is different from the original spelling is designated a subsequent spelling (*Code,* Article 33). Not every original or subsequent spelling is correct.

ORIGINAL SPELLINGS

If the first form of a name to be published is consistent and unambiguous, the original is defined as correct unless it contravenes some stipulation of the *Code* (Articles 11, 27 to 31, and 34) or unless the original publication contains clear evidence of an inadvertent error in the sense of the *Code,* or, among names belonging to the family-group, unless correction of the termination or the stem of the type genus is required. An original spelling that fails to meet these requirements in defined as incorrect.

If a name is spelled in more than one way in the original publication, the form adopted by the first reviser is accepted as the correct original spelling, provided that it complies with mandatory stipulations of the *Code* (Articles 11 and 24 to 34).

Incorrect original spellings are any that fail to satisfy requirements of the *Code,* represent an inadvertent error, or are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and, therefore, cannot enter into homonymy or be used as replacement names; and they call for correction. For example, a name originally published with a

diacritical mark, apostrophe, dieresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel in a name derived from a German word or personal name unfortunately requires the insertion of *e* after the vowel. Where original spelling is judged to be incorrect solely because of inadequacies of the Greek or Latin scholarship of the author, nomenclatorial changes conflict with the primary propose of zoological nomenclature as an information retrieval system. One looks forward with hope to a revised *Code* wherein rules are emplaced that enhance stability rather than classical scholarship, thereby facilitating access to information.

SUBSEQUENT SPELLINGS

If a subsequent spelling differs from an original spelling in any way, even by the omission, addition, or alteration of a single letter, the subsequent spelling must be defined as a different name. Exceptions include such changes as an altered termination of adjectival specific names to agree in gender with associated generic names; changes of family-group names to denote assigned taxonomic rank; and corrections that eliminate originally used diacritical marks, hyphens, and the like. Such changes are not regarded as spelling changes conceived to produce a different name. In some instances, however, species-group names having variable spellings are regarded as homonyms as specified in the *Code* (Article 58).

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If "demonstrably intentional" (*Code,* Article 33, p. 73), the change is designated as an emendation. Emendations may be either justifiable or unjustifiable. Justifiable emendations are corrections of incorrect original spellings, and these take the authorship and date of the original spellings. Unjustifiable emendations are names having their own status in nomenclature, with author and date of their publication. They are junior, objective synonyms of the name in its original form.

Subsequent spellings, if unintentional, are defined as incorrect subsequent spellings. They have no status in nomenclature, do not enter into homonymy, and cannot be used as replacement names.

AVAILABLE AND UNAVAILABLE NAMES

Editorial prefaces of some previous volumes of the *Treatise* have discussed in appreciable detail the availability of the many kinds of zoological names that have been proposed under a variety of circumstances. Much of that information, while important, does not pertain to the present volume, in which authors have used fewer terms for such names. The reader is referred to the *Code* (Articles 10 to 20) for further details on availability of names. Here, suffice it to say that an available zoological name is any that conforms to all mandatory provisions of the *Code.* All zoological names that fail to comply with mandatory provisions of the *Code* are unavailable and have no status in zoological nomenclature. Both available and unavailable names are classifiable into groups that have been recognized in previous volumes of the *Treatise,* although not explicitly differentiated in the *Code.* Among names that are available, these groups include inviolate names, perfect names, imperfect names, vain names, transferred names, improved or corrected names, substitute names, and conserved names. Kinds of unavailable names include naked names (see *nomina nuda* below), denied names, impermissible names, null names, and forgotten names.

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the *Code,* which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition, or indication (*Code,* Article 12) and names

published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen novum*) of a preexisting available name (*Code,* Article 13a), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (*Code,* Article 13b). *Nomina nuda* have no status in nomenclature, and they are not correctable to establish original authorship and date.

VALID AND INVALID NAMES

Important considerations distinguish valid from available names on the one hand and invalid from unavailable names on the other. Whereas determination of availability is based entirely on objective considerations guided by articles of the *Code,* conclusions as to validity of zoological names may be partly subjective. A valid name is the correct one for a given taxon, which may have two or more available names but only a single correct, hence valid, name, which is also generally the oldest name that it has been given. Obviously, no valid name can also be an unavailable name, but invalid names may be either available or unavailable. It follows that any name for a given taxon other than the valid name, whether available or unavailable, is an invalid name.

One encounters a sort of nomenclatorial no-man's land in considering the status of such zoological names as *nomina dubia* (doubtful names), which may include both available and unavailable names. The unavailable ones can well be ignored, but names considered to be available contribute to uncertainty and instability in the systematic literature. These can ordinarily be removed only by appeal to the ICZN for special action. Because few systematists care to seek such remedy, such invalid but available names persist in the literature.

NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES

SPECIES-GROUP NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here, both because the topic is well understood and relatively inconsequential and because the *Treatise* deals with genus-group names and higher categories. When the form of adjectival specific names is changed to agree with the gender of a generic name in transferring a species from one genus to another, one need never label the changed name as *nomen correctum.* Similarly, transliteration of a letter accompanied by a diacritical mark in the manner now called for by the *Code,* as in changing originally *bröggeri* to *broeggeri,* or eliminating a hyphen, as in changing originally published *cornu-oryx* to *cornuoryx,* does not require the designation *nomen correctum.* Of course, in this age of computers and electronic databases, such changes of name, which are perfectly valid for the purposes of scholarship, run counter to the requirements of nomenclatorial stability upon which the preparation of massive, electronic databases is predicated.

GENUS-GROUP NAMES

Conditions warranting change of the originally published, valid form of generic and subgeneric names are sufficiently rare that lengthy discussion is unnecessary. Only elimination of diacritical marks and hyphens in some names in this category and replacement of homonyms seem to furnish basis for valid emendation. Many names that formerly were regarded as homonyms are no longer so regarded, because two names that differ only by a single letter or in original publication by the presence of a diacritical mark in one are now construed to be entirely distinct.

As has been pointed out above, difficulty typically arises when one tries to decide whether a change of spelling of a name by a subsequent author was intentional or unintentional, and the decision has often to be made arbitrarily.

FAMILY-GROUP NAMES

Family-group Names: Authorship and Date

All family-group taxa having names based on the same type genus are attributed to the author who first published the name of any of these groups, whether tribe, subfamily, or family (superfamily being almost inevitably a later-conceived taxon). Accordingly, if a family is divided into subfamilies or a subfamily into tribes, the name of no such subfamily or tribe can antedate the family name. Moreover, every family containing differentiated subfamilies must have a nominate subfamily (*sensu stricto*), which is based on the same type genus as the family. Finally, the author and date set down for the nominate subfamily invariably are identical with those of the family, irrespective of whether the author of the family or some subsequent author introduced subdivisions.

Corrections in the form of family-group names do not affect authorship and date of the taxon concerned, but in the *Treatise* recording the authorship and date of the correction is desirable because it provides a pathway to follow the thinking of the systematists involved.

Family-Group Names: Use of *nomen translatum*

The *Code* specifies the endings only for subfamily (-inae) and family (-idae) names, but all family-group taxa are defined as coordinate (*Code,* Article 36, p. 77): "A name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date for taxa based upon the same name-bearing

type (type genus) at other ranks in the family group, with appropriate mandatory change of suffix [Art. 34a]." Such changes of rank and concomitant changes of endings as elevation of a tribe to subfamily rank or of a subfamily to family rank, if introduced subsequent to designation of a subfamily or family based on the same nominotypical genus, are *nomina translata*. In the *Treatise* it is desirable to distinguish the valid alteration in the changed ending of each transferred family-group name by the term *nomen translatum,* abbreviated to *nom. transl.* Similarly for clarity, authors should record the author, date, and page of the alteration.

Family HEXAGENITIDAE Lameere, 1917

[*nom. transl.* DEMOULIN, 1954, p. 566, *ex* Hexagenitinae LAMEERE, 1917, p. 74]

This is especially important for superfamilies, for the information of interest is the author who initially introduced a taxon rather than the author of the superfamily as defined by the *Code.* The latter is merely the individual who first defined some lower-ranked, family-group taxon that contains the nominotypical genus of the superfamily. On the other hand, the publication that introduces the superfamily by *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the taxon.

Superfamily AGNOSTOIDEA M'COY, 1849

[*nom. transl.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, *ex* Agnostinae M'COY, 1849, p. 402]

Family-group Names: Use of *nomen correctum*

Valid name changes classed as *nomina correcta* do not depend on transfer from one category of the family group to another but most commonly involve correction of the stem of the nominotypical genus. In addi-

tion, they include somewhat arbitrarily chosen modifications of endings for names of tribes or superfamilies. Examples of the use of *nomen correctum* are the following.

Family STREPTELASMATIDAE
Nicholson, 1889

[*nom. correct.* WEDEKIND, 1927, p. 7, *pro* Streptelasmidae NICHOLSON in NICHOLSON & LYDEKKER, 1889, p. 297]

Family PALAEOSCORPIDAE
Lehmann, 1944

[*nom. correct.* PETRUNKEVITCH, 1955, p. 73, *pro* Palaeoscorpionidae LEHMANN, 1944, p. 177]

FAMILY-GROUP NAMES:
REPLACEMENTS

Family-group names are formed by adding combinations of letters, which are prescribed for family and subfamily, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but among all those included it must be the first published as name giver to a family-group taxon. Once fixed, the family-group name remains tied to the nominotypical genus even if the generic name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* requires replacement of a family-group name only if the nominotypical genus is found to have been a junior homonym when it was proposed (*Code,* Article 39, p. 79), in which case ". . . it must be replaced either by the next oldest available name from among its synonyms, including those of its subordinate taxa, or, if there is no such name, by a new replacement name based on the valid name of the former type genus." Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name. Recommendation 40A of the *Code* (p. 81), however, specifies that for subsequent application of the rule of priority, the family-group name ". . . should be cited with its own author and date, followed by the date of the replaced name in parentheses." Many family-group names that have been in use for a long time are *nomina nuda,* since they fail to satisfy criteria of availability (*Code,* Article 11f). These demand replacement by valid names.

The aim of family-group nomenclature is to yield the greatest possible stability and uniformity, just as in other zoological names. Both taxonomic experience and the *Code* (Article 40) indicate the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of the same worker may change from time to time. The retention of first-published, family-group names that are found to be based on junior objective synonyms, however, is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. Moreover, to displace a widely used, family-group name based on the senior objective synonym by disinterring a forgotten and virtually unused family-group name based on a junior objective synonym because the latter happens to have priority of publication is unsettling.

A family-group name may need to be replaced if the nominotypical genus is transferred to another family-group. If so, the first-published of the generic names remaining in the family-group taxon is to be recognized in forming a replacement name.

Suprafamilial Taxa: Taxa above Family-Group

International rules of zoological nomenclature as given in the *Code* affect only lower-rank categories: subspecies to superfamily. Suprafamilial categories (suborder to phylum) are either not mentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological Nomenclature* (1953, Articles 59 to 69) proposed adopting rules for naming suborders and higher taxa up to and including

phylum, with provision for designating a type genus for each, in such manner as not to interfere with the taxonomic freedom of workers. Procedures were outlined for applying the rule of priority and rule of homonymy to suprafamilial taxa and for dealing with the names of such taxa and their authorship, with assigned dates, if they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

The Colloquium on Zoological Nomenclature, which met in London during the week just before the 15th International Congress of Zoology convened in 1958, thoroughly discussed the proposals for regulating suprafamilial nomenclature, as well as many others advocated for inclusion in the new *Code* or recommended for exclusion from it. A decision that was supported by a wide majority of the participants in the colloquium was against the establishment of rules for naming taxa above family-group rank, mainly because it was judged that such regulation would unwisely tie the hands of taxonomists. For example, a class or order defined by an author at a given date, using chosen morphologic characters (e.g., gills of bivalves), should not be allowed to freeze nomenclature, taking precedence over another class or order that is proposed later and distinguished by different characters (e.g., hinge teeth of bivalves). Even the fixing of type genera for suprafamilial taxa would have little, if any, value, hindering taxonomic work rather than aiding it. No basis for establishing such types and for naming these taxa has yet been provided.

The considerations just stated do not prevent the editors of the *Treatise* from making rules for dealing with suprafamilial groups of animals described and illustrated in this publication. Some uniformity is needed, especially for the guidance of *Treatise* authors. This policy should accord with recognized general practice among zoologists; but where general practice is indeterminate or nonexistent, our own procedure in suprafamilial no-

menclature needs to be specified as clearly as possible. This pertains especially to decisions about names themselves, about citation of authors and dates, and about treatment of suprafamilial taxa that, on taxonomic grounds, are changed from their originally assigned rank. Accordingly, a few rules expressing *Treatise* policy are given here, some with examples of their application.

1. The name of any suprafamilial taxon must be a Latin or Latinized, uninominal noun of plural form, or treated as such, with a capital initial letter and without diacritical mark, apostrophe, diaeresis, or hyphen. If a component consists of a numeral, numerical adjective, or adverb, this must be written in full.

2. Names of suprafamilial taxa may be constructed in almost any manner. A name may indicate morphological attributes (e.g., Lamellibranchiata, Cyclostomata, Toxoglossa) or be based on the stem of an included genus (e.g., Bellerophontina, Nautilida, Fungiina) or on arbitrary combinations of letters (e.g., Yuania); none of these, however, can end in -idae or -inae, which terminations are reserved for family-group taxa. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (e.g., order Decapoda LATREILLE, 1803, crustaceans, and order Decapoda LEACH, 1818, cephalopods; suborder Chonetoidea MUIR-WOOD, 1955, and genus *Chonetoidea* JONES, 1928). Worthy of notice is the classificatory and nomenclatorial distinction between suprafamilial and family-group taxa that, respectively, are named from the same type genus, since one is not considered to be transferable to the other (e.g., suborder Bellerophontina ULRICH & SCOFIELD, 1897 is not coordinate with superfamily Bellerophontacea MCCOY, 1851 or family Bellerophontidae MCCOY, 1851).

3. The rules of priority and homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatorial stability and to avoid confusion these rules are widely

applied by zoologists to taxa above the family-group level wherever they do not infringe on taxonomic freedom and long-established usage.

4. Authors who accept priority as a determinant in nomenclature of a suprafamilial taxon may change its assigned rank at will, with or without modifying the terminal letters of the name, but such changes cannot rationally be judged to alter the authorship and date of the taxon as published originally. A name revised from its previously published rank is a transferred name (*nomen translatum*), as illustrated in the following.

Order CORYNEXOCHIDA Kobayashi, 1935

[*nom. transl.* MOORE, 1959, p. 217, *ex* suborder Corynexochida KOBAYASHI, 1935, p. 81]

A name revised from its previously published form merely by adoption of a different termination without changing taxonomic rank is a *nomen correctum*.

Order DISPARIDA Moore & Laudon, 1943

[*nom. correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, *pro* order Disparata MOORE & LAUDON, 1943, p. 24]

A suprafamilial name revised from its previously published rank with accompanying change of termination, which signals the change of rank, is recorded as a *nomen translatum et correctum.*

Order HYBOCRINIDA Jaekel, 1918

[*nom. transl. et correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, *ex* suborder Hybocrinites JAEKEL, 1918, p. 90]

5. The authorship and date of nominate subordinate and supraordinate taxa among suprafamilial taxa are considered in the *Treatise* to be identical since each actually or potentially has the same type. Examples are given below.

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* TEICHERT in TEICHERT & others, 1964, p. 128, *ex* order Endoceroidea TEICHERT, 1933, p. 214]

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT in TEICHERT & others, 1964, p. 165, *pro* order Endoceroidea TEICHERT, 1933, p. 214]

TAXONOMIC EMENDATION

Emendation has two distinct meanings as regards zoological nomenclature. These are alteration of a name itself in various ways for various reasons, as has been reviewed, and alteration of the taxonomic scope or concept for which a name is used. The *Code* (Article 33a and Glossary, p. 254) concerns itself only with the first type of emendation, applying the term to intentional, either justified or unjustified changes of the original spelling of a name. The second type of emendation primarily concerns classification and inherently is not associated with change of name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleontologists, who have emended zoological names refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation *emend.* then must accompany the name with statement of the author and date of the emendation. On the other hand, many systematists think that publication of *emend.* with a zoological name is valueless because alteration of a taxonomic concept is introduced whenever a subspecies, species, genus, or other taxon is incorporated into or removed from a higher zoological taxon. Inevitably associated with such classificatory expansions and restrictions is some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat more extensive revisions are put forward, generally with a published statement of the reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as an aid to subsequent workers in taking account of the altered no-

menclatorial usage and to indicate where in the literature cogent discussion may be found. Authors of contributions to the *Treatise* are encouraged to include records of all especially noteworthy emendations of this nature, using the abbreviation *emend.* with the name to which it refers and citing the author, date, and page of the emendation. Examples from *Treatise* volumes follow.

Order ORTHIDA
Schuchert & Cooper, 1932

[*nom. transl. et correct.* Moore in Moore, Lalicker, & Fischer, 1952, p. 220, *ex* suborder Orthoidea Schuchert & Cooper, 1932, p. 43; *emend.,* Williams & Wright, 1965, p. 299]

Subfamily ROVEACRININAE
Peck, 1943

[Roveacrininae Peck, 1943, p. 465; *emend.,* Peck in Moore & Teichert, 1978, p. 921]

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE SPECIES

In the *Treatise* the name of the type species of each genus and subgenus is given immediately following the generic name with its accompanying author, date, and page reference or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names of this species is cited, accompanied by an asterisk (*), with notation of the author, date, and page of original publication, except if the species was first published in the same paper and by the same author as that containing definition of the genus of which it is the type. In this instance, the initial letter of the generic name followed by the trivial name is given without repeating the name of the author and date. Examples of these two sorts of citations follow.

Orionastraea Smith, 1917, p. 294 [*Sarcinula phillipsi McCoy, 1849, p. 125; OD].
Schoenophyllum Simpson, 1900, p. 214 [*S. aggregatum; OD].

If the cited type species is a junior synonym of some other species, the name of this latter also is given, as follows.

Actinocyathus D'Orbigny, 1849, p. 12 [*Cyathophyllum crenulate Phillips, 1836, p. 202; M; =Lonsdaleia floriformis (Martin), 1809, pl. 43; validated by ICZN Opinion 419].

In some instances the type species is a junior homonym. If so, it is cited as shown in the following example.

Prionocyclus Meek, 1871b, p. 298 [*Ammonites serratocarinatus Meek, 1871a, p. 429, *non* Stoliczka, 1964, p. 57; =Prionocyclus wyomingensis Meek, 1876, p. 452].

In the *Treatise* the name of the type species is always given in the exact form it had in the original publication except that diacritical marks have been removed. Where other mandatory changes are required, these are introduced later in the text, typically in a figure caption.

Fixation of Type Species Originally

It is desirable to record the manner of establishing the type species, whether by original designation (OD) or by subsequent designation (SD). The type species of a genus or subgenus, according to provisions of the *Code,* may be fixed in various ways in the original publication; or it may be fixed subsequently in ways specified by the *Code* (Article 68) and described in the next section. Type species fixed in the original publication include (1) *original designation* (in the *Treatise* indicated by OD) when the type species is explicitly stated or (before 1931) indicated by n. gen., n. sp. (or its equivalent) applied to a single species included in a new genus, (2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the *Treatise* by the specific name), (3) established by *monotypy* if a new genus or subgenus has only one originally included species (in the *Treatise* indicated as M), and (4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as the type.

Fixation of Type Species Subsequently

The type species of many genera are not determinable from the publication in which the generic name was introduced. Therefore, such genera can acquire a type species only

by some manner of subsequent designation. Most commonly this is established by publishing a statement naming as type species one of the species originally included in the genus. In the *Treatise* such fixation of the type species by subsequent designation in this manner is indicated by the letters SD accompanied by the name of the subsequent author (who may be the same person as the original author) and the publication date and page number of the subsequent designation. Some genera, as first described and named, included no mentioned species (for such genera established after 1930, see below); these necessarily lack a type species until a date subsequent to that of the original publication when one or more species is assigned to such a genus. If only a single species is thus assigned, it automatically becomes the type species. Of course, the first publication containing assignment of species to the genus that originally lacked any included species is the one concerned in fixation of the type species, and if this publication names two or more species as belonging to the genus but did not designate a type species, then a later SD designation is necessary. Examples of the use of SD as employed in the *Treatise* follow.

Hexagonaria Gurich, 1896, p. 171 [*Cyathophyllum hexagonum* Goldfuss, 1826, p. 61; SD Lang, Smith, & Thomas, 1940, p. 69].

Mesephemera Handlirsch, 1906, p. 600 [*Tineites lithophilus* Germar, 1842, p. 88; SD Carpenter, herein].

Another mode of fixing the type species of a genus is action of the International Commission of Zoological Nomenclature using its plenary powers. Definition in this way may set aside application of the *Code* so as to arrive at a decision considered to be in the best interest of continuity and stability of zoological nomenclature. When made, it is binding and commonly is cited in the *Treatise* by the letters ICZN, accompanied by the date of announced decision and reference to the appropriate numbered opinion.

Subsequent designation of a type species is admissible only for genera established prior to 1931. A new genus-group name established after 1930 and not accompanied by fixation of a type species through original designation or original indication is invalid (*Code,* Article 13b). Effort of a subsequent author to validate such a name by subsequent designation of a type species constitutes an original publication making the name available under authorship and date of the subsequent author.

HOMONYMS

Most generic names are distinct from all others and are indicated without ambiguity by citing their originally published spelling accompanied by name of the author and date of first publication. If the same generic name has been applied to two or more distinct taxonomic units, however, it is necessary to differentiate such homonyms. This calls for distinction between junior homonyms and senior homonyms. Because a junior homonym is invalid, it must be replaced by some other name. For example, *Callophora* Hall, 1852, introduced for Paleozoic trepostomate bryozoans, is invalid because Gray in 1848 published the same name for Cretaceous-to-Holocene cheilostomate bryozoans. Bassler in 1911 introduced the new name *Hallophora* to replace Hall's homonym. The *Treatise* style of entry is given below.

Hallophora Bassler, 1911, p. 325, *nom. nov. pro Callophora* Hall, 1852, p. 144, *non* Gray, 1848.

In like manner, a replacement generic name that is needed may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is generally avoided). An exact bibliographic reference must be given for the replaced name as in the following example.

Mysterium De Laubenfels, herein, *nom. nov. pro Mystrium* Schrammen, 1936, p. 183, *non* Roger, 1862 [*Mystrium porosum* Schrammen, 1936, p. 183; OD].

Otherwise, no mention of the existence of a junior homonym generally is made.

Synonymous Homonyms

An author sometimes publishes a generic name in two or more papers of different date, each of which indicates that the name is new. This is a bothersome source of errors for later workers who are unaware that a supposed first publication that they have in hand is not actually the original one. Although the names were separately published, they are identical and therefore definable as homonyms; at the same time they are absolute synonyms. For the guidance of all concerned, it seems desirable to record such names as synonymous homonyms. In the *Treatise* the junior of one of these is indicated by the abbreviation *jr. syn. hom.*

Not infrequently, identical family-group names are published as new names by different authors, the author of the name that was introduced last being ignorant of previous publication(s) by one or more other workers. In spite of differences in taxonomic concepts as indicated by diagnoses and grouping of genera and possibly in assigned rank, these family-group taxa, being based on the same type genus, are nomenclatorial homonyms. They are also synonyms. Wherever encountered, such synonymous homonyms are distinguished in the *Treatise* as in dealing with generic names.

A rare but special case of homonymy exists when identical family names are formed from generic names having the same stem but differing in their endings. An example is the family name Scutellidae RICHTER & RICHTER, 1925, based on *Scutellum* PUSCH, 1833, a trilobite. This name is a junior homonym of Scutellidae GRAY, 1825, based on the echinoid genus *Scutella* LAMARCK, 1816. The name of the trilobite family was later changed to Scutelluidae (ICZN, Opinion 1004, 1974).

SYNONYMS

In the *Treatise,* citation of synonyms is given immediately after the record of the type species. If two or more synonyms of differing date are recognized, these are arranged in chronological order. Objective synonyms are indicated by accompanying designation obj., others being understood to constitute subjective synonyms, of which the types are also indicated. Examples showing *Treatise* style in listing synonyms follow.

Mackenziephyllum PEDDER, 1971, p. 48 [**M. insolitum;* OD] [=*Zonastraea* TSYGANKO in SPASSKIY, KRAVTSOV, & TSYGANKO, 1971, p. 85, *nom. nud.; Zonastraea* TSYGANKO, 1972, p. 21 (type, *Z. graciosa,* OD)].

Kodonophyllum WEDEKIND, 1927, p. 34 [**Streptelasma Milne-Edwardsi* DYBOWSKI, 1873, p. 409; OD; =*Madrepora truncata* LINNE, 1758, p. 795, see SMITH & TREMBERTH, 1929, p. 368] [=*Patrophontes* LANG & SMITH, 1927, p. 456 (type, *Madrepora truncata* LINNE, 1758, p. 795, OD); *Codonophyllum* LANG, SMITH, & THOMAS, 1940, p. 39, obj.].

Some junior synonyms of either the objective or the subjective sort may be preferred over senior synonyms whenever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a genus. This requires action of the ICZN, which may use its plenary powers to set aside the unwanted name, validate the wanted one, and place the concerned names on appropriate official lists.

OTHER EDITORIAL MATTERS
BIOGEOGRAPHY

Purists, *Treatise* editors among them, would like nothing better than a stable world with a stable geography that makes possible a stable biogeographical classification. Global events of the past few years have shown how rapidly geography can change, and in all likelihood we have not seen the last of such change as new, so-called republics continue to spring up all over the globe. One expects confusion among readers in the future as they try to decipher such geographical terms as U.S.S.R., Yugoslavia, or Ceylon. Such confusion is unavoidable, as books must be completed and published at some real time. Libraries would be limited indeed if publication were always to be delayed until the political world had settled down.

Insofar as possible, trilobite genera from the former Soviet Union are referred to the

republics in which they are found, but in some instances other kinds of information may be given instead. In addition, such terms as central Europe and western Europe are likely to mean different things to different people. Some imprecision is introduced by the use of all such terms, of course, but it is probably no greater than the imprecision that stems from the fact that the work of paleontology is not yet finished, and the geographical ranges of many genera are imperfectly known.

NAMES OF AUTHORS: TRANSLATION AND TRANSLITERATION

Chinese scientists have become increasingly active in systematic paleontology in the past two decades. Chinese names cause anguish among English-language bibliographers for two reasons. First, no scheme exists for one-to-one transliteration of Chinese characters into roman letters. Thus, a Chinese author may change the roman-letter spelling of his name from one publication to another. For example, the name Chang, the most common family name in the world reportedly held by some one billion people, might also be spelled Zhang. The principal purpose of a bibliography is to provide the reader with entry into the literature. Quite arbitrarily, therefore, in the interest of information retrieval, the *Treatise* editorial staff has decided to retain the roman spelling that a Chinese author has used in each of his publications rather than attempting to adopt a common spelling of an author's name to be used in all citations of his work. It is entirely possible, therefore, that the publications of a Chinese author may be listed in more than one place under more than one name in the bibliography.

Second, most but by no means all Chinese list their family name first followed by given names. People with Chinese names who study in the West, however, often reverse the order, putting the family name last as is the Western custom. Thus, for example, Dr. Yi-Maw Chang, recently of the staff of the Pa-

leontological Institute, was Chang Yi-Maw when he lived in Taiwan. When he came to America, he became Yi-Maw Chang, and his subsequent bibliographic citations are listed as Chang, Yi-Maw. The *Treatise* staff has adopted the convention of listing family names first, inserting a comma, and following this with given names or initials. We do this even for Chinese authors who have not reversed their names in the Western fashion.

Several systems exist for transliterating the Cyrillic alphabet into the roman alphabet. We have adopted the American Library Association/Library of Congress romanization table for Russian and other languages using the Cyrillic alphabet.

MATTERS SPECIFIC TO THIS VOLUME

This volume departs from previous volumes of the *Treatise* in several important respects. Stratigraphical ranges of genera are typically given as zones rather than exclusively as universal stage names. In order to represent these zones clearly, we have used *or* in place of the solidus (/) and *to* in place of the en-dash (–). Replacing the dash with *to* eliminates ambiguity in zones with hyphenated names. This use of refined stratigraphy has obviated the traditional *Treatise* range charts of genera and higher taxa. In its place is presented a detailed chart of Cambrian stratigraphy that correlates stage names and zones in numerous geological regions. Finally, unlike previous volumes of the *Treatise,* the classification of the trilobites is presented here in preliminary form. Publication of a final classification must await the completion of the research that is underway for preparation of future volumes on the trilobites.

ACKNOWLEDGMENTS

stages of editing and into production. In this they have been ably assisted by members of the other editorial team, Jill Hardesty and Karen Renteria; by Jack Keim with photography; and by Jean Burgess with word processing. Jill Krebs, the remaining member of the Paleontological Institute staff, is involved with preparation of PaleoBank, the paleontological database for future *Treatise* volumes, and has not been closely involved with the trilobite *Treatise.*

This editorial preface and other, recent ones are extensive revisions of the prefaces prepared for previous *Treatise* volumes by former editors, including the late Raymond C. Moore, the late Curt Teichert, and Richard A. Robison. I am indebted to them for preparing earlier prefaces and for the leadership they have provided in bringing the *Treatise* project to its present status.

Finally, I am pleased to extend on behalf of the members of the staff of the Paleontological Institute, both past and present, our most sincere thanks to Professor H. B. Whittington for the unwavering scholarship, dedication to the task, and scrupulous attention to detail that have marked his involvement with the project from the outset and, indeed, his entire career as a specialist on the Trilobita.

REFERENCES

Ride, W. D. L., C. W. Sabrosky, G. Bernardi, and R. V. Melville, eds. 1985. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature. University of California Press. Berkeley & Los Angeles. xx + 338 p.

Roger L. Kaesler
Lawrence, Kansas
July 15, 1997

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well established throughout the world, but minor divisions (e.g., substages, stages, and subseries) are more likely to be provincial in application. The stratigraphical units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to revision of Part O. They are adapted from the International Union of Geological Sciences 1989 Global Stratigraphic Chart, compiled by J. W. Cowie and M. G. Bassett.

Paleozoic Erathem
  Permian System
    Upper Permian Series
    Lower Permian Series
  Carboniferous System
    Upper Carboniferous Subsystem
      Stephanian Series
      Westphalian Series
      Namurian Series (part)
    Lower Carboniferous Subsystem
      Namurian Series (part)
      Visean Series
      Tournaisian Series
  Devonian System
    Upper Devonian Series
    Middle Devonian Series
    Lower Devonian Series

Silurian System
    Pridoli Series
    Ludlow Series
    Wenlock Series
    Llandovery Series
Ordovician System
  Upper Ordovician Subsystem
    Cincinnatian Series
    Champlainian Series (part)
  Lower Ordovician Subsystem
    Champlainian Series (part)
    Canadian Series
Cambrian System
    Lower Cambrian Series
    Middle Cambrian Series
    Upper Cambrian Series

AUTHOR'S PREFACE

The introduction is intended to correct and amplify the general description given by Harrington in the first edition of *Treatise,* Part O (in Moore, 1959, p. 38–117), in the light of research published by the end of 1993. Historical matters such as early studies and the development of ideas on classification are omitted. Particularly the discovery and description of new silicified material have greatly added to knowledge of exoskeletal morphology, as the section on this subject shows. In the following section new and earlier information on the limbs is summarized, before considering possible musculature, mode of walking, and sensory devices. The publication of Memoir 67 on paleoecology by the Geological Society of America in 1957 and the publication in 1955 of Professor A. Seilacher's studies on trace fossils attributed to trilobites stimulated work in these fields. In conjunction with the increasing knowledge of sedimentary rocks and diagenetic processes, much research has been published on matters unrepresented in the 1959 edition. Other new studies have resulted in plausible reconstructions of Paleozoic world geography and enabled fresh thinking on faunal realms. The sections on mode of life, habits, occurrence, and use of numerical and cladistic methods are no more than an introduction to these subjects by reference to examples in which additional works are listed.

I am indebted to Dr. Euan N. K. Clarkson, Edinburgh University, for kindly contributing the account of the trilobite eye and for his collaboration in describing coaptative structures. Professor Brian D. E. Chatterton, University of Alberta, and Dr. Stephen E. Speyer have provided an entirely new account of ontogeny; Dr. Richard A. Fortey, Natural History Museum, London, has provided the classification to be used in this revision and in collaboration with Dr. R. M. Owens, National Museum of Wales, an account of evolution. Dr. Nadine V. Wilmot collaborated in describing the microstructure of the exoskeleton and provided the originals of Figures 70 and 71.

Throughout the text, when considering a specific exoskeletal structure, reference is made to structures found in related taxa or the affinities of a particular genus are indicated. As Fortey points out in his discussion of classification, many family-group names are long established, widely understood, and accepted. Such familiar names are used here to indicate relationship, either formally or informally. For example, *Cheirurus* and related genera may be referred to as Cheiruroidea (the superfamily), Cheiruridae (the family), or Cheirurinae (the subfamily). Informally, a superfamily group may be referred to as cheiruroids or a family group as cheirurids. Such informal terms as cheirurine or cheiruride lack precise meaning and will not be used. At a higher taxonomic level there is little or no agreement on natural groups, and a new, as yet incomplete, grouping into orders and suborders is outlined below by Fortey. In the text, names of these ordinal and subordinal taxa are used formally to indicate that it is the group defined in this new arrangement that is being referred to— i.e., as Olenellina (the suborder) or Proetida (the order). This procedure means that a suborder composed of a single superfamily, for example Eodiscina or Calymenina, may be referred to also as eodiscoids or calymenoids, but this is not the case with suborders that include more than one superfamily. For example, the suborder Agnostina is not embraced by the informal term agnostoid, which refers only to the superfamily Agnostoidea.

In the preparation of this introduction I have benefited from discussions and correspondence with Drs. W. T. Dean, R. A. Fortey, C. P. Hughes, P. D. Lane, R. M. Owens, A. W. A. Rushton, J. H. Shergold, D. J. Siveter, and A. T. Thomas, but responsibility for its content remains with me. I express my gratitude to the Leverhulme Trust for their support of my research and the

Department of Earth Sciences, University of Cambridge, for the provision of facilities in the preparation of this account, including all the new figures. Mrs. Sandra J. Last has put much skill and effort into the preparation of the text.

Authorship of the systematic sections is indicated, the diagnoses of the class Trilobita, orders, and suborders being by R. A. Fortey and me. I am indebted to these authors for their willingness to contribute and for their patience and promptness in answering queries and giving additional information at the editorial stage. A grant from *Treatise* funds enabled Professor W. T. Chang to substitute photographs for drawings of Redlichiina. Most helpful has been Dr. J. H. Shergold's willingness to provide the section on Cambrian correlation. Work began on this revision in 1980, and two further volumes on systematics are proposed. I am happy, now that Volume 1 is completed, to pass the reins of coordinating authorship into the hands of Dr. R. A. Fortey and to wish him well in a daunting task.

<div align="right">

H. B. Whittington
Sedwick Museum
Downing Street
Cambridge
England

</div>

REPOSITORIES AND THEIR ABBREVIATIONS

Abbreviations and locations for museums and institutions holding type material, which are used throughout the systematic sections of this volume, are listed below.

AGSO: Australian Geological Survey Organisation (formerly Bureau of Mineral Resources, BMR), Canberra, Australia

AMF: Australian Museum, Sydney, Australia

AMNH: American Museum of Natural History, New York, USA

ANU: Australian National University, Canberra, Australia

AUGD: South Australian Museum, Adelaide, Australia

BAF CB: Universidad de Buenos Aires, Departmento de Biología, Buenos Aires, Argentina

BGS: British Geological Survey (formerly the Geological Survey and Museum, GSM), London, U.K.

BGU: Geological Museum, Buryat Geological Board, Ulan-Ude, Russia

BMNH: British Museum (Natural History), London, U.K. (now Natural History Museum, London, NHM)

BU: Department of Geology, Birmingham University, Birmingham, U.K.

CAGC: Chinese Academy of Geological Sciences, Beijing, China

CIGMR: Chengdu Institute of Geology and Mineral Resources, Chengdu, Sichuan, China

CNIGR: Central Scientific Research Geological Exploration Museum (Chernyshev Museum), St. Petersburg, Russia

CSGM: Central Siberian Geological Museum, United Institute of Geology, Geophysics and Mineralogy, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia

CU: Cornell University, Ithaca, New York

CUGB: China University of Geosciences, Beijing, China

GGU: Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), Copenhagen, Denmark

GIN: Geological Institute, Academy of Sciences, Moscow, Russia

GIT: Geological Institute of Tallinn, Estonia

GMAN: Geological Museum, Geological Institute, Kazakhstan Academy of Sciences, Alma Ata, Kazakhstan

GMU: Geological Museum, Ukrainian Academy of Sciences, Kiev, Russia

GPCN: Paleontological Division, Museum of West Siberian Geological Production Company, Novosibirsk, Russia

GSC: Geological Survey of Canada, Ottawa, Ontario, Canada

GSE: Institute of Geological Sciences, Edinburgh, Scotland

GSI: Geological Survey of India, Calcutta, India

HBG: Hunan Provincial Bureau of Geology, Changsha, Hunan, China

HMB: Museum for Natural Science, Humboldt-University, Berlin, Germany

ICS: Institute for Cambrian Studies, Boulder, Colorado, USA

IGGN: see CSGM

IGiG: Institute of Geology and Geophysics, Uzbekistan Academy of Sciences, Tashkent, Uzbekistan

IGR: Institut of Geology, University of Rennes, France

IGUW: Institute of Geology, University of Warsaw, Warsaw, Poland

IPM: Institut de Paléontologie, Museum National d'Histoire Naturelle, Paris, France

IRScNB: Institut Royal des Sciences Naturelle de Belgique, Brussels, Belgium

KazIMS: Kazakhstan Scientific Research Institute of Mineral Resources, Alma Ata, Kazakhstan

KUMIP: Museum of Natural History, University of Kansas, Division of Invertebrate Paleontology, Lawrence, Kansas, USA

KGC: Kunming Geological School, Kunming, China

LACMIP: Los Angeles County Museum, Los Angeles, California, USA

LGSB: Laboratory of Geology, Sorbonne, Paris, France

LO: Geological Institute Museum, Department of Historical Geology, University of Lund, Lund, Sweden

LU: Department of Geology and Mineralogy, Laval University, Montreal, Quebec, Canada

MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA

MGUH: Geological Museum, Copenhagen University, Copenhagen, Denmark

MHN: Museo de Historia Natural de Argentina, Mendoza, Argentina

MLU: Museum für Mitteldeutsche Erdgeschichte, Martin-Luther Universität, Halle, Germany

MMG: Museum of the Ministry of Geology, Tashkent, Uzbekistan

MMK: Geological Museum, Copenhagen University, Copenhagen, Denmark

MNHN: Institut de Paléontologie, Museum National d'Histoire Naturelle, Paris, France

MWSGPC: Paleontological Division, Museum of West Siberian Geological Production Company, Novokuznetsk, Russia

NIGMR: Nanjing Institute of Geology and Mineral Resources, Nanjing, China

NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China

NMING: National Museum of Ireland, Dublin, Ireland

NMP: Narodní Muzeum of Natural History, Prague, Czech Republic

NMVP: National Museum of Victoria, Melbourne, Australia

NMW: National Museum of Wales, Cardiff, U.K.

NYSM: New York State Museum, Albany, New York, U.S.A.

OMR: Regional Museum of B. Horák, Rokycany, Czech Republic

OUM: Oxford University Museum, Oxford, U.K.

PIN: Paleontological Institute, Russian Academy of Sciences, Moscow, Russia

PIW: Paleontological Institute, Würzburg University, Würzburg, Germany

PM: Palaeontological Museum, Uppsala University, Uppsala, Sweden

PMO: Palaeontological Museum, University of Oslo, Oslo, Norway

PU: Department of Geology, Princeton University, Princeton, New Jersey

RM: Swedish Museum of Natural History, Stockholm, Sweden

SAMA: South Australian Museum, Adelaide, Australia

SG: Museo di Paleontologia, Servizio Geologico d'Italia, Rome, Italy

SGM: Geological Survey of Morocco (Service Geologique du Maroc), Rabat, Morocco

SGU: Swedish Geological Survey, Uppsala, Sweden

SM: Sedgwick Museum, Department of Earth Sciences, University of Cambridge, Cambridge, U.K.

SMF: Senckenberg Museum, Frankfurt am Main, Germany

SMNH: Shanghai Museum of Natural History, Shanghai, China

SNIIGGIMS: see CSGM

TsGM: Central Scientific and Geological Museum, St. Petersburg, Russia

UBA: Department of Geology, University of Buenos Aires, Buenos Aires, Argentina

UBC: Department of Geology, University of British Columbia, Vancouver, British Columbia, Canada

UCR: Department of Earth Sciences, University of California, Riverside, California, U.S.A.

UM: Department of Geology, University of Montpellier, Montpellier, France

UMC: Department of Geology, University of Missouri-Columbia, Columbia, Missouri, USA

UMU: Geological-Paleontological Museum, Münster University, Münster, Germany

UMUT: University Museum, University of Tokyo, Tokyo, Japan

UP: Museum of Paleontology, University of Pisa, Pisa, Italy

UQF: Department of Geology, University of Queensland, Brisbane, Australia

USNM: U.S. National Museum, Washington, D.C., USA

UTGD: Department of Geology, University of Tasmania, Hobart, Tasmania

VNIGNI: All Union Scientific Institute of Oil Prospecting, Moscow, Russia

XIGMR: Museum of the Xinjiang Institute of Geology and Mineral Resources, Geological Bureau of Xinjiang Uygur Autonomous Region, Urumqi, China

YIGS: Yunnan Institute of Geological Sciences, Kunming, Yunnan, China

YPM: Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA

YPM(PU): Yale University (Princeton University specimens), Peabody Museum of Natural History, New Haven, Connecticut, USA

ZSGU: West Siberian Research Institute for Geology, Geography and Mineral Resources, Novokuznetsk, Russia

MORPHOLOGY OF THE EXOSKELETON

H. B. WHITTINGTON

This section deals exclusively with the mineralized portion of the cuticle, the exoskeleton, other portions of the trilobite body being considered in the following section. In both these sections reference is to the exoskeleton and body of a trilobite in which the specific number of thoracic segments is present, a **holaspis.** To avoid ambiguity, all paired structures are described in the singular.

SIZE, FORM, AND ORIENTATION

The exoskeletons of trilobites are found in a wide variety of marine sediments, the original mineral matter apparently little changed or recrystallized, replaced, or removed to leave a mold. The exoskeletons may be preserved complete, or lacking ventral sclerites and librigena, partially or wholly disarticulated, or in a fragmentary state. When preserved in limestone, in a concretion, or in coarser clastic sediments, the exoskeleton may retain its original convexity; in finer clastic sediments the exoskeletons are flattened and distorted as a result of compaction of the sediment. Distortion may also result from subsequent stress of the enclosing rock, such as that producing cleavage. Exoskeletons preserved by silicification, which may be freed from the limestone matrix by dissolving it away with acid, have given much knowledge of morphology and growth. Improved methods of casting, in latex or plastic compounds, have greatly facilitated study of exoskeletal molds.

The exoskeleton is ovoid or subelliptical in outline and convex, the convexity of individual portions and of the entire exoskeleton differing greatly between taxa. It extends inward, for a distance that varies between taxa, beneath the ventral side of the animal. Spines, hollow projections from the exoskeleton, may be developed in any portion of the exoskeleton. These spines are typically closed

structures, apart from the minute canals and openings described below in the section on exoskeletal microstructure and sculpture (p. 74). Another exception is the intergenal spine during the instar stages of development of *Olenellus* (PALMER, 1957, pl. 19, fig. 2, 3, 12), which is not closed on the ventral side. Presumably it became closed during the last instar stage when it was reduced to a small remnant.

While many holaspid exoskeletons are between 3 and 10 cm in length along the midline (excluding anterior or posterior spines in this line), one example, *Acanthopleurella stipulae,* is 1.07 to 1.50 mm in length and is believed to be the smallest known (FORTEY & RUSHTON, 1980). RAYMOND (1931) listed and discussed large known trilobites, including Middle Cambrian paradoxidids; Ordovician asaphids, lichids, and homalonotids; and Devonian lichids, homalonotids, and dalmanitids. Lengths range from 30 to 70 cm, the maximum being that of the Ordovician *Uralichas,* which RABANO (1989) gave as 66 cm. BERGSTRÖM and LEVI-SETTI (1978) described a specimen of *Paradoxides davidis* with a sagittal length of 37 cm, and DAILY and others (1979, p. 16) recorded an individual of *Redlichia* with a length of 35 cm. Dr. R. J. F. JENKINS, University of Adelaide, informs me (personal communication,1989) that this latter figure may be incorrect, the largest specimens he has traced being about 25 cm in length. In the early Middle Cambrian of Morocco occur an Olenellina, specimens of which attain a maximum length of 23 cm, and a paradoxidoid of a maximum length of 39 cm (GEYER, 1993). N. C. HUGHES (1993, p. 9) considered that the largest individuals of the Upper Cambrian *Dikelocephalus* were 40 to 45 cm in length. A complete exoskeleton of an isotelid of Ordovician (Ashgill) age, with a sagittal length of 43 cm, has been recorded from the Hudson Bay area of Canada (M. E. JOHNSON, SKINNER, &
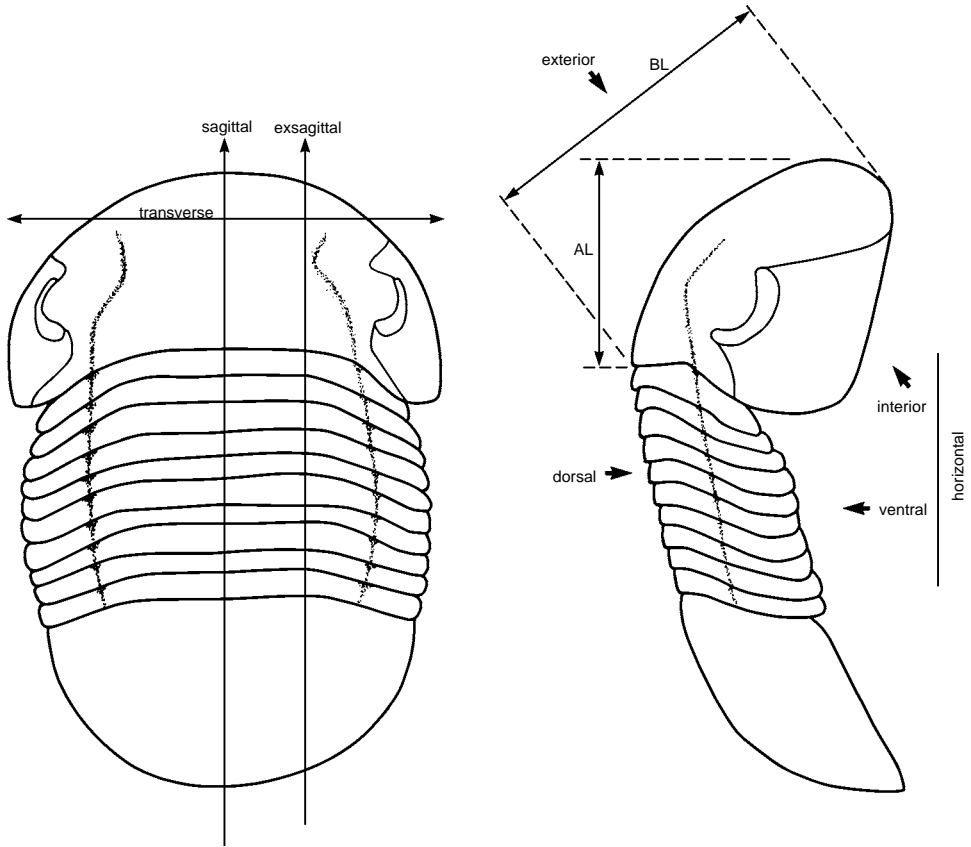
Fig. 1. Dorsal and right-lateral outlines of the Silurian illaenid *Bumastus,* ✕1 (new). See text (p. 2–3) for discussion of orientation and directions.

MacLeod, 1988, fig. 13), and Reimann (1943) considered that the Devonian lichid *Terataspsis grandis* attained a length of at least 50 cm. It is common experience when collecting to find fragments of larger portions of the exoskeleton than any found entire (e.g., Raymond, 1931), and records of large Devonian dalmanitids and homalonotids appear to be based on such fragments.

In order to describe without ambiguity what is meant by length and width of an exoskeleton or any portion of it, the direction in which a measurement is being made is best referred to either a longitudinal or a transverse direction in the entire exoskeleton (Fig. 1). **Sagittal** (abbreviated to *sag.*) is the direction along the axial midline, **exsagittal** (abbreviated as *exs.*) is that direction parallel to but outside the sagittal line, and **transverse** (abbreviated as *tr.*) is the direction at right angles to sagittal. Thus an axial ring may be described as wide (tr.), i.e., wide in a transverse direction, but short (sag. and exs.), i.e., short in the midline or outside it but parallel to it. As W. Zhang and Jell (1987, p. 35) have advocated, it would be advantageous if long and short were used uniformly with reference to longitudinal (sag. and exs.) dimensions and broad and narrow with reference to transverse (tr.) dimensions. To describe the direction away from the sagittal line, **abaxial** is used, whereas **adaxial** is toward the sagittal line. In illustrations of trilobite exoskeletons, partial or complete, con-

ventions may be needed to explain the direction in which the specimen is being viewed. These conventions are not necessary if the specimen is flattened in the bedding plane, when a view at right angles to this plane will suffice. In specimens retaining some or all of the original convexity, views described with respect to the animal as dorsal and right lateral (Fig. 1) may be given, supplemented by anterior, posterior, ventral, or oblique views. The line AL may be considered to lie in the horizontal plane with respect to the animal, but then the dorsal view does not show fully the external surface of the cephalon. Hence WHITTINGTON and EVITT (1954) used views termed *exterior* and *interior,* taken at right angles to the vertical plane in which the line BL lies. BRUTON (1968a) preferred the term *palpebral* for the exterior view which is approximately vertical to the surface of the palpebral lobe. The problems inherent in the use of the term *horizontal* with reference to the exoskeleton were made evident by FORTEY (1975b, p. 15). How to orient the exoskeleton or its parts for the purpose of taking measurements has been debated (TEMPLE, 1975); for example, the measurement of BL rather than AL is recommended for length of cephalon (cf. BRUTON & OWEN, 1988). What is important is that each study should state precisely what has been measured and how the specimen was oriented, the latter being less obviously necessary when dealing with flattened material.

When the exoskeleton is preserved in calcareous rock, it may have been partially stripped off as the rock was split to reveal the specimen. Such specimens, where exfoliated, show a mold of the inner surface of the exoskeleton similar to the internal molds that are extracted from clastic rocks. The features shown by the external surface of the exoskeleton are different from the **visceral features**, those of the inner or **parietal surface** of the exoskeleton. It is important that the external and internal (parietal) features of an exoskeleton be described from the exoskeleton or from casts made from molds or of exfoliated specimens. Confusion arises when the parietal surface is described as it appears on the mold (of an exfoliated specimen) or an internal mold is described as if it showed the external surface of the exoskeleton.

DIVISIONS OF THE EXOSKELETON

The trilobite exoskeleton is divided by shallow infolds, evident externally as furrows, appearing on the inner surface as low ridges (Fig. 2). The longitudinal **axial furrow** isolates the convex median **axis** from the lateral portion. The axis is crossed by transverse furrows (lateral glabellar, occipital, articulating, and inter-ring furrows) at similar intervals (gradually decreasing posteriorly) from one another; these furrows are considered to correspond to the boundaries of the somites of the body. On the lateral region of the exoskeleton, each furrow (posterior border and pleural furrow) commences opposite a transverse axial furrow, and extends outward and slightly backward. The exoskeleton is also divided by transverse articulations (Fig. 2), which separate an anterior group of fused somites, the **cephalon;** each of the series of **segments** forming the **thorax;** and a posterior group of fused somites, the **pygidium.** The lateral portion of the cephalon is the **gena,** which may extend in front of the axis to the sagittal line. The **pleural region** is the lateral portion of either thorax or pygidium and in the latter may extend behind the axis to the sagittal line. The posterior border furrow of the gena and the pleural furrows of the thorax run outward and slightly backward in relation to the articulations. It has been assumed that the articulations lie at the boundaries of the somites, i.e., that each thoracic segment is the exoskeleton of a somite. Others have argued that the posterior border furrow of the cephalon and the pleural furrows of the thoracic segments and pygidium mark the boundaries of the somites and that the articulations are secondary divisions (see discussion of cephalic segmentation, p. 132). The furrows, infolds of the exoskeleton, are primary features of trilobites, some or all of
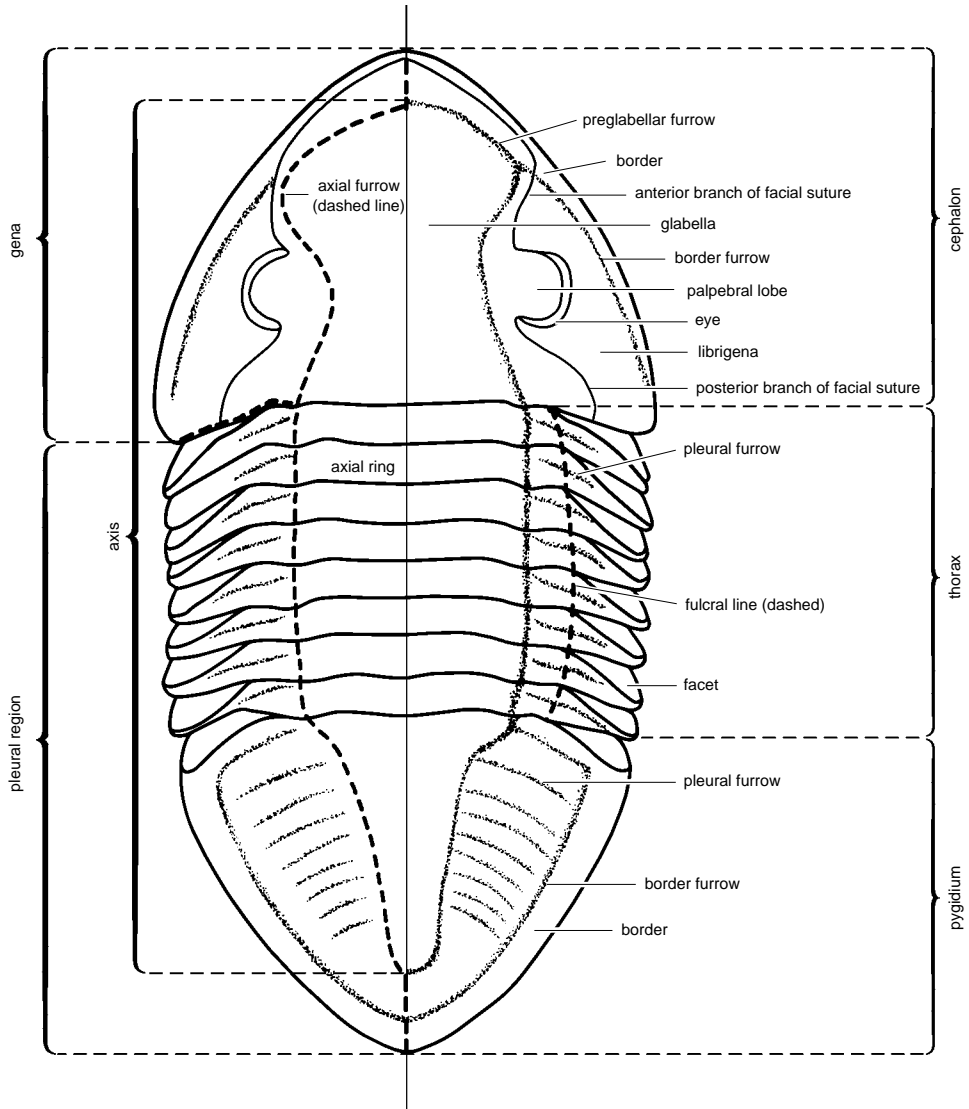
Fig. 2. Terminology of the exoskeleton illustrated by the Ordovician asaphid *Isotelus,* ×8 (new). *Dashed line* on left side outlines limits of axial region, gena, and pleural region. Articulating furrows are hidden beneath posterior margins of glabella and axial rings of thorax.

them appearing early in development (see section on ontogeny, p. 173).

The exoskeleton is continued on the ventral side beneath the outer portions of the gena and pleural region as the **doublure.** Beneath the anterior of the axis there is a ventral sclerite, the **hypostome,** which may be attached to the doublure anteriorly.

CEPHALON

The outline of the cephalon in dorsal aspect varies from subcircular to semielliptical and subtriangular and may be transversely subelliptical. The convexity varies widely between taxa. The size of the cephalon in relation to the thorax and pygidium varies

considerably, and a trilobite may be described as **micropygous** (pygidium small in relation to cephalon), **isopygous** (pygidium and cephalon of similar size), or **macropygous** when the pygidium is larger than the cephalon (see section on the pygidium for further discussion of these terms, p. 59). The cephalon may be evenly convex and unfurrowed; but in most taxa the raised axial region, the **glabella**, is outlined by the **axial** and **preglabellar furrows,** and the **occipital ring** is set off from the rest of the glabella by the **occipital furrow**. The gena bears the **eye lobe** (if present), and with rare exceptions the **facial suture** traverses the eye lobe, an anterior and a posterior branch crossing the gena and extending on to the doublure. The facial suture divides the gena into an inner, adaxial portion, the **fixigena,** and an outer, abaxial portion, the **librigena**. That portion of the cephalon that lies adaxial to the facial sutures is the **cranidium**.

GLABELLA

A small circular or oval depression, the **fossula**, when developed, may be used to separate the preglabellar furrow from the axial furrow, the two furrows that are continuous and outline the glabella (Fig. 3). The fossula lies immediately in front of the junction of the eye ridge with the axial furrow. The size relative to the cephalon, shape, and convexity of the glabella vary greatly; and in some trilobites the glabella may not be outlined by furrows, but wholly or only posteriorly by a convexity differing from that of the rest of the cephalon. In the majority of trilobites the most posterior subdivision of the glabella, the **occipital ring,** is defined by the **occipital furrow,** and an occipital doublure is present, longest sagittally (Fig. 4–5). Abaxially the occipital ring may be inflated, and a **lateral occipital lobe** may be set off by its independent convexity (Fig. 3). A shallow furrow, which curves in an arc across the occipital ring, has been termed the **band furrow** in olenids (Nikolaisen & Henningsmoen, 1985, fig. 2) and some asaphids (Henningsmoen, 1960, p. 218),

but it may be that in these flattened specimens this supposed furrow is an impression made by the anterior margin of the doublure of the ring. A narrow **posterior band** of the occipital ring, lower than the main body of the ring and set off from it by a change in slope is characteristic of the odontopleurid *Ceratocephala* (Whittington & Evitt, 1954, p. 55).

Further subdivision of the glabella (Fig. 3–5) in front of the occipital ring may be indicated by furrows or pits, usually in lateral pairs, the **lateral glabellar furrows**. The best defined of these furrows is generally that next to the occipital furrow, with furrows in front of this becoming successively shorter (tr.) and less well defined. In the olenid *Hypermecaspis* (Fortey, 1974b, p. 45), however, the furrow next to the occipital is shorter (tr.) than those in front, a relatively unusual situation. A similar short furrow was termed an intervening furrow in *Asilluchus* Öpik (1963, p. 67) but may well be the basal lateral glabellar furrow. In the oryctocephalid *Sandoveria* (Shergold, 1969, p. 13, fig. 3) a glabellar furrow regarded as the intervening furrow curves back to meet the occipital furrow, isolating an intervening glabellar lobe considered to intervene between the occipital ring and the basal lateral glabellar lobe. The occipital apodeme lies in the occipital furrow behind this intervening lobe, so that the latter might alternatively be regarded as the basal lateral lobe. In this case there would be five pairs of lateral glabellar lobes in *Sandoveria.* Up to four pairs of lateral glabellar furrows are present in many trilobites, and a fifth pair is said to be present in the immature glabella of *Daguinaspis* (Hupé, 1951; 1953a, p. 261). These furrows are numbered from the posterior forward as S (sulcus) O, the occipital furrow, and S1, S2, S3, etc. (Fig. 4.2–5). Between these lateral furrows are the **lateral glabellar lobes,** numbered correspondingly L (lobe) 1, L2, L3, etc.; the lateral occipital lobe is designated LO. These lateral lobes may be inflated and so have a convexity independent from that of the adjacent portions of the glabella. The
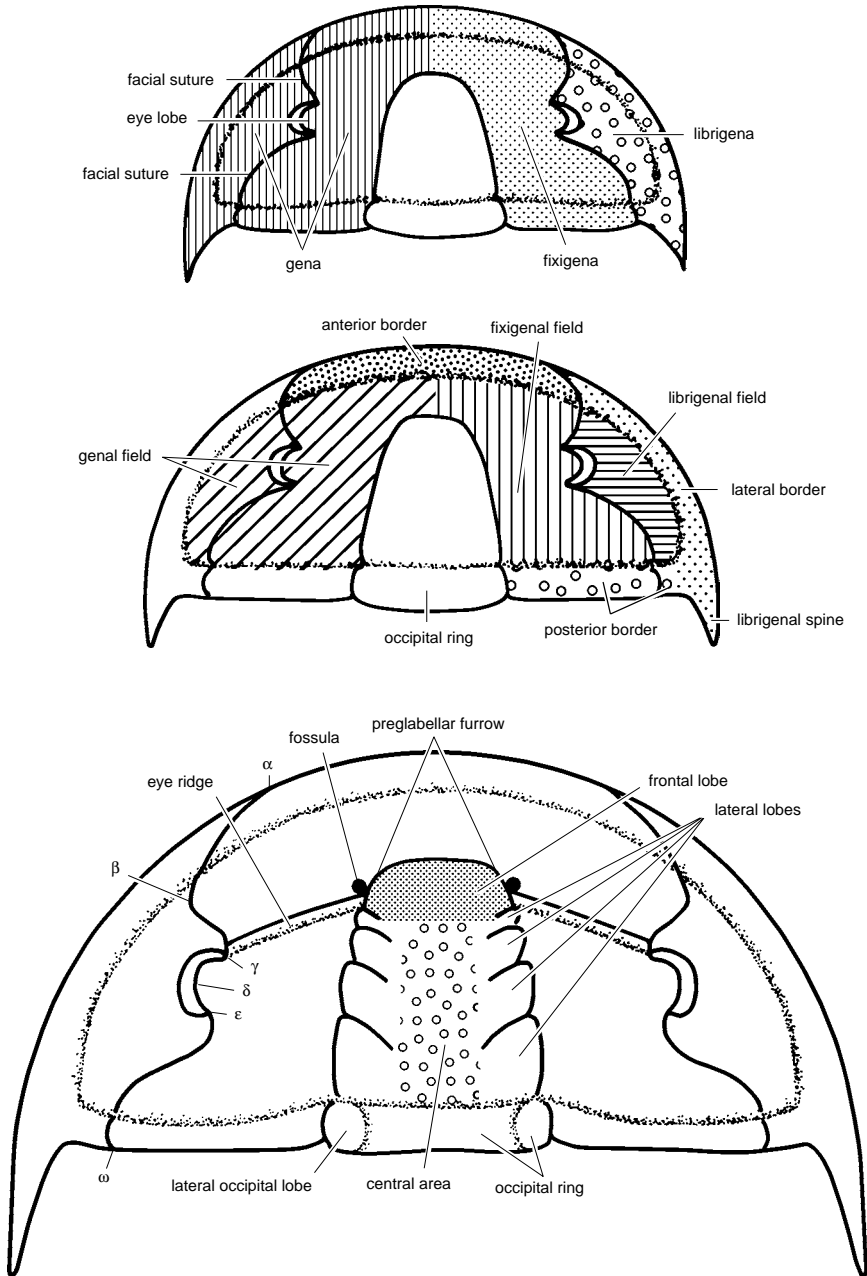
FIG. 3. Terminology of the cephalon illustrated by a ptychopariid trilobite; the labelled portions are differentiated by shading. Greek letters denote salient points on facial suture: β is farthest abaxial point of anterior branch, which reaches the cephalic margin at α; γ to ε is palpebral suture, and δ is the farthest abaxial point of this suture; posterior branch reaches cephalic margin at ω (new).

lateral glabellar furrows vary in depth, length (tr.), and direction; may extend to the axial furrow; and may be subcircular or oval de-pressions, adjacent to or some distance from the axial furrow. A pair may extend adaxially to form a continuous **transglabellar furrow**.

In the Agnostina a different notation and terminology, initiated by Robison (1964, 1982), has been applied to the glabella (Fig. 6.1). The basal lobes and narrow (sag. and exs.) occipital band are excluded from the glabella, which is divided by the transglabellar furrow into the **anteroglabella** and **posteroglabella**. The posterior portion of the posteroglabella projects back between the basal lobes as the **glabellar culmination** and may be inflated and prominent, rounded, or angulate. Lateral furrows of the glabella are numbered F1 to F3 from the posterior forward, F3 being the transglabellar furrow. Axial rings defined at the anterior margin by these furrows are numbered M1 to M3 from the posterior forward. This terminology was not applied to the Eodiscina by Jell (1975a), who regarded the basal lobe as occipital and used the notation S and L for glabellar furrows and lobes as applied to all trilobites except the Agnostina (Fig. 5). In trilobites (except Agnostina) the portion of the glabella in front of the most anterior pair of lateral furrows is the **frontal lobe** (Fig. 3), for which Henningsmoen (1957a, p. 12, fig. 1) used the abbreviation LA. The portion of the glabella lying between the frontal lobe, occipital furrow, and adaxial ends of the lateral glabellar furrows is the central area of the glabella. The frontal lobe and central area may be referred to as the fronto-median glabellar lobe. Other subdivisions of the glabella are developed in particular taxa, including the **occiput** in trinucleids (C. P. Hughes, Ingham, & Addison, 1975, p. 558, fig. 1), the **intercalating ring** in phacopids (Richter & Richter, 1926, fig. 14) (both of these lying immediately anterior to the occipital furrow), and the **median preoccipital lobe** in the proetid *Ditomopyge* (Weller, 1935). In lichids a **longitudinal furrow** may be directed exsagittally and join the inner ends of the lateral glabellar furrows, enclosing two or three lateral lobes or a single **composite lateral lobe** between the longitudinal and axial furrows (Fig. 7.2–6). There have been differing interpretations of the origins of these lobes, whether they are part of the glabella, and whether the most posterior was an oc-

cipital lobe. Studies of ontogeny have shed light on some of the problems, in particular the recognition of the **bulla** swelling in early growth stages and its development into the **bullar lobe**. The **posterolateral cranidial lobe**, a swelling adjacent to the base of the glabella, appears to belong to the fixigena and not the glabella. The history of views on glabellar lobation in lichids was reviewed by Thomas and Holloway (1988), and the terminology they accepted is given in Figure 7. The most posterior lateral lobe is considered to be part of L1, which is consequently subdivided into L1a (the more posterior) and L1b. In two subfamilies (Selenopeltinae and Ceratocephalinae) of the Odontopleuridae, subdivisions of L1 and L2 have been recognized by Ramsköld (1991b, fig. 6). L1 is subdivided into L1a (exterior), L1b (interior), and L1c (anterior) sublobes; and L2 is subdivided into L2a (interior) and L2b (exterior) sublobes.

On the inner surface of the exoskeleton, occipital and lateral glabellar furrows are reflected as ridges. In particular species, SO, S1, and S2 may be deepened a short distance adaxial to the axial furrow, and this deepening is reflected on the inner surface as a knob or bladelike extension of the ridge that projected into the body as an **apodeme** (Fig. 5). Such apodemes are characteristic of Cheirurinae and Deiphoninae but not of Acanthoparyphinae or Sphaerexochinae (Chatterton & Perry, 1984), for example; are well developed in encrinurids (Chatterton & Ludvigsen, 1976, pl. 14–15; Evitt & Tripp, 1977) and pterygometopids (Ludvigsen & Chatterton, 1982, pl. 6–7); and are less strongly developed in odontopleurids (Chatterton & Perry, 1983). In Phacopoidea (Campbell, 1976; Størmer, 1980) areas of muscle attachment other than apodemes have been described as pits in the external surface or darker areas distributed widely on the exoskeleton. In asaphids (Fortey, 1975b, p. 17; 1980c, fig. 1, 3), illaenids (Jaanusson, 1954, p. 549–551), styginids (Lane & Thomas, 1983, fig. 1–2), and raphiophorids (Whittington, 1965, pl. 10–12; Fortey, 1975b, pl. 22, 24–25),

smooth areas that may be slightly depressed and appear as raised areas on the internal mold are considered to be areas of muscle attachment corresponding to the glabellar furrows (see Fig. 20). As some of these examples show (Fig. 8), these areas may appear dark, particularly when the specimen is immersed in liquid. A particular such area, the **lunette**, in the illaenid *Bumastoides* (Fig. 9.1–2) is crescentic in outline and raised on the inner surface of the exoskeleton. Smooth or dark areas, representing areas of muscle attachment or glabellar furrows, have been recognized in other trilobites such as olenids (HENNINGSMOEN, 1957a, p. 92), *Telephina* (WHITTINGTON, 1965, pl. 37), and *Remopleurides* (WHITTINGTON, 1959a, pl. 5).

In Agnostina the external surface of the glabella and occipital (basal) lobes may display smooth patches, some faintly depressed (Fig. 10) (see also HUNT, 1967, pl. 22, fig. 44–47). Similar patches may be outlined by an impressed rim on the internal mold (FORTEY, 1980b, p. 30; SHERGOLD, 1975, pl. 3, fig. 3, pl. 11, fig. 5), indicating that the exoskeleton was thickened. In other specimens similar areas may appear dark (ROBISON, 1984, p. 42). These areas are considered to have been for muscle attachment, and study of these impressions in internal molds by ÖPIK (1963, 1967) and SHERGOLD (1975) has given rise to a complex terminology for them and the associated ridges, grooves, and pits (Fig. 11.1). A paired ridge, the **axial glabellar carina**, may run sagittally between the **axial glabellar node** and the **terminal glabellar node,** and a **notula** is a minute pit (in the internal mold) associated with a muscle area. A possibly analogous structure, a sagittal ridge (carina) on the internal mold of the glabella, has been recognized in such illaenids as *Panderia* (BRUTON, 1968a, pl. 1, fig. 1–3) and *Stenopareia* (OWEN & BRUTON, 1980, pl. 3, fig. 10). In asaphids rows of impressions on either side of the sagittal line of the internal mold of the glabella, in some examples separated by a low sagittal ridge, were described by HENNINGSMOEN (1960, p. 213); a low sagittal ridge is
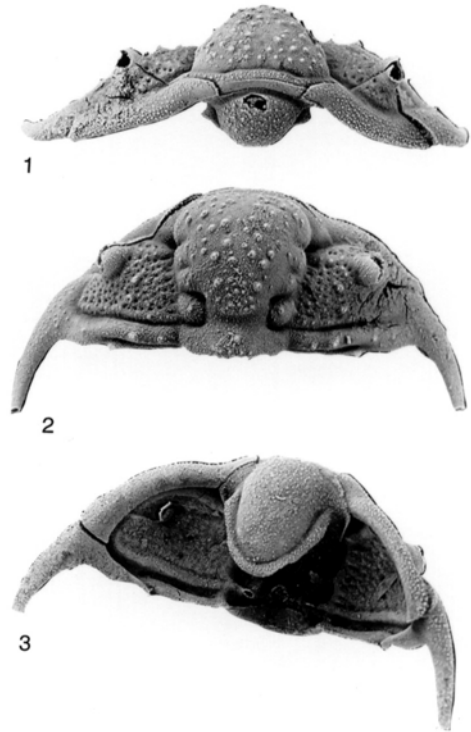
FIG. 4. Cephalon of the cheirurid *Ceraurus whittingtoni* EVITT, 1953, Middle Ordovician, Virginia, USA. The visual surface of the eye lobe is missing. *1,* Anterior view, ×3 (new); *2,3,* dorsal and oblique ventral views, ×3 (Whittington, 1960b, fig. 1a,c).

present in the glabella of *Stegnopsis* (WHITTINGTON, 1965, p. 347, pl. 22, fig. 3).

The glabella may bear median or paired spines or nodes on the frontal or frontomedian lobes, and in many taxa there is a median or paired occipital spine or node. A spectacular example is the encrinurid *Perirehaedulus* (Fig. 12), which also shows a sagittally directed **anteromedian depression** or **longitudinal median glabellar furrow** extending back from the anterior margin of the frontal glabellar lobe. Such a furrow or an associated pit or more elongate (tr.) median depression in the preglabellar furrow is characteristic of encrinurids (FORTEY, 1980b, pl. 22; EVITT & TRIPP, 1977). Similar depressions are present in some pliomerids (WHITTINGTON, 1961b), and cheirurids (muscle scars in Fig. 4.1) show a median
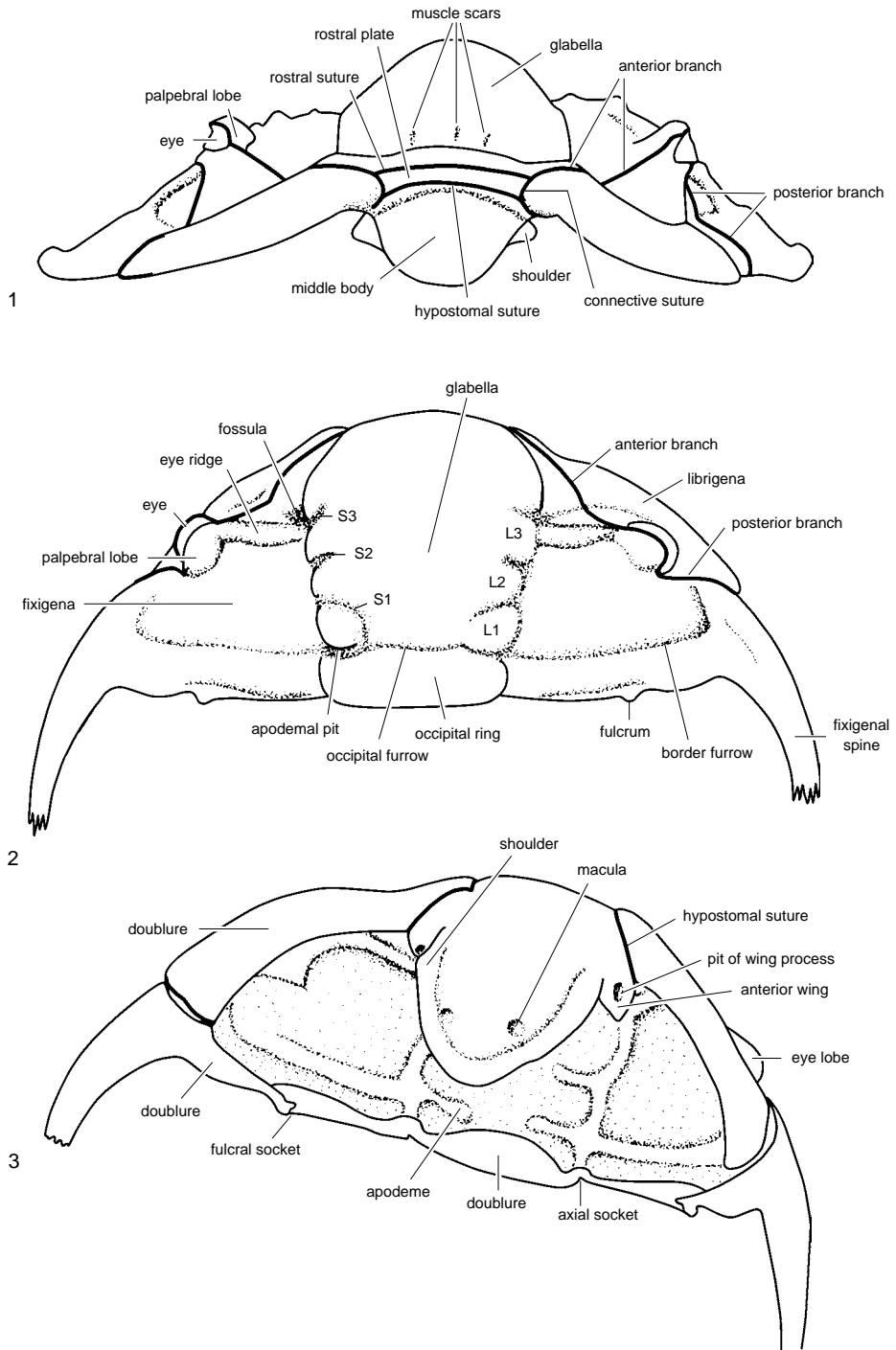
Fig. 5. Diagrammatic representation of anterior (*1*), dorsal (*2*), and oblique (*3*) views of *Ceraurus whittingtoni* Evitt, 1953 (see Fig. 4) to show terminology of the cephalic features (new).
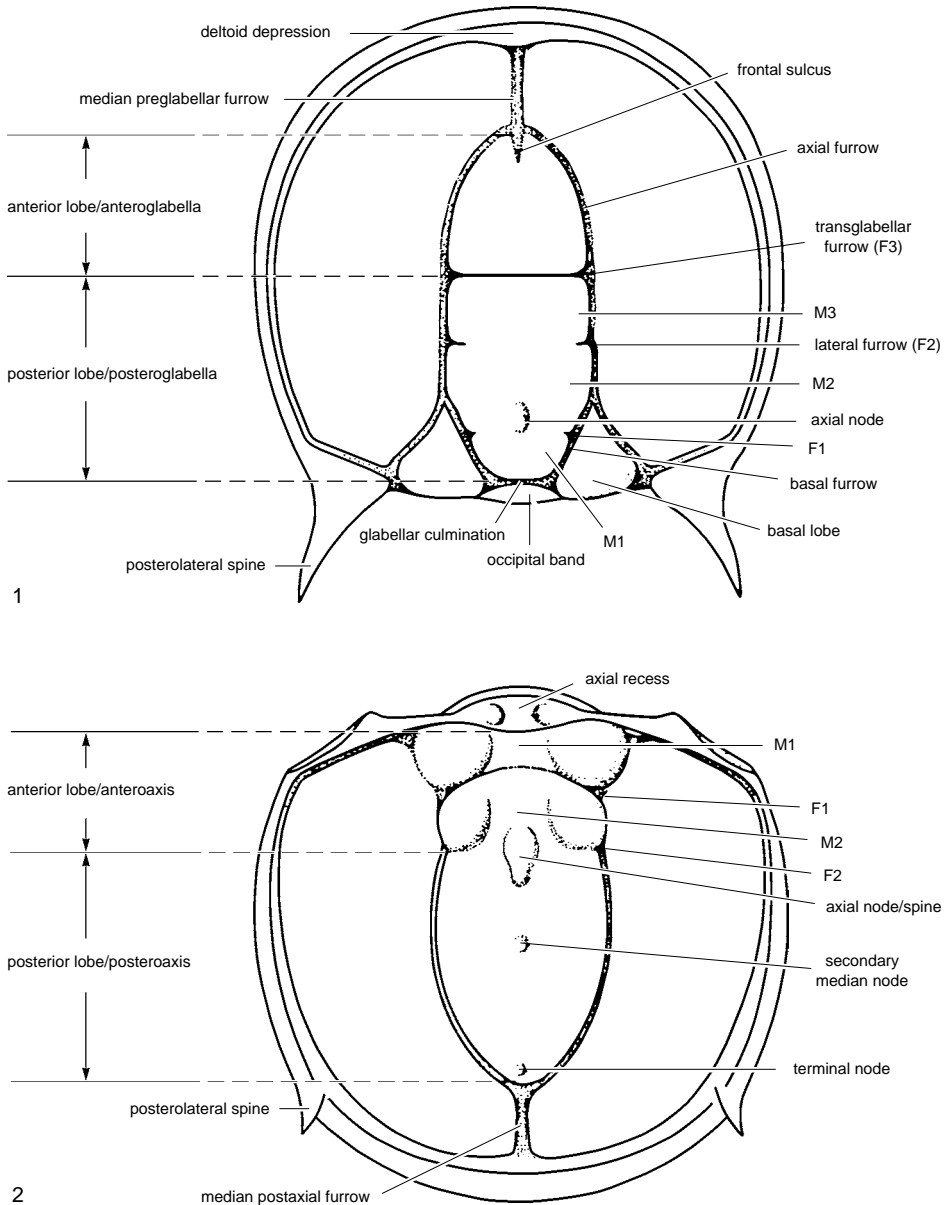
FIG. 6. Terminology applied to the external surface of the Agnostina; *1,* cephalon and *2,* pygidium (Shergold, Laurie, & Sun, 1990, fig. 1–2).

furrow flanked by a pair of depressions. A necklace arrangement of pits on the frontal lobe in phacopids (STØRMER, 1980, p. 263) has long been known and includes deep pits in the preglabellar furrow. These pits and grooves, which form projections on the inner surface, have been regarded as points of muscle attachment. In *Dalmanites* a pair of smooth areas on the frontal glabellar lobe, pierced by minute pores, were regarded as muscle-attachment areas by RAMSKÖLD (1985, p. 35).
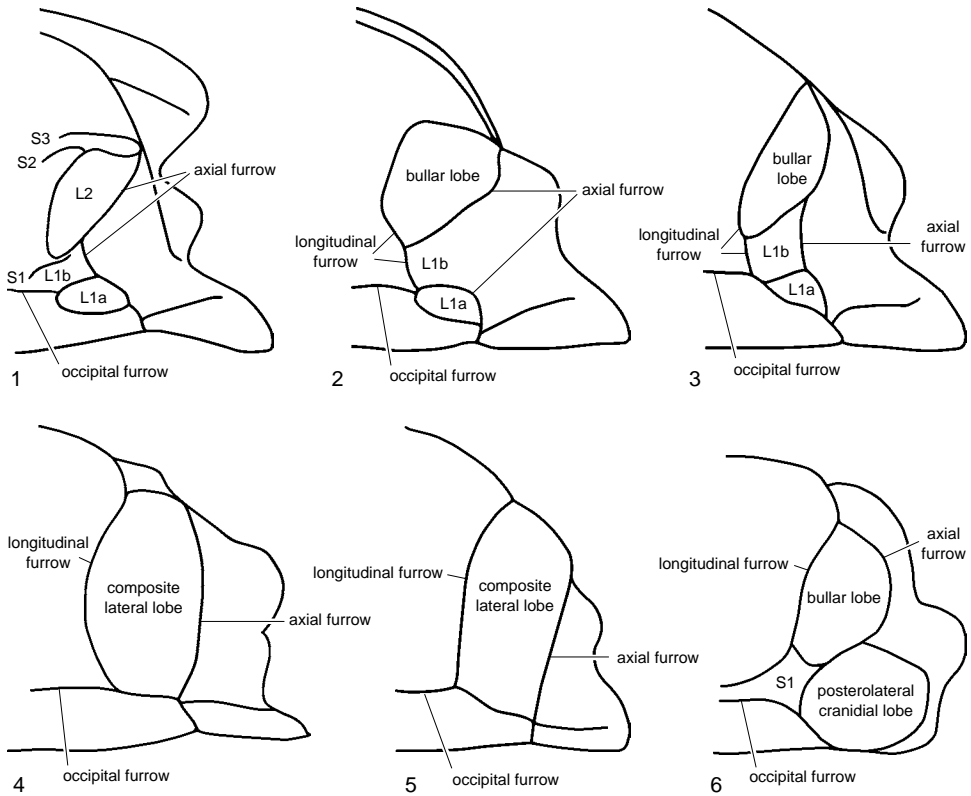
FIG. 7. Cranidial morphology of Lichida. Composite lobe formed by fusion of bullar lobe with L1b or L1a. *1, Lichakephalus; 2, Platylichas (Platylichas); 3, Dicranopeltis; 4, Echinolichas; 5, Amphilichas; 6, Acanthopyge (Jasperia)* (Thomas & Holloway, 1988, fig. 2).

GENA

The gena has a convex border in many trilobites, the area enclosed within this border being the **genal field** (Fig. 3). The term **acrolobe** (Fig. 13) was applied to the area within the border in Agnostina by ÖPIK (1967), but whether it was intended to include the axial region is not specified. The border extends to the midline in front of the glabella, and there may be a **preglabellar field** between the preglabellar furrow and the border (Fig. 14). The preglabellar field may be long (sag. and exs.) or short, flattened and gently sloping, or convex and steeply sloping. In such Cambrian trilobites as *Ctenocephalus* and *Nepea* (see Fig. 23), the preglabellar field is occupied by a prominent, subcircular **preglabellar boss**; in others there may be a **median preglabellar ridge**. This

ridge may be narrow (tr.), of constant width, or may be broader, widening forward to merge with the anterior border to form the structure distinguished as the **plectrum** by

FIG. 8. *Illaenus lacertus* WHITTINGTON, Upper Ordovician, Baffin Island, Canada. Dorsal view of enrolled exoskeleton, immersed in liquid, showing darker muscle areas of glabella, ×3 (Whittington, 1954b, pl. 61, fig. 1).

FIG. 9. *Bumastoides milleri* (BILLINGS), Middle Ordovician, Ontario, Canada. *1,2,* Dorsal and anterior views of internal mold of cranidium, showing impression of lunette, ×3; *3,* dorsal view of cephalon of enrolled specimen, ×4.5; *4,* exterior view of thorax and pygidium, latter broken to show mold of outer surface of doublure, ×4.5 (Whittington, 1954b, pl. 62, fig. 18, 25–26, 29).

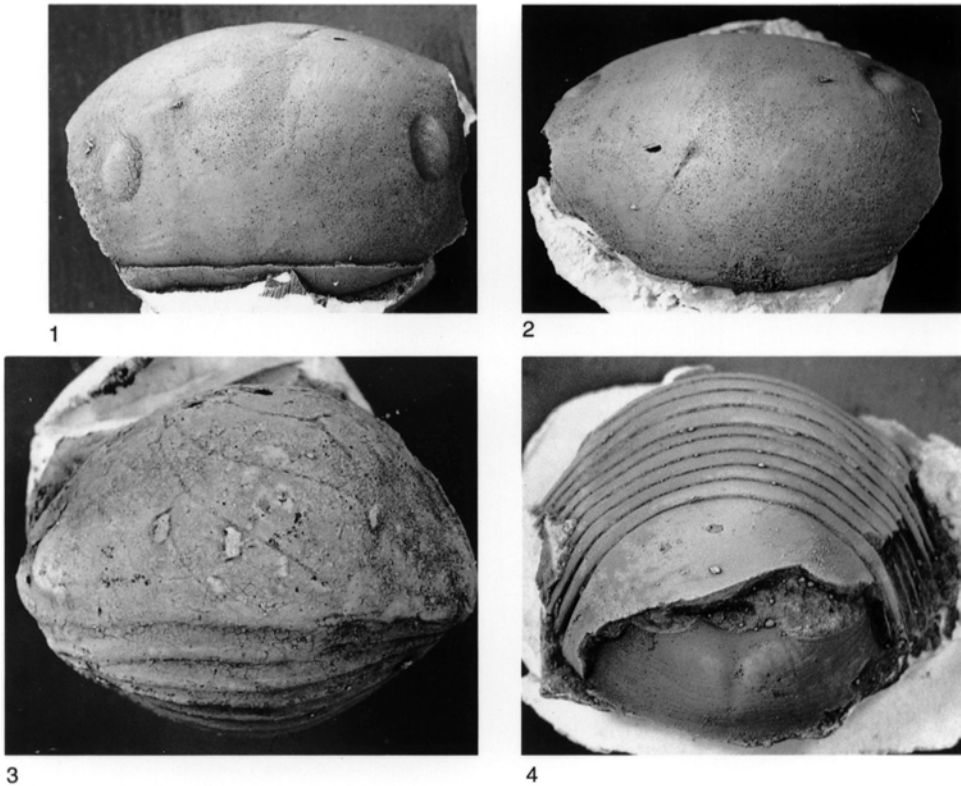ÖPIK (1967, p. 58). FORTEY (1990a, p. 547, fig. 9) has described the plectrum stage in the development of Ptychoparioidea. In other trilobites there may be a **median preglabellar furrow** (e.g., Fig. 6). In some proetids a **transverse preglabellar ridge** occurs immediately inside the border furrow (see Fig. 19). The gena bears the eye lobe (when present), and in many trilobites an **eye ridge** runs inwards and forward from the anterior end of the eye lobe to the axial furrow opposite the anterolateral portion of the glabella. Where present, the fossula lies immediately in front of the intersection of the eye ridge and the axial furrow. The gena is divided by the inner edge or furrow of the border, by the eye ridge, and by the facial suture; terminology for these separate areas is given in Figure 14.

The eye lobe is convex, and may be strongly so, or raised on a stalk. In trilobites having a facial suture (Fig. 5), the eye lobe is divided by the suture, in an abaxially curving arc (points γ, δ, and ε in Fig. 3), into the adaxial **palpebral lobe** and an abaxial **visual surface**. Below the visual surface there may be a ridge and furrow, the **eye socle** and **eye socle furrow** (Fig. 15), separating it from the genal field. Abaxial to the eye lobe in proetids, however, there may be a smooth **subocular area** or a depressed **subocular groove** bounded on the outside by a **subocular ridge**. The palpebral lobe, subsemicircular in dorsal outline, is separated from the fixigena by a change in slope or a **palpebral furrow**. It may be subdivided (by this change in slope or furrow) into a convex

palpebral rim bordering the facial suture and a lower adaxial portion. The **palpebral ledge** is a flattened edge or furrow abaxial to the rim. The palpebral lobe and eye ridge may form a continuous structure, the **palpebro-ocular ridge**. Olenellina lack the facial suture; consequently the gena is not subdivided by it, nor is the palpebral lobe outlined abaxially (Fig. 16). Hence a different terminology has been employed. HUPÉ (1953a) used ocular lobe (*lobe oculaire*) for the combined eye ridge (*crête oculaire*) and eye lobe (*lobe palpebral*), without mention of the visual surface. ÖPIK (1961a) termed the eye ridge and eye lobe the palpebral lobe, divided longitudinally into inner and outer portions by a furrow, the ocular striga. BERGSTRÖM (1973a) used anterior and posterior (rather than outer and inner) palpebro-ocular ridge. Here **ocular lobe** is preferred for the combined eye ridge and eye lobe, including the visual surface. This lobe divides the genal field into interocular and extraocular areas and is itself divided by the **ocular furrow** into inner and outer bands (Fig. 16). The ocular furrow is the ocular striga of ÖPIK or epipalpebral furrow of COWIE and MCNAMARA (1978). In many specimens of Olenellina, the ocular lobe is broken so that only the outline is preserved (e.g., FRITZ, 1972; 1991). In rare specimens (e.g., WHITTINGTON, 1989, fig. 8–9) the visual surface is sharply outlined, as it is partially even when the lobe is broken (e.g., FRITZ, 1972, pl. 1, fig. 7–8, pl. 15, fig. 16; 1991, pl. 11, fig. 8–9). ÖPIK (1967, p. 54) argued that there was a **circumocular suture** surrounding the visual surface in this and other Cambrian trilobites. In Olenellina and protolenids the inner and outer ridges of the ocular lobe may divide adjacent to the glabella, the posterior ridge reaching the axial furrow immediately in front of the outer end of glabellar S3, the anterior either merging with the anterolateral edge of the frontal glabellar lobe or the pair uniting around the anterior margin of the preglabellar furrow to form a **parafrontal band** (HUPÉ, 1953a, p. 105). This band is developed in ellipsocephaloids, particularly in protoleninids (GEYER, 1990b)

FIG. 10. *Galbagnostus galba* (BILLINGS), Middle Ordovician, Table Head, Newfoundland. *1,2,* External surface of cephalon, dorsal and oblique views; *3,* dorsal view of pygidium, to show sculpture and smooth areas, ×20 (Whittington, 1965, pl. 3, fig. 7, 15; pl. 4, fig. 9).
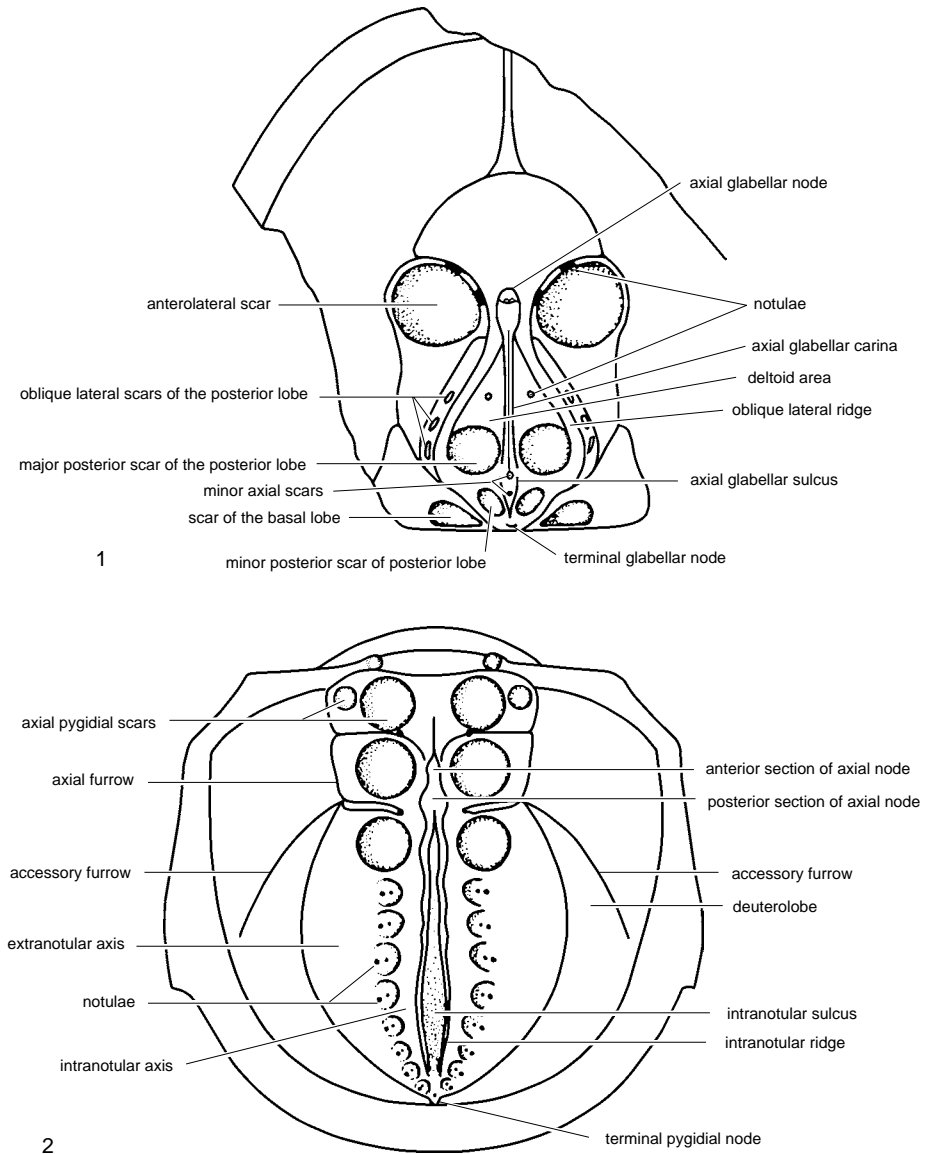
FIG. 11. Terminology applied to the visceral features of the Agnostina revealed by the parietal surface of the exoskeleton; *1,* cephalon and *2,* pygidium. This surface is preserved in many examples as an internal mold of the exoskeleton and illustrated as such (Shergold, Laurie, & Sun, 1990, fig. 6).

and in the redlichioid *Lemdadella* (SDZUY, 1978). It has been observed in the Middle Cambrian *Asthenopsis*, and in some specimens of *A. opalensis* the eye ridge is divided along most of its length into three parallel ridges (JELL, 1978b). In a small cephalon of *Daguinaspis,* HUPÉ (1951) described a third branch from the eye ridge adjacent to the glabella and illustrated similar structures in *Fallotaspis* (HUPÉ, 1953a, pl. 1, fig. 1–3); this structure was used by HUPÉ (1951) in his discussion of cephalic segmentation. The most recent consideration of the morphology of the palpebro-ocular ridge and the

parafrontal band was by PILLOLA (1991, p. 79–84, fig. 47), who concluded that the trisegmented eye ridge is best known in Lower Cambrian trilobites. In younger forms the structure of the eye ridge is simplified.

A pattern of radiating, distally anastomosing ridges, the **genal caeca**, is developed with varying intensity on the frontal area and adjacent librigenal field or over the entire genal field in many Cambrian and Ordovician trilobites (ÖPIK, 1961a) and in Silurian and Devonian proetids (ŠNAJDR, 1980, pl. 63, fig. 3–4). The ridges are numerous and narrow in comparison with the size of the cephalon. They may become stronger as they approach and cross the border furrow or may not be evident on the border. The pattern of the genal caeca is well displayed by *Harpides*, extending from the axial and preglabellar furrows across the genal field and border to the narrow marginal rim (Fig. 17.1). This cephalic border (described below as the fringe) is wide (sag. and tr.), gently concave dorsally, and bilaminar, the two lamellae lying close together. The external surface of the lamella on the underside bears a pattern of radiating ridges corresponding to those on the upper lamella (Fig. 17.2). This suggests that the ridges enclose a system of canals that lay between the lamellae [cf. FORTEY's (1974b, p. 53) description of the olenid *Tropidopyge*]. FRITZ (1972, p. 23) has shown that in certain Olenellina the median ridge of the preglabellar field is part of the genal caeca (Fig. 18). In *Redlichia* a ridge on the preocular area of the fixigena, directed out close to the anterior branch of the facial suture or situated more adaxially to it, was termed the **facial line** (WHITEHOUSE, 1939, p. 189; ÖPIK, 1961a, fig. 8; W. CHANG, 1966, fig. 1, as the preocular facial line). This ridge is similar in width to those of the genal caeca and has been considered to be part of this system of canals by some authors (ÖPIK, 1970b, p. 25, pl. 4, fig. 1). In harpids and harpetids, pits lie between the ridges of the genal caeca, and in some olenids (FORTEY, 1974b, fig. 4), for example, pits occur in the
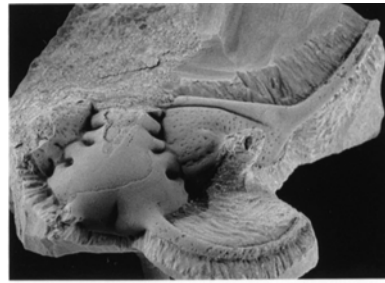
FIG. 12. *Perirehaedulus caprus* (THOMAS in THOMAS & NARBONNE), Silurian, Arctic Canada. *1,2,* Anterior and dorsal views of the holotype, an incomplete cranidium, ×3 (Thomas & Narbonne, 1979, pl. 4, fig. c, e).

border furrow between the ridges. The genal caeca may radiate from the eye ridge, the eye lobe, or the axial furrow behind the eye ridge (Fig. 17.1). Thus the eye ridge runs across the radiating caeca, as does the **genal ridge**, curving outward and backward toward the genal angle. The genal ridge may branch abaxially and may not reach the genal angle. It is present in Olenellina (Fig. 16), in redlichioids (the para-ocular facial line of W. CHANG, 1966, fig. 1), and, for example, in *Churkinia* (PALMER, 1968, pl. 1, fig. 6). In trilobites lacking an eye lobe or eye tubercle (e.g., *Conocoryphe, Lonchodomas, Anisonotella*), a single genal ridge may extend outward from the axial furrow and curve back to the genal angle. The **intergenal ridge**
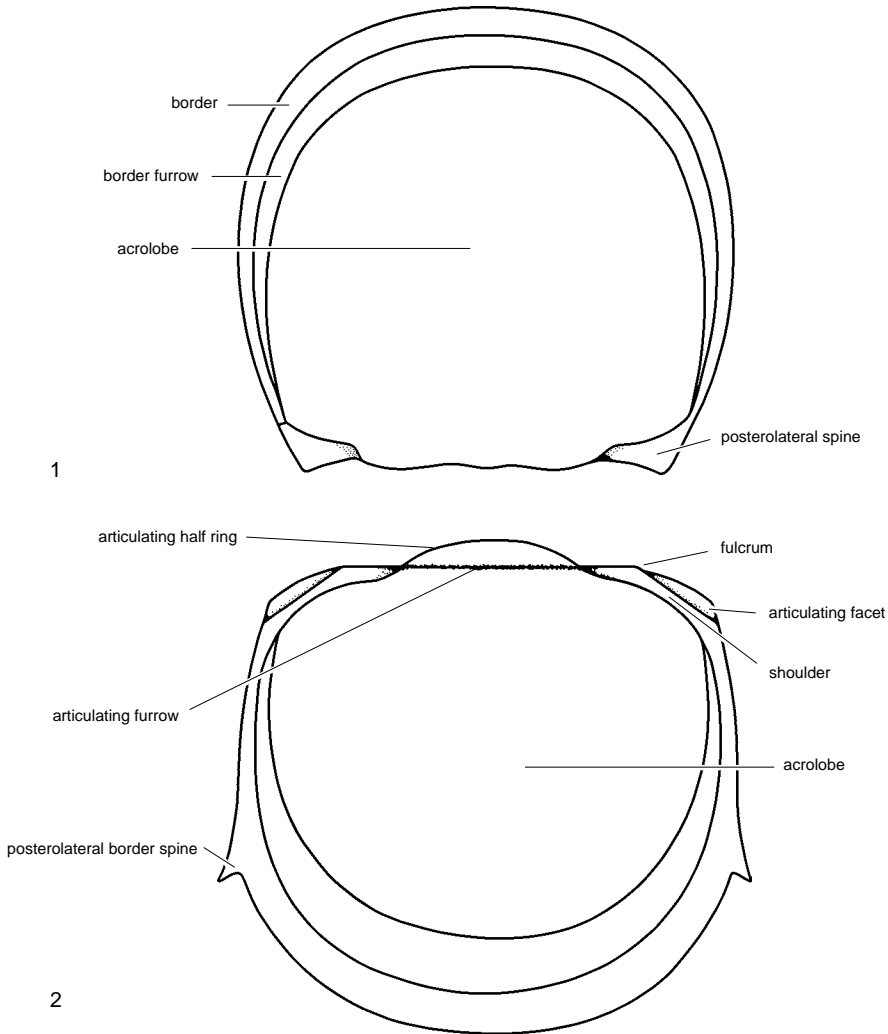
Fig. 13. Terminology applied to the external surface of the Agnostina; *1,* cephalon and *2,* pygidium (Shergold, Laurie, & Sun, 1990, fig. 1–2).

in Olenellina is a ridge that arises from the posterior end of the inflated palpebral (interocular) area and curves outward and backward to the posterior border and base of the intergenal spine (Fig. 16). The ridge is prominent in early developmental stages of *Olenellus* (PALMER, 1957) and *Elliptocephala* (WHITTINGTON, 1957a) and is retained in the holaspis. In *Elliptocephala* a less prominent ridge, the **posterior ocular line** or **ridge**, runs back from the posterior end of the eye lobe to the border, outside the intergenal ridge (Fig. 16). Both ridges are present in holaspides of *Fallotaspis* (HUPÉ, 1953a, pl. 1, fig. 1) and *Eofallotaspis* (SDZUY, 1978, pl. 1, fig. 1, 4).

In Agnostida (ÖPIK, 1961a; ROBISON, 1978, p. 4; JELL, 1975a) a radiating, branching pattern of ridges, **rugae**, separated by furrows or **scrobiculae** that rarely anastomose, extends from the axial furrow to the border furrow. These ridges are relatively
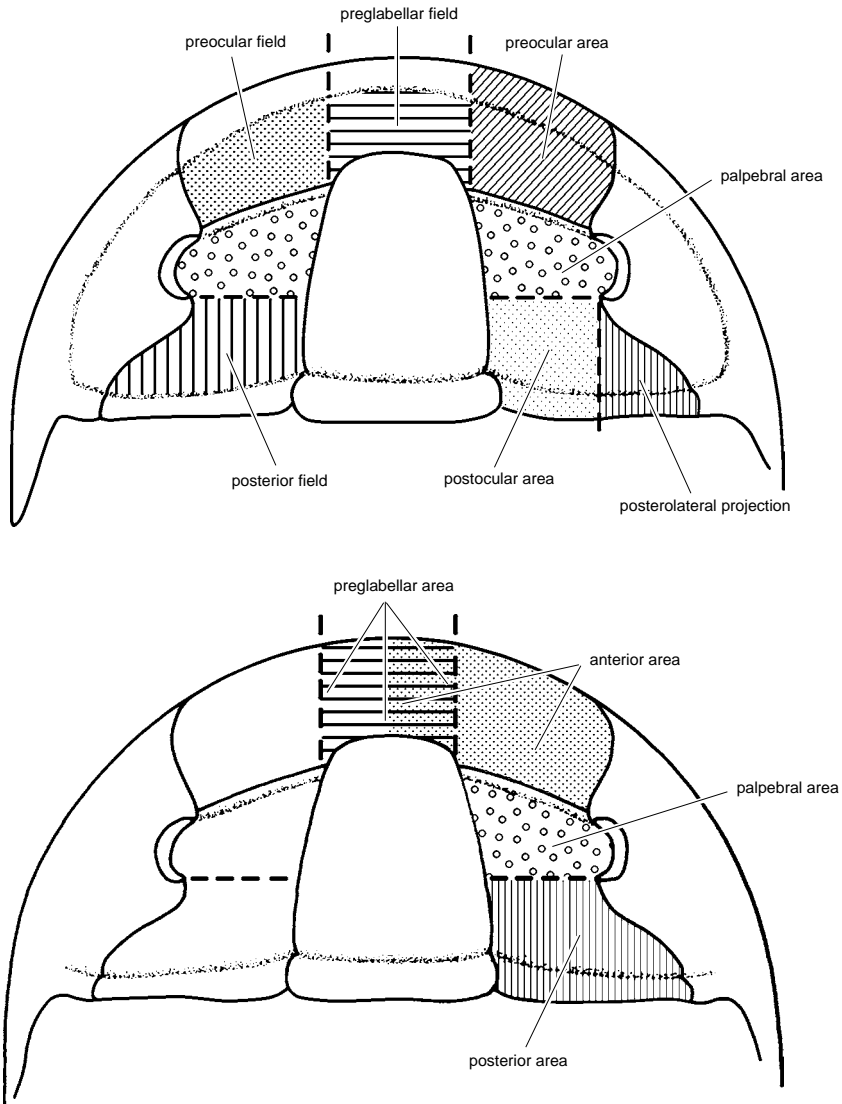
Fig. 14. Terminology of areas and fields of the cephalon illustrated by a ptychopariid trilobite, labelled portions differentiated by shading (new).

much coarser than those of other trilobites and have few main connections to the axial furrow; according to ROBISON these ridges are always anteromedially divided, unlike those in other trilobites. In the Ordovician *Galbagnostus* (WHITTINGTON, 1965, p. 307) and *Arthrorhachis* (FORTEY, 1980b, p. 31) a much finer pattern of radiating ridges has been detected crossing the border furrow.

The **tropidium** (Fig. 19) is a ridge, concentric with the cephalic margin, which traverses the preglabellar and genal fields inside the margin of the doublure (OWENS, 1973; MORZADEC, 1983, pl. 1, fig. 4–6); it may form more than one continuous ridge. OWENS termed similar discontinuous ridges **tropidial ridges**. ORMISTON (1971) described silicified material that showed that the
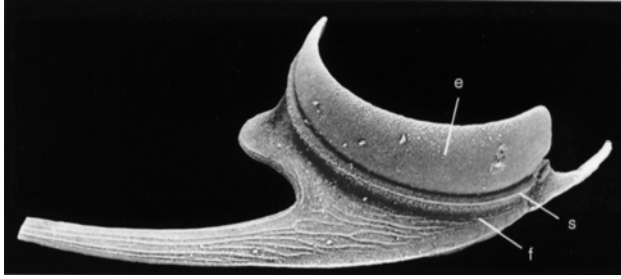
Fig. 15. *Remopleurides plaesiourus* Whittington, Middle Ordovician, Virginia. Oblique view of isolated free cheek to show visual surface of eye (*e*), eye socle (*s*), and eye socle furrow (*f*), ×6 (Whittington, 1959a, pl. 5, fig. 6–7).

tropidium was not reflected as a groove in the parietal surface. According to Šnajdr (1980, p. 18) the tropidium is present as a groove on the parietal surface in forms with a thin exoskeleton; when the exoskeleton is thick it is not so represented.

On the genal field adjacent to the base of the glabella there may be a low, elongated (exs.) swelling, the **baccula** (Fortey, 1975b) (see Fig. 73). This swelling may be connected to the anterolateral corner of the occipital ring, separated from L1 by a furrow, separated from the glabella by the axial furrow, or separated in addition from the genal field by the **baccular furrow**. The different forms of the baccula in unrelated trilobites

have led some authors to consider it part of the glabella, others to regard it as part of the genal field. In *Harpides* (Fig. 17) and harpids such as *Dolichoharpes* (Chatterton & Ludvigsen, 1976, pl. 7, fig. 8–9, 16), a semicircular depressed area lacking reticulate ridges lies at the inner posterior corner of the genal field, opposite L1, and is termed the **ala.** An area in a similar position in styginids (Fig. 20), also smooth, has been called the lateral muscle impression (Fortey, 1980b, p. 59; Lane & Thomas, 1983, fig. 1–2); it has been compared with the lunette in *Bumastoides* (Fig. 9.1–2) and other illaenids. The **paraglabellar area** in homalonotids (Cooper, 1982) is in the same position. Some, if not
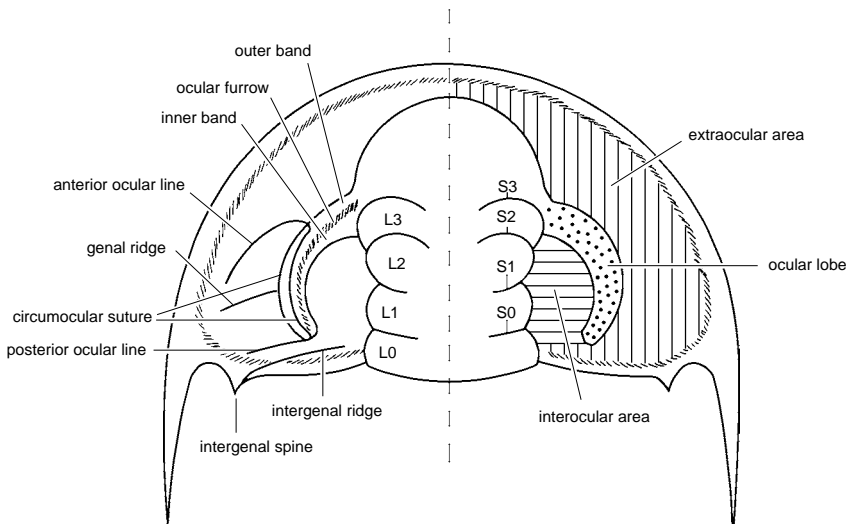
Fig. 16. Terminology of the cephalon of Olenellina, after Hupé (1953a) and Fritz (1991) (new).
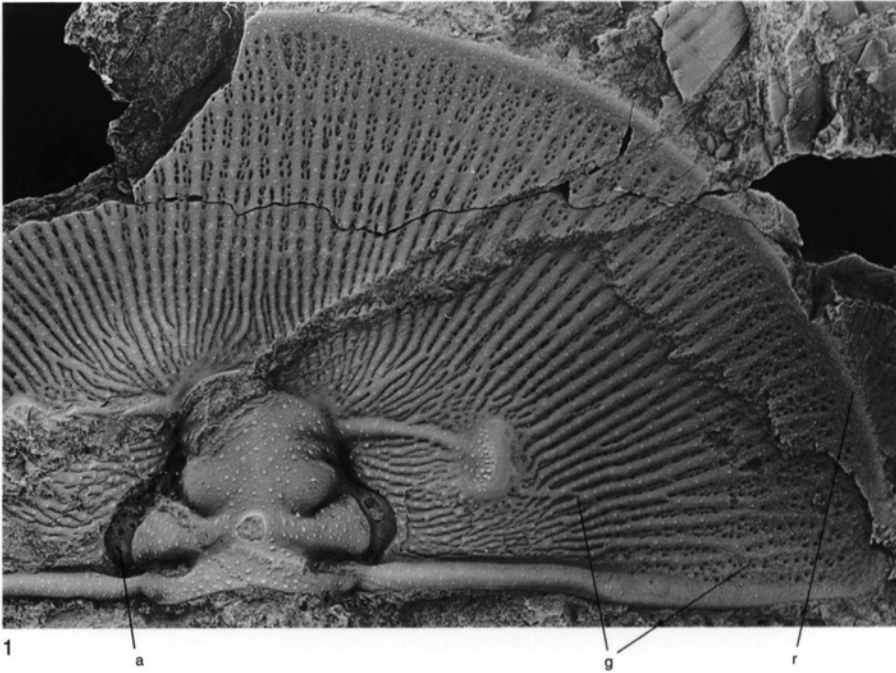
FIG. 17. *Harpides atlanticus* BILLINGS, Middle Ordovician, Table Head, Newfoundland. *1,* Dorsal view of incomplete genicranium, to show radiating pattern of genal caeca, ×5; *2,* exterior view of fragment of lower lamella of fringe, showing genal caeca as raised ridges, with intervening pits and strong concentric ridges, ×9. Abbreviations: *a,* ala; *g,* genal ridge; *r,* rim (Whittington, 1965, pl. 5, fig. 3; pl. 6, fig. 2).
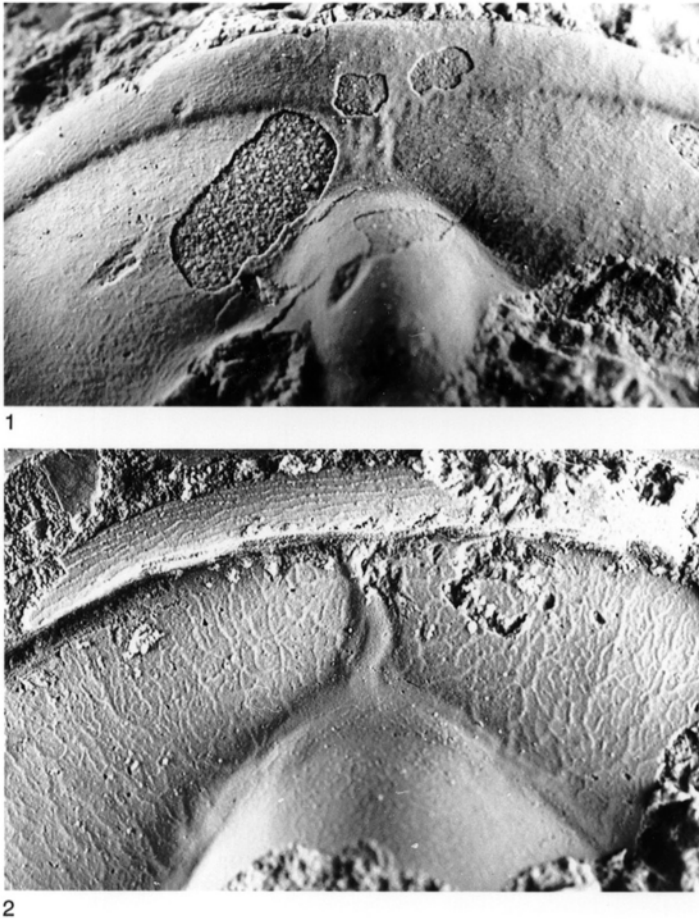
FIG. 18. The median preglabellar ridge in two Olenellina, Lower Cambrian, Canada, which suggests that the ridge is composite and part of the genal caeca. *1, Nevadella baculenta* FRITZ, 1972, ×10; *2, Olenellus* sp., ×8 (Fritz, 1972, pl. 5, fig. 3; pl. 13, fig. 14).

all of these areas, project from the parietal surface and appear as depressions in the internal mold. They are considered to be areas of muscle attachment, but the paraglabellar area in *Trimerus* (WHITTINGTON, 1993b) bears impressions of the genal caeca and hence cannot have been an attachment area.

The genal angle may be rounded, but in many trilobites it bears the prominent genal spine, called **librigenal** or **fixigenal** according to whether the suture is **opisthoparian** (Fig. 3) or **proparian** (Fig. 5), i.e., whether the spine is borne by the librigena or the fixigena. These terms indicate merely the position of the genal spine of the holaspid trilobite with reference to the suture and do not imply homology. The genal spine may be short or long so that it extends back beyond the rest of the body. In trilobites lacking a genal spine, the posterior branch of the suture may cross the border at the genal angle, a condition called **gonatoparian**.

The form of the anterior and lateral cephalic **border** (Fig. 3) varies. In many trilobites the border is dorsally convex, defined by border furrows (Fig. 4), and, in combination with the ventrally convex doublure, forms a tubular structure around the outer edge. This structure is continued into the base of the genal spine, where present, and

into the distal extremity of the posterior border. The inner edge of the doublure of the lateral cephalic border (Fig. 4) lies a short distance ventrally of the border furrow. This tubular type of anterior and lateral cephalic border characterizes many Cambrian trilobites (see Fig. 27–28, 30, 37) and is present in many post-Cambrian forms such as proetids and Phillipsiinae (see, for example, Fig. 31.4). In the latter example, however, the doublure is flattened, giving a sharply flexed cephalic margin, as it is in Agnostina (see Fig. 27.1). This modification is associated the close fit of cephalic and pygidial doublures when fully enrolled (see section on enrollment, p. 67). In *Isotelus* (Fig. 2) lateral and anterior borders are ill-defined by the change in slope between glabella and genal field and the faintly convex border. The doublure is flat abaxially beneath the lateral border, curving up adaxially to lie close beneath the dorsal surface of the librigena (CHATTERTON & LUDVIGSEN, 1976, pl. 2). This type of border is characteristic of asaphids (JAANUSSON, 1953a, 1953b; HENNINGSMOEN, 1960) and styginids (ŠNADJR, 1960); it is also developed in the bathyurid *Punka* (FORTEY, 1979), but *Bathyurus* (see Fig. 31.2) has a tubular border. In trilobites in which the frontal glabellar lobe is expanded, for example in some cheirurids (see Fig. 34.1) or in phacopids (see Fig. 36.2), the anterior border faces anteriorly and may be greatly restricted, the lateral borders retaining their tubular form and facing upward and outward. In such encrinurids as *Encrinuroides* (see Fig. 34.3) the anterior border faces anteriorly, and the preglabellar field (between the preglabellar furrow and anterior border furrow) is long (sag. and exs.) and convex. The anterior branches of the suture, together with the narrow (tr.) rostral suture, divide the preglabellar field transversely. This division has resulted in the use of special terms (EVITT & TRIPP, 1977)—anterior border of cranidium and precranidial lobe—the latter for the lobe of the librigena between the connective and facial sutures and anterior border furrow. Lateral and anterior borders may be lost altogether by effacement in
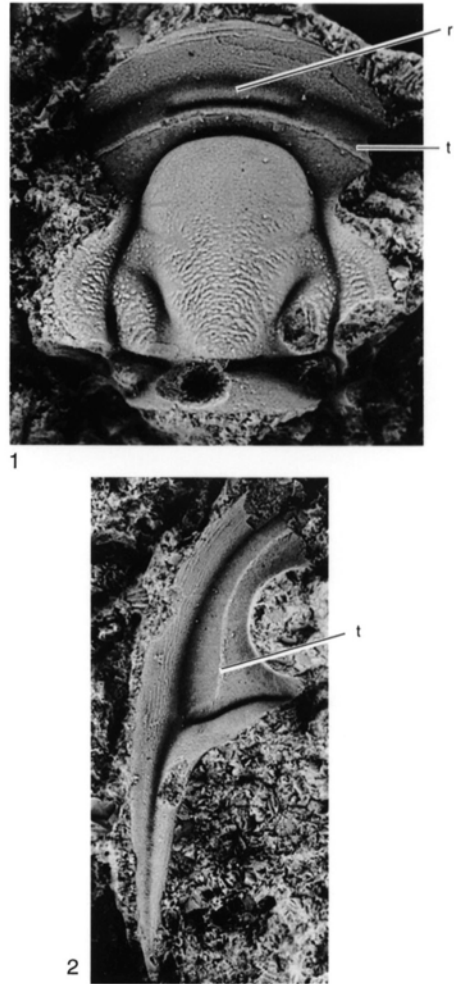
FIG. 19. *Warburgella stokesii* (MURCHISON), Silurian, Wenlock Limestone, U.K. *1,* Cranidium, showing transverse preglabellar ridge (*r*) and tropidium (*t*) on preglabellar field, ×13; *2,* librigena, showing tropidium continued on genal field, ×6 (Owens, 1973, pl. 13, fig. 12–13).

some illaenids (see Fig. 1, 33), but the tubular form is retained laterally by the doublure.

A different type of cephalic border is that of the trinucleid *Cryptolithus* (see Fig. 29.1, 129). The border slopes steeply downward anteriorly and laterally and has a vertical edge, the doublure underlying it closely. Pits in the outer surfaces of border and doublure join the two surfaces by opposed, funnel-shaped structures. The cephalic suture runs around the steep margin of the border and
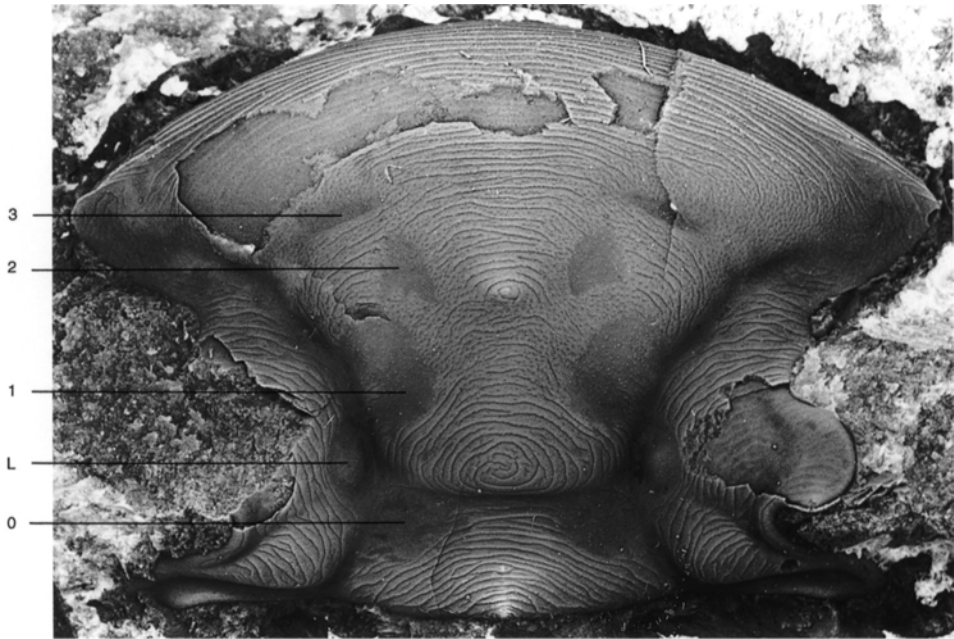
FIG. 20. *Kosovopeltis? pompilius* (BILLINGS), Lower Devonian, Maine. Dorsal view of cranidium, showing sculpture and lateral (*L*) and glabellar (*0–3*) muscle impressions, ×6 (Whittington, 1960a, pl. 54, fig. 25).

curves inward to the posterior border at the genal angle; it also divides the funnel-shaped structures. This type of border, the **fringe**, thus consists of two pitted lamellae, the **upper** and **lower lamellae**, separated by the suture, with the lower lamella extended into the genal spine. Details of the structure of the fringe in trinucleids were given by C. P. HUGHES, INGHAM, and ADDISON (1975). Similar in structure is the fringe of harpetids (WHITTINGTON, 1949; CHATTERTON & LUDVIGSEN, 1976), harpidids (Fig. 17), and dionidids (WHITTINGTON, 1952a). A single row of pits in the anterior border furrow is developed in a number of different trilobites, and in *Redlichia* (see Fig. 30.2) and certain olenids (FORTEY, 1974b) these are opposed by pits in the doublure.

The posterior cephalic border has the form of a raised ridge, defined on the inner side by a change in slope or the border furrow. This border extends transversely in the horizontal plane from the axial furrow to the **fulcrum** (Fig. 5), abaxial to which it is flexed

down. The doublure extends adaxially from the genal angle, narrowing (exs.) and disappearing at the fulcrum. In trilobites, such as *Olenellus* (see Fig. 45), in which the posterior border curves outward and downward from the axial furrow, there is no fulcrum dividing the border into inner and outer portions, but the doublure extends inward to a corresponding position in an exsagittal line with the inner edge of the thoracic doublure. The posterior cephalic border thus duplicates the form of the thoracic segments in being either fulcrate or nonfulcrate (see discussion of thorax below); such duplication is necessary for articulation of cephalon and anterior thoracic segment. In trilobites in which the thoracic pleural furrow is effaced, as in illaenids (WHITTINGTON, 1963, pl. 16), the posterior border furrow is also effaced, and the posterior cephalic border consequently is not defined (see Fig. 33). Nevertheless, the posterior edge of the cephalon is fulcrate (i.e., bent down at the fulcrum) and so articulates with the fulcrate thorax.
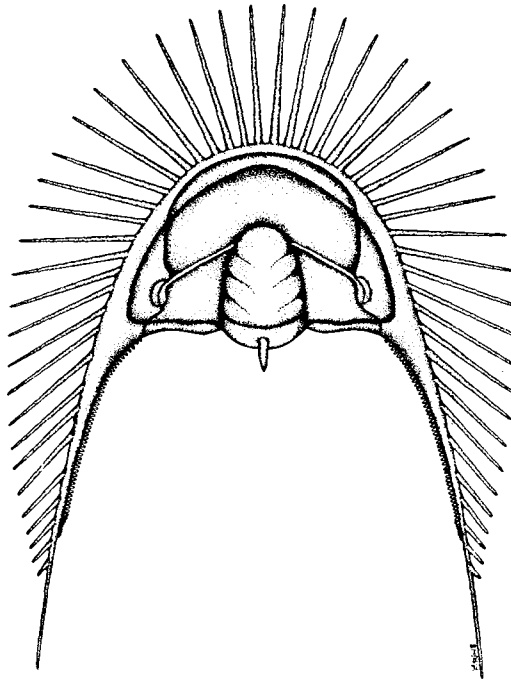
Fig. 21. Reconstruction of cephalon of *Bowmania americana* (WALCOTT), Upper Cambrian, North America; based on new material from R. LUDVIGSEN and from LUDVIGSEN, 1982, fig. 24 (new).

In many trilobites the only relatively large cephalic border spine is the **genal spine**. This spine is backwardly directed and may terminate at some point beside the thorax or extend behind the body. In most trilobites this spine tapers progressively to a sharp point. Exceptions include the Cambrian *Peachella* (PALMER & REPINA, 1993, fig. 4.2) and such Carboniferous proetids as *Spinibole* and *Cystispina* (BRAUCKMANN, 1978; OWENS & TILSLEY, 1995). In *Spinibole* the genal spine is long, tubular, and bluntly pointed; in *Cystispina* the club-shaped spine is divided into two cysts. Many additional cephalic border spines (less prominent than the genal spine) are present in such Cambrian trilobites as *Bowmania* (Fig. 21), and in some post-Cambrian odontopleurids (Fig. 22) there are many additional border spines. These spines may project almost horizontally as in *Bowmania* or be downwardly and outwardly directed as in *Acidaspsis*. The anterior border and doublure of the cephalon may be

drawn out into a **frontal spine**, as in asaphids such as *Megistaspis (Megistaspidella)* (JAANUSSON, 1956b; WANDÅS, 1984). An extraordinary example of such a spine, three times the length (sag.) of the rest of the cephalon, is that of the dalmanitid *Psychopyge* (MORZADEC, 1988). In other dalmanitids the spine may be shorter, but bifid or trifid (CAMPBELL, 1977), and has been referred to as a **frontal process**. Short spines (the **median** and **anterior fixigenal** spines) project from the lateral border in holaspid cheirurids such as *Sphaerocoryphe* and are remnants of relatively longer spines in earlier growth stages. In the Devonian *Paracalmonia* a similar short spine is present on the border of the librigena. Striking is the long, upward curving **intergenal spine** in the Cambrian *Nepea* (Fig. 23). Similarly situated but smaller intergenal spines are present in the developmental stages of Olenellina, *Paradoxides* (WHITTINGTON, 1957b), and dolichometopids (ÖPIK, 1982); and remnants may be

Fig. 22. Reconstruction of cephalon of *Acidaspis brighti* Murchison, Silurian, Europe, North America. *1,* Dorsal, *2,* anterior, and *3,* right lateral views, ×3 (Whittington, 1956b, fig. 1).
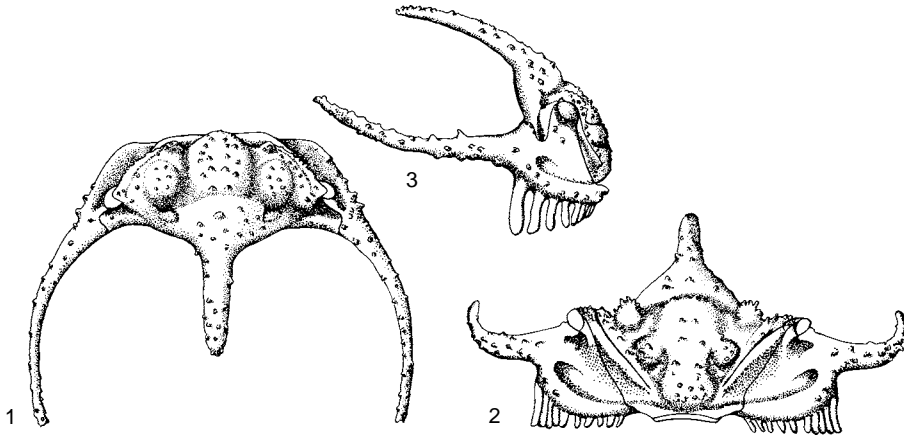
retained in holaspides (Fig. 16). In most trilobites the adaxial portion of the posterior cephalic border is directed transversely, the abaxial portion curved back (to different degrees) into the base of the genal spine. In some Olenellina and redlichioids, however, the genal spine is advanced, in that the base of the spine is situated on a transverse line in advance of the occipital ring at the mid-length of the cephalon or even farther forward. In these forms the posterior cephalic border is flexed forward, in Olenellina at or adaxial to the intergenal spine (Fig. 16), in redlichioids at about where it is crossed by the posterior section of the facial suture. This marked flexure in the posterior border was termed the **intergenal angle** by W. Chang (1966, fig. 1). A terminology for the angle between the lateral and posterior borders and the genal spine was proposed by Henningsmoen (1957a, fig. 1). An unusual cephalic spine is the posterolateral spine of the fixigena in *Ancyropyge* (Ormiston, 1967), as prominent as the librigenal and occipital spines.

In the posterolateral corner of the genal field of the metagnostids *Geragnostus*, *Galbagnostus* (Fig. 10.2), and *Arthrorhachis* (Whittington, 1965, p. 297; Hunt, 1967, pl. 22, fig. 35, 47), there is a smooth, oval area that differs from the muscle areas of the

glabella in being slightly raised; what this area represents is uncertain. A structure in the same position in a different metagnostid has been interpreted as an eye lobe (Ahlberg, 1988). Størmer (1980, p. 263–266) described pits and darker areas in the genal field (including the palpebral lobe and furrow) of *Chasmops* and interpreted them as areas of muscle attachment. Similar pits are present in the genal field in cheirurids, pliomerids, and encrinurids; whether these were areas of muscle insertion is an open question.

CEPHALIC SUTURES AND THE VENTRAL CEPHALIC EXOSKELETON

The **facial suture,** divided into an **anterior** and **posterior branch** (or **section**) by the eye lobe when present, may divide the dorsal cephalic exoskeleton into the cranidium and librigena (Fig. 3), and this suture may be met by other sutures in the ventral exoskeleton (Fig. 5). The dorsal and ventral sutures comprise the **cephalic sutures**. On molting the exoskeleton parted along these sutures, so that not only may the sutures be visible in entire exoskeletons, but the parts into which it separated (librigena, cranidium, rostral plate, hypostome) may be preserved. The course of the sutures is different in different

trilobites, and a particular pattern has long been recognized as characteristic of some family groups (as has the form of the hypostome), hence the importance that has been placed on cephalic sutures in classification (STUBBLEFIELD, 1936). The extraction and study of silicified specimens has provided much new information, and the preservation in full relief has enabled a better appreciation of the course of the sutures. The following account of cephalic sutures, the nature of the hypostome, and its relationship to the rest of the cephalic exoskeleton is based on recent reviews (WHITTINGTON, 1988a, 1988b). FORTEY and CHATTERTON (1988, fig. 5, p. 178; see FORTEY, 1990a, for further discussion) introduced the term **natant** condition to describe that in which the hypostome was detached from the cephalic doublure, and **conterminant** condition for that in which the hypostome was attached by a suture to the doublure, the latter extending inward to a position beneath the preglabellar furrow.

PATTERNS OF CEPHALIC AND FACIAL SUTURES

In cephala having an opisthoparian facial suture (Fig. 1–3) the two branches may subtend abaxially an oblique angle, the anterior branches curving inward to become confluent along the margin. This arrangement characterizes many species and has been called **ptychopariid** (see Fig. 27.4), a term carrying the implication that the **connective suture** is present on the doublure, defining the abaxial margin of the rostral plate. In the conterminant condition this suture connects the facial suture to the hypostomal suture (Fig. 4.1–5). When in the conterminant condition only a **median suture** transects the doublure, no rostral plate is developed, and the cephalic suture is termed **asaphid** (see Fig. 35). In the remopleuridioid *Kainella* the anterior branch is strongly outwardly directed from the eye lobe, then curves inward to cross the anterior border and meet the median suture. This pattern, in which the anterior branches subtend a wide angle in front of the eye lobes, is
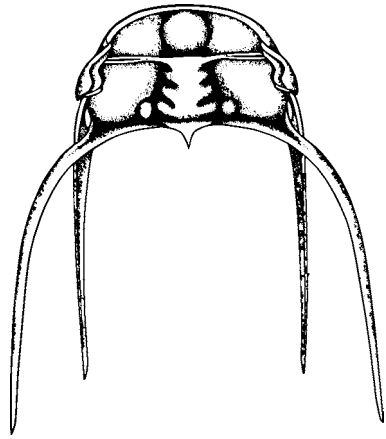
FIG. 23. Reconstruction of cephalon of *Nepea narinosa* WHITEHOUSE, Middle Cambrian, Australia, dorsal view. The upper of the two pairs of spines is the intergenal spine, ×2 (Öpik, 1970a, fig. 2).

described as **kainelliform**. In *Centropleura* (ÖPIK, 1961b, fig. 37) the anterior branch of the suture curves to run outward and backward, before curving forward to the cephalic margin and is termed **retrodivergent**. In the **cedariidiform** type of suture the posterior branch is directed outward from the eye lobe, then curves back over the posterior border to a point just inside the base of the genal spine, as in *Cedaria*. The proparian suture (Fig. 5), typical of the post-Cambrian Cheirurina and Phacopina, is also present in such unrelated Cambrian forms as *Norwoodella*. Special variants of this suture are the **burlingiiform** type (as in *Burlingia* and *Schmalenseeia*), in which both anterior and posterior branches run outward and forward from the eye lobe to the margin, and the **dalmanitidiform** (as in *Dalmanites*), where the anterior branches are confluent along the dorsal surface of the anterior border. In trilobites having either opisthoparian or proparian facial sutures, the anterior branches may be confluent; but the doublure is not crossed by a median or connective suture; this is described as the **nileiform** (see Fig. 36.1) facial suture.

The above kinds of facial sutures all cross the eye lobe, but facial sutures may be present when the eye lobe is absent. For

Fig. 24. Dorsal view of genicranium of *Brachymetopus ornatus* Woodward, Carboniferous (Dinantian), U.K., ×6 (Owens, 1986, pl. 5, fig. 10).

example, a ptychopariid facial suture is present in the Devonian proetid *Erbenicoryphe* (see Fig. 119), and a proparian suture occurs in the Devonian phacopid *Trimerocephalus* (see Fig. 118.4). On the other hand, a prominent eye lobe may be present, although the facial suture is lacking, as in *Brachymetopus* (Fig. 24).

A **marginal** or **submarginal** suture characterizes trinucleids (see Fig. 29.1), harpetids, and dionidids; and a variant is seen in *Entomaspis* (Rasetti, 1952a), where two branches run outward and backward from the eye lobe to the base of the genal spine where they join the marginal suture (**entomaspidiform** type). In trilobites with a marginal suture the cephalic exoskeleton is divided into a dorsal portion, for which Henningsmoen (1959, p. 155) coined the term **genicranium**, and a ventral portion, which he called the **doublural plate**; the latter is referred to in harpetids and trinucleids as the **lower lamella** of the fringe.

In some trilobites either branch of the facial suture may be situated on or beside a narrow ridge, the **sutural ridge**. In Olenellina Størmer (1942, fig. 14; pl. 2, fig. 1, 3–5) showed not only the intergenal and posterior ocular ridges but also described a fainter ridge curving from the anterior end of the eye lobe, outward and backward over the genal field (see Fig. 122). Some species of

Fallotaspis Hupé (1953a, fig. 20, 23; pl. 1, fig. 3, 5) also have an anterior ocular line or ridge extending backward to cross the posterior border just outside the base of the genal spine. There has been much discussion of the significance of the anterior and posterior ocular lines (Størmer, 1942, p. 137–139 and references; Hupé, 1953a, p. 118–119, fig. 68; Harrington in Moore, 1959, p. 62–63; Bergström, 1973b, p. 285). Harrington, following Hupé, concluded that they represented the fused facial suture and applied the name **metaparian** to such a suture. Størmer was not convinced of this interpretation, and there is no evidence for it from what we know of ontogeny in Olenellina. The notion of secondary fusion of facial sutures in Olenellina is considered improbable (Whittington, 1989).

The above terms that purport to describe the course of all or part of the cephalic suture or supposed suture have only limited use because the exact course differs even between species attributed to one genus.

DOUBLURE AND ROSTRAL PLATE

At the inner edge of the doublure the exoskeleton becomes thin except along the hypostomal suture (e.g., Whittington & Evitt, 1954, pl. 12, fig. 30). As a result of compaction, the trace of the inner edge of the doublure of the lateral and anterior borders may be impressed on to the dorsal exoskeleton to give a **paradoublural line.** In uncompressed trilobites this line may be marked by a slight change in slope of the dorsal exoskeleton. The doublure may extend inward beneath the genal field for a short distance adaxially, closely beneath the dorsal exoskeleton, but never extends below the eye lobe.

The cephalic doublure may be impressed by a **vincular furrow,** subparallel to the margin (see Fig. 36.2), or by one or more notches (Fig. 27.1) or folds below the lateral or posterolateral border. These vincular structures are coaptative (see section on enrollment and coaptation, p. 67). In certain asaphids, silicified specimens (Ross,

1951b, pl. 12, fig. 3–8; CHATTERTON & LUDVIGSEN, 1976, pl. 2, fig. 10, 12–14) show not only a vincular fold near the lateral margin but a small opening in the doublure posterolaterally that has one margin raised, the **panderian opening** (see Fig. 35.3). In other trilobites this opening is presumed to have lain within a small embayment in the inner margin of the doublure (see Fig. 29.3, 31.4, 35.1).

In Olenellina (see Fig. 30.1) there were no facial sutures, but the cephalic doublure is divided by a **perrostral suture** that runs along the arc of the doublure from beneath one genal angle to the other, a short distance abaxially from the inner margin. This suture isolates a narrow (sag. and tr.), crescentic **rostral plate**. A similarly shaped rostral plate is isolated in the brachymetopid *Australosutura* (Fig. 25) by the **rostral suture** that curves over the doublure between the inner, posterior edges. In *Brachymetopus* (Fig. 24) the rostral plate is crescentic (OWENS, 1986) as in *Australosutura* (Fig. 25), but facial sutures are absent. A crescentic ventral plate has been described in the cephalon of the metagnostid *Arthrorhachis* (see Fig. 27.1). Such ventral, rostral plates are the widest known (measured along the arc of the doublure) and are present in extremely different trilobites.

A narrower rostral plate is present in trilobites in which the connective suture crosses the anterior portion of the doublure; the shape of the plate is determined by the course of the suture, the distance separating the pair of sutures, and the form of the doublure. JAANUSSON (1956a, p. 37) proposed that the ptychopariid type of cephalic suture in which a rostral plate is present should be subdivided as **euptychopariid** and **stenoptychopariid**, referring respectively to forms in which the rostral plate was broad (see Fig. 27.4) or narrow (tr.) (see Fig. 31.1). The connective suture may be straight, inward as well as backwardly directed, giving a subrectangular or rhomboidal outline to the rostral plate, or the suture may be sinuous or run in a curve concave abaxially, resulting in
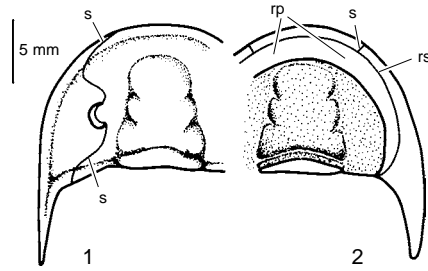
FIG. 25. Cephalon of *Australosutura* sp., Carboniferous; *1,* dorsal and *2,* ventral views. Abbreviations: *rp,* rostral plate; *rs,* rostral suture; *s,* facial suture (Whittington, 1988b, fig. 13).

an hourglass-shaped outline (see Fig. 28.1b, 31.2b). In certain encrinurids (see Fig. 34.3) the connective suture is close to the midline, and the rostral plate is an extremely narrow (tr.) strip. The doublure may be flat or gently convex anteriorly but may be sharply flexed, as in calymenids (see Fig. 34.2) or illaenids (see Fig. 33). In the former group the outer, anterior portion of the rostral plate (shown in the ventral view, Fig. 34.2b) is referred to as the **border sector;** the inner portion (which is bent sharply upwards and so hidden in the ventral view but shown in section in Fig. 34.2d) is the **doublure sector.** The anterior margin of the rostral plate, the rostral suture, lies in most trilobites on the margin of the border or on the ventral side; however, in xystridurids (see Fig. 30.3) and homalonotids it is dorsal to the margin.

NATURE OF CEPHALIC SUTURES

The course of the cephalic sutures and the nomenclature of sections of them and of the portions into which they divide the cephalon have been given above. The **hypostomal suture** is described below, a suture that separates hypostome from cephalic doublure. In entire specimens of the cephalon preserved in limestone, the suture lines may be visible as impressed lines; in such specimens in shale or silt compaction may have caused slight displacement along the suture lines so that they are readily visible. Portions of the cephalic exoskeleton, separated at the sutures, comprise the vast majority of fossils.

Such material that has been silicified has shown that the relatively thick exoskeleton is truncated at a flat edge along suture lines, and the precise fit along these lines is revealed by rare silicified specimens in which the portions are in juxtaposition (Fig. 4). This sutural edge of the exoskeleton contrasts with the thin edge at the inner margin of the doublure, to which the unmineralized ventral integument was attached. Silicified material of *Proetus* (WHITTINGTON & CAMPBELL, 1967, pl. 2, fig. 3), for example, shows the difference in appearance between these edges.

In specimens of the odontopleurid *Ceratocephala* from Bohemia (BRUTON, 1968b, p. 49) facial sutures cannot be seen, and they are described as fused and indistinct in a species described by CHATTERTON and PERRY (1983, p. 48); in other species (e.g., BRUTON, 1966, p. 25) there is clear evidence of these sutures. Other examples could be cited, and *Stelckaspis* is characterized (CHATTERTON & PERRY, 1983, p. 32) as having fused facial sutures in the holaspid stages and lacking sutural ridges. Whether facial sutures can be traced in a specimen may depend on the mode of preservation (cf. BRUTON, 1968b, p. 49), and it may also depend on whether a specimen is the exoskeleton of a molt or of a whole animal that died between molts. In the latter the suture may not have been functional, whereas in the former it would have been. In Upper Cambrian (RASETTI, 1952c, p. 892) and Ordovician trilobites (LUDVIGSEN, 1979b, p. 4) the median suture may be present in some species of a genus but absent in others. In such examples the absence of this suture does not appear to have taxonomic significance.

HYPOSTOME

The **hypostome** is a ventral cephalic exoskeletal plate, situated beneath the anterior portion of the glabella and consisting of a convex, oval or subcircular **middle body** surrounded by borders (Fig. 4, 26). The width corresponds to that of the frontal glabellar lobe, and in Cambrian trilobites the plate appears to have extended back to a point beneath L2 or L1. In younger trilobites the length (sag.) is greater, in some instances reaching to a point beneath the occipital ring. The middle body of the hypostome is subdivided into a larger **anterior lobe** and smaller **posterior lobe** by a **middle furrow** directed inward and backward from the lateral border furrow; the posterior lobe may have a convexity that is independent from that of the anterior lobe. The middle furrow dies out adaxially, and at the inner end there may be a flat or convex area, the **macula**, situated in the furrow or on either side of the slope down to the furrow, characteristically on the posterior side of this slope. The macula may be flat, lie in a deep depression, or be gently or strongly convex; it may be oval or lenticular in outline. Examples of the macula have been described in which the external surface is smooth (LINDSTRÖM, 1901; WHITTINGTON, 1988a, p. 600; 1988b, p. 336) or in which it is tuberculate (ORMISTON, 1967, pl. 2, fig. 6); examples in which the exoskeleton is thinner than in adjacent areas or shows an internal cellular structure have also been described. An anteromedian protuberance of the middle body, the **rhynchos** (see Fig. 34.2–3), is a coaptative device present, for example, in remopleuridids, calymenids, and encrinurids.

An anterior border of the hypostome may not be developed. If developed it may be flat, narrow, and downward- and forward-sloping or narrow and convex and complete or incomplete medially. The lateral and posterior borders, separated from the middle body by furrows, are of many different forms and are extended dorsally and inwardly as a doublure. In post-Cambrian species a rounded projection, the **shoulder**, is present at the anterior end of the lateral border; in older species such a projection lies farther back on the lateral border. The anterolateral edge of the hypostome is extended upward and outward as an **anterior wing**; on the inner surface of the wing a **wing process** may project,
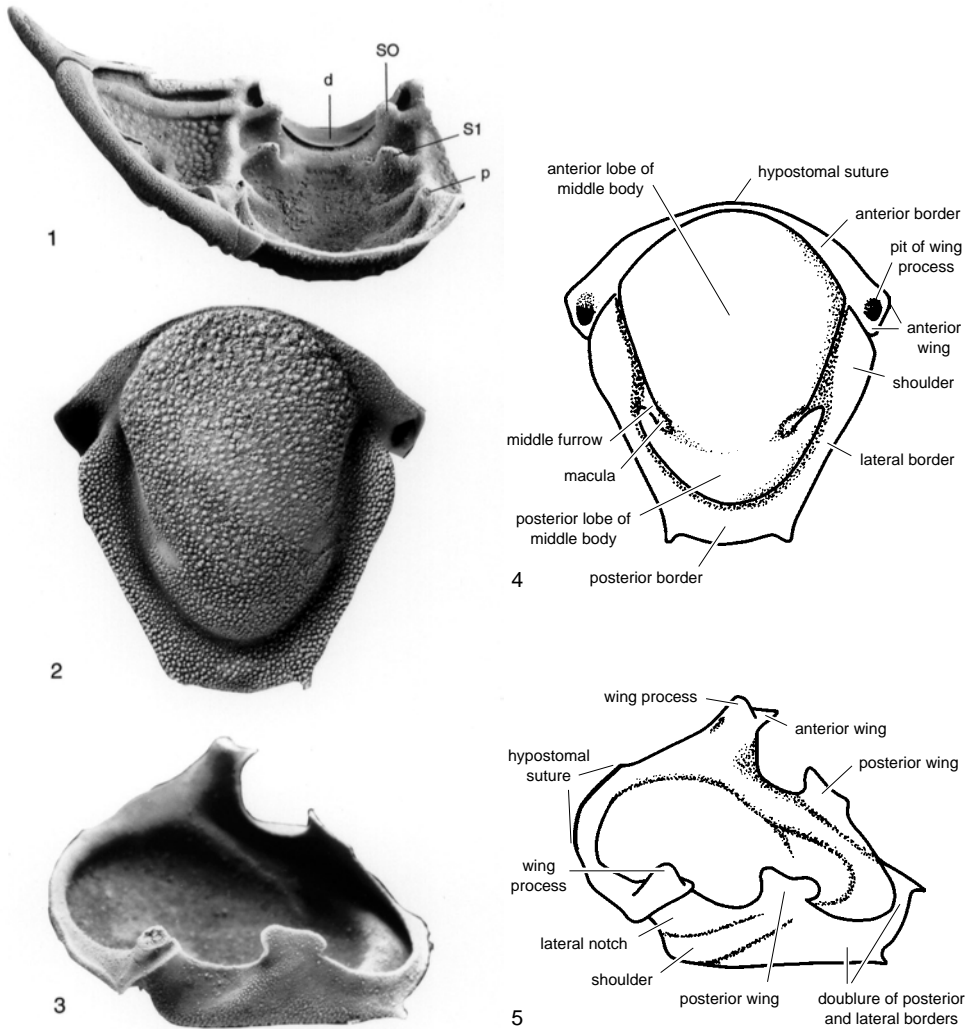
Fig. 26. Incomplete cephalon and hypostome of *Ceraurinella typa* Whittington & Evitt. *1,* Anteroventral view of cranidium with attached right free cheek, to show doublure of occipital ring (*d*), apodemes of SO and S1, and pit (*p*) in fossular apodeme, ×6 (Whittington & Evitt, 1954, pl. 10). *2,3,* Hypostome in ventral and oblique interior views, ×9 (Whittington & Evitt, 1954, pl. 11). *4,5,* Diagrammatic representation of hypostome to indicate terminology of ventral and oblique views, respectively (new).

a corresponding pit being present on the outer surface. In specimens in which the hypostome has been found in place, the tip of the wing or the wing process lies immediately beneath the fossular apodeme (Fig. 26.1) projecting from the dorsal exoskeleton. Where the internal surface of the hypostome is known, a **posterior wing** projects dorsally from the inner edge of the doublure of the lateral border, beneath the shoulder. Between the shoulder and anterior wing is the embayment of the **lateral notch**, which is broad in many Cambrian trilobites and in Proetida and is a narrow channel in such groups as Phacopida. The posterior border may bear one or more spines and may have a median notch developed or be deeply forked as in some Asaphida. The

remopleuridid *Hypodicranotus* (WHITTINGTON, 1952b; LUDVIGSEN & CHATTERTON, 1991) is unique in that the prongs of the fork extend back beneath the thorax to the pygidium. The varied structures of the doublure of the posterior border, revealed by silicified specimens, include a median projection, a median groove, and sharp granulation (WHITTINGTON, 1988b, p. 335).

Hypostomal Attachment Conditions

The hypostomes of holaspid trilobites and their relationship to the rest of the cephalic exoskeleton were described by WHITTINGTON (1988a, 1988b). It was shown that in species of particular genera or families the hypostome was inserted into the ventral cephalic integument and in others that it was attached at a suture to the cephalic doublure. In the same year FORTEY and CHATTERTON (1988, p. 178) proposed terms to describe the different attachment conditions and portrayed both holaspid and protaspid hypostomes. FORTEY (1990a) discussed different hypostomal conditions in more detail, as well as their possible evolution and importance to classification. In the light of this work, the cephalic types proposed by HARRINGTON (in MOORE, 1959, p. 67), which have been little used and are known to be partly in error, are not given here. Hypostomal conditions are described in the terms of FORTEY and CHATTERTON.

In the **natant** condition the hypostome is inserted into the ventral integument of the cephalon below the anterior portion of the glabella, not attached to the inner edge of the doublure but lying a short distance behind it. In the remarkable specimens of *Agnostus pisiformis* (MÜLLER & WALOSSEK, 1987), a natant hypostome is preserved in place (see Fig. 78, 80, 82); in species of other genera in which only the exoskeleton is preserved (e.g., WHITTINGTON, 1988a, pl. 55, fig. 8–9; FORTEY, 1990a, pl. 1) it is slightly displaced. Many Cambrian (Fig. 27.2–4, 28) and fewer post-Cambrian trilobites (Fig. 27.1, 29) have the hypostome in this position. They are restored with the anterior wing lying beneath the anterior end of the axial furrow, in front of the intersection of this furrow with the eye ridge (if this ridge is developed), or beneath the corresponding position, the fossula, in *Cryptolithus* and *Ampyx.* In the latter two genera and in *Proetus* (Fig. 29.3), a preglabellar field is absent, this field being well developed in the Cambrian examples. In some trilobites with a natant hypostome the doublure is not crossed by sutures (Fig. 28.2; 29.1–2), while in others it is traversed by connective sutures that isolate a rostral plate of differing sizes and shapes (Fig. 27.2–3, 28.1, 29.3). In *Proetus* the anterior edge of the hypostome lay close to the inner edge of the doublure. Well-preserved silicified specimens (WHITTINGTON & CAMPBELL, 1967, pl.

FIG. 27. Cephala with natant hypostome. *1, Arthrorhachis* sp., Middle Ordovician, with dashed outline of possible hypostome (Whittington, 1988b, fig. 1). *2, Pagetia ocellata* JELL, Middle Cambrian (Whittington, 1988a, fig. 1). *3, Dolerolenus* sp., Lower Cambrian (Whittington, 1988a, fig. 7). *4, Ptychoparia striata* (EMMRICH), Middle Cambrian (Whittington, 1988a, fig. 11). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton.

Abbreviations for this figure and Figures 28–37: *ab,* anterior boss; *ap,* anterior pit or fossula; *aw,* anterior wing; *bs,* border sector of rostral plate; *cs,* connective suture; *d,* doublure of cephalon; *ds,* doublure sector of rostral plate; *g,* girder; *gr,* genal ridge; *h,* hypostome; *hs,* hypostomal suture; *imd,* inner margin of cephalic doublure; *ln,* lateral notch of hypostome; *m,* median suture; *mc,* macula; *mt,* median tongue (narrow median extension inward of the posterior doublure of the hypostome); *oa,* oval area of middle body of remopleuridid hypostome; *p,* pit in anterior cephalic doublure of remopleuridid; *pa,* panderian notch; *pi,* pit in anterior border furrow or corresponding pit in doublure; *pr,* perrostral suture; *pw,* posterior wing of hypostome; *pyg,* pygidium; *rf,* rostral flange; *rh,* rhynchos; *rp,* rostral plate; *rs,* rostral suture; *s,* facial suture; *sh,* shoulder; *v,* vincular furrow or notch; *wp,* wing process.
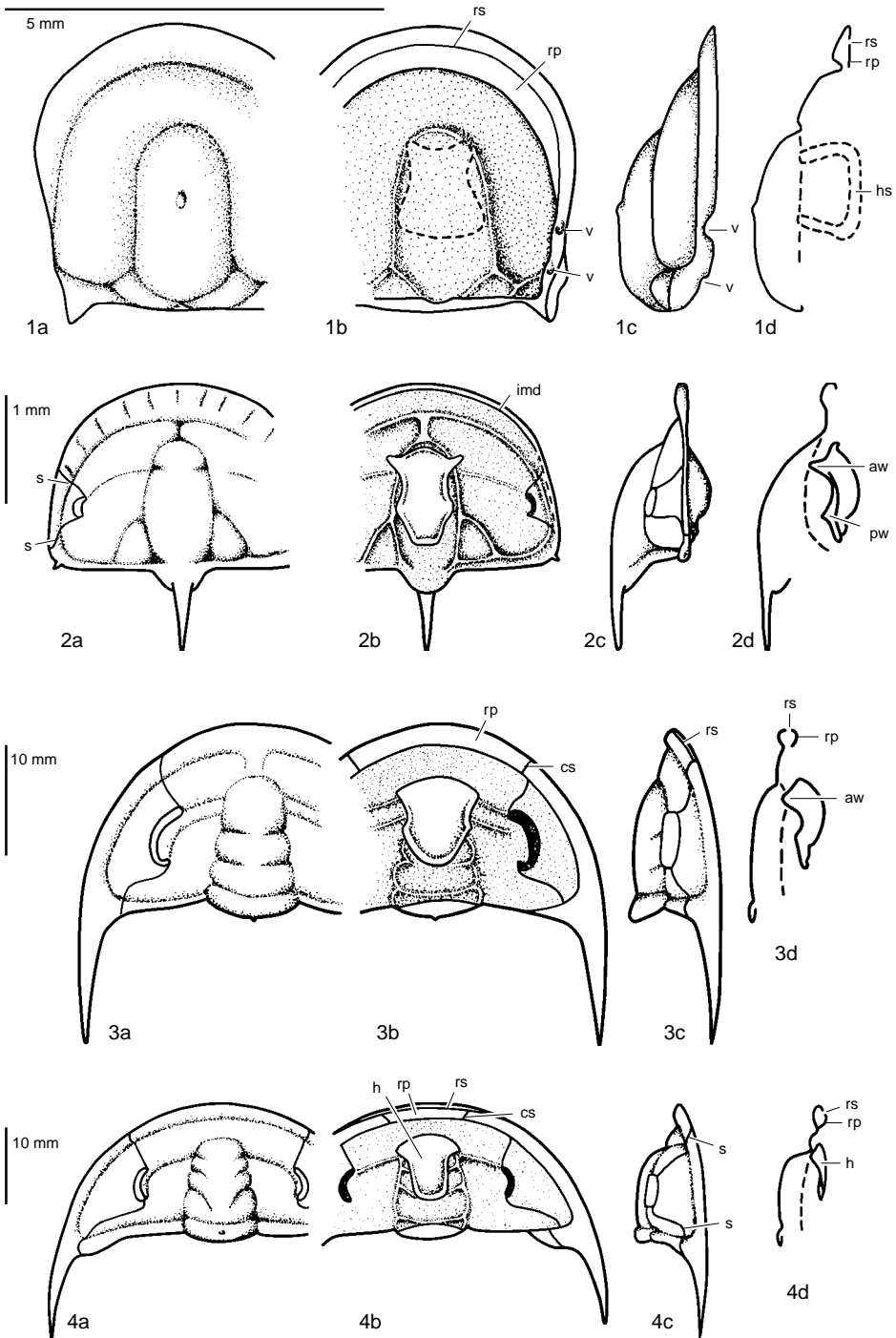
FIG. 27. *For explanation, see facing page.*
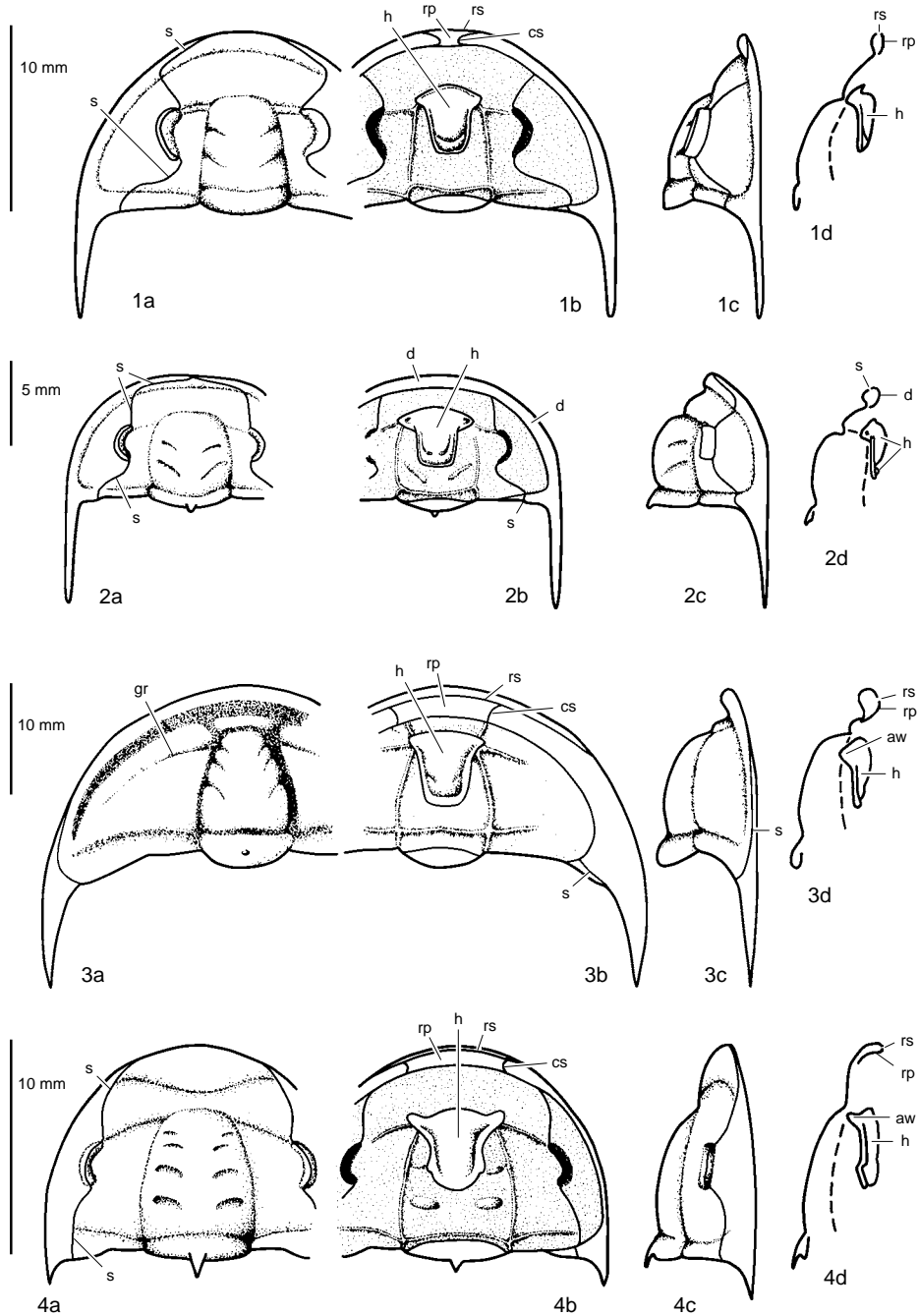
FIG. 28. Cephala with natant hypostome. *1, Aphelaspis* sp., Upper Cambrian (Whittington, 1988a, fig. 17). *2, Parabolinella* sp., Upper Cambrian (Whittington, 1988a, fig. 19). *3, Conocoryphe sulzeri* (SCHLOTHEIM), Middle Cambrian (Whittington, 1988a, fig. 12). *4, Agraulos ceticephalus* (BARRANDE), Middle Cambrian (Whittington, 1988a, fig. 14). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.
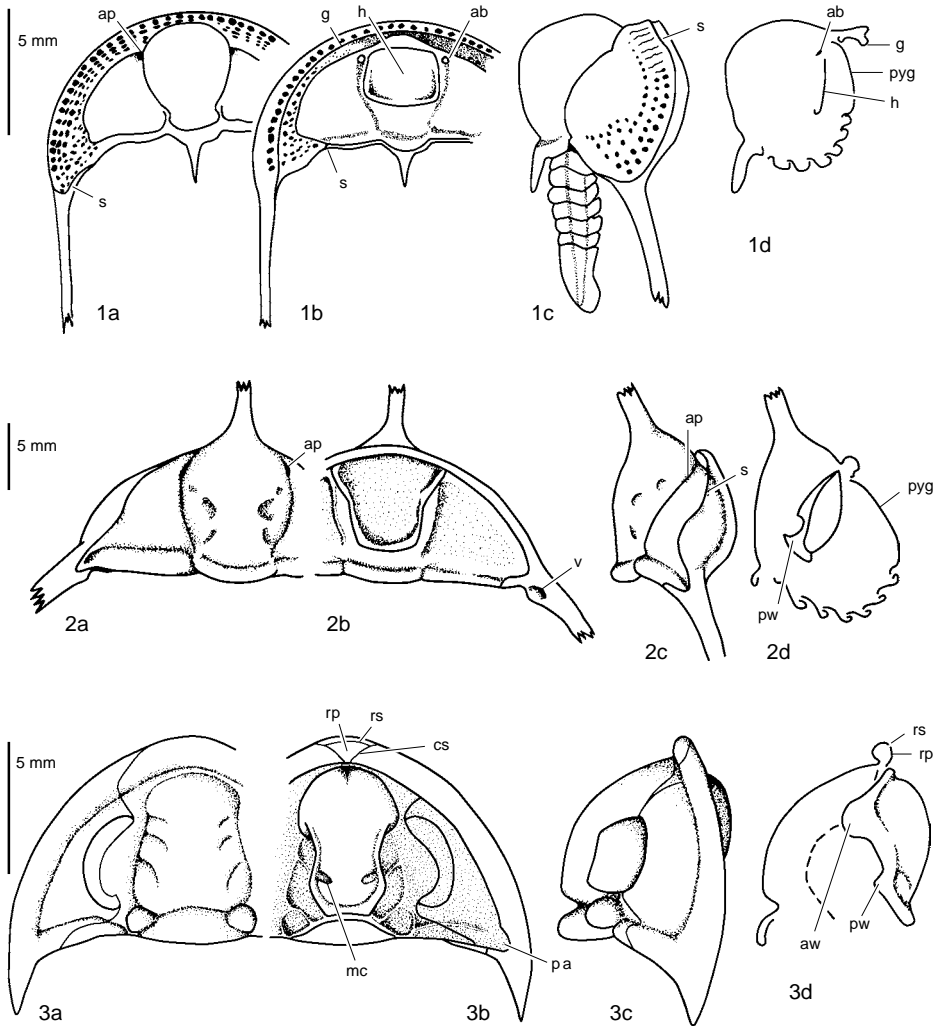
FIG. 29. Cephala of post-Cambrian trilobites with a natant hypostome. *1, Cryptolithus* sp., Ordovician (Whittington, 1988b, fig. 15). *2, Ampyx* sp., Ordovician (Whittington, 1988b, fig. 16). *3, Proetus (Proetus)* sp., Silurian (Whittington, 1988b, fig. 11). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral (including thorax and pygidium in part 1), and *d,* sagittal section of enrolled exoskeleton (of cephalon only in part 3) combined with a right lateral view of the hypostome. The position of the rostral suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

2, fig. 1) show that the anterior edge of the hypostome was rounded and slotted, not a thick, flat sutural edge. This suggested that the hypostome was natant.

FORTEY (1990a, fig. 11) drew attention to the similarity in morphology between examples of the natant hypostome. This generalization embraced what we know of hypostomes in Eodiscina (Fig. 27.2), but that of

Agnostus pisiformis (MÜLLER & WALOSSEK, 1987, p. 11, fig. 5) and other Agnostina (ROBISON, 1972b) is different. The hypostome in Agnostina is highly convex and lacks borders, the more heavily sclerotized portions surround and divide the middle body, and the anterior and posterior wings are elongate and dorsally directed. The middle body is divided into a pair of oval

areas, the hypostomal lobes (see Fig. 80), which were less heavily sclerotized; openings in silicified specimens described by Robison may represent similar areas. An outline of this type of hypostome is suggested for *Arthrorhachis* (Fig. 27.1), an example of a unique find among Agnostina of a species having a wide rostral plate and rostral suture. Müller and Walossek (1987, p. 44–46, fig. 26) discussed the similarities and differences between the hypostome of Agnostina and that of other trilobites and commented that the hypostome was a homologous structure in all trilobites.

In a wide range of trilobite groups the hypostome is attached to the inner margin of the cephalic doublure by the **hypostomal suture**. This is the **conterminant** condition. In *Holmia* (Fig. 30.1) the hypostome is wide (tr.) anteriorly, corresponding in width to the frontal portion of the glabella, and the anterior wing is large and triangular, its tip lying beneath the axial furrow immediately in front of the eye lobe. The hypostomal suture is narrow (tr.), the anterior wing curving up dorsal to the rostral plate. The form and relationship of the hypostome to the dorsal exoskeleton is similar in *Xystridura* (Fig. 30.3) to that in *Holmia*. In *Xystridura*, however, there is a facial and a rostral suture, the latter on the dorsal surface of the border, and the connective suture curves back to reach the inner margin of the doublure beneath the genal angle. In *Redlichia* (Fig. 30.2) the hypostome is narrower (tr.) anteriorly, corresponding to the form of the frontal lobe of the glabella, but a relatively large anterior wing is present. A furrow in the external surface of the rostral plate in *Redlichia* runs beneath the anterior border furrow, and pits in each of the furrows project inward and interlock (according to Öpik, 1958; cf. Fortey, 1990a, fig. 6).

Many post-Cambrian trilobite groups are characterized by having the hypostome attached to a doublure in which rostral and connective sutures define a rostral plate. Among Cambrian trilobites, *Welleraspis* (Fig. 31.1) is a probable example, but specimens of Cambrian trilobites showing such an arrangement, with the hypostome preserved in place, have not been figured. Among post-Cambrian trilobites, a number of such specimens are known, as well as undistorted silicified material that allows reconstruction in three dimensions. Examples are *Dysplanus* (Fig. 31.3), *Bathyurus* (Fig. 31.2), *Paladin* (Fig. 31.4), *Acanthopyge* (Fig. 32.1), and *Acidaspis* (Fig. 32.2), in all of which the anterior wing extends up so that the tip lies closely beneath the ridge formed on the parietal surface by the axial furrow; in *Dysplanus* and *Paladin* a wing process is developed. The large size of the anterior wing in *Bathyurus* means that, if the hypostome were attached, it must have been inclined steeply downward and backward. The angle of inclination of the hypostome was less in *Paladin*, while in *Acanthopyge* it was moderate but the hypostome was large in relation to the rest of the cephalon. In *Illaenus* (Fig. 33) and *Bumastus* the rostral plate was curved posteriorly through 180° to form an inwardly facing **rostral flange**, the hypostomal suture extending along the inner edge of the flange and the adjacent edges of the doublure. The backward and upward inclination of the hypostome has been recorded in *Illaenus* (Jaanusson, 1954), and in species of this genus and of *Bumastus* the anterior wing is large; in *Bumastus* the tip may have been situated close beneath the fossular apodeme.

While in most of the above-mentioned genera the tip of the wing process lies close to, against, or in a pit in the fossular apodeme, this device is particularly well developed in such genera as *Ceraurus* (Fig. 5), *Ceraurinella* (Fig. 26), *Deiphon* (Fig. 34.1), *Encrinuroides* (Fig. 34.3), and *Calymene* (Fig. 34.2). In addition to process and apodeme being in contact, the distal portion of the wing was wrapped around the apodeme to aid in keeping the process in position. The size of the wing and its process and the convexity of the cephalon lead to a downwardly sloping attitude of the hypostome, strongly so in *Deiphon* and other cheirurids. The presence of the rhynchos in some encrinurids and calymenids appears to be related to co-
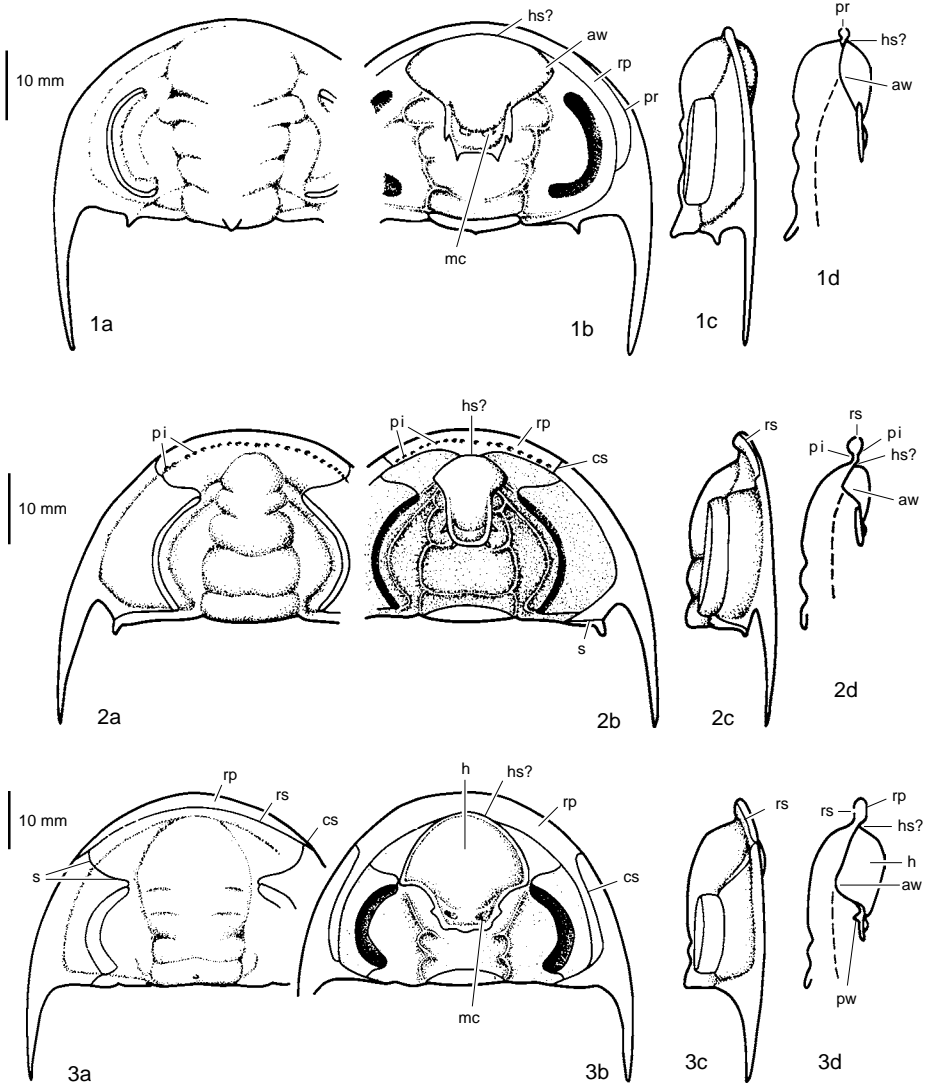
FIG. 30. Cephala in which the hypostome was probably conterminant. *1, Holmia kjerulfi* (LINNARSSON), Lower Cambrian (Whittington, 1988a, fig. 3). *2, Redlichia* sp., Lower to Middle Cambrian (Whittington, 1988a, fig. 6). *3, Xystridura* sp., Middle Cambrian (Whittington, 1988a, fig. 9). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral or perrostral suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

aptation—that is, to the fit of the pygidium below the cephalon when the hypostome is inclined downward.

The combination of an attached hypostome and a median suture crossing the doublure is known in species of the Upper Cambrian genera *Proceratopyge* and *Eurekia* (Fig. 35.1–2). In these species the hypostomal suture is narrow (tr.), and an anterior wing extends upward to the ridge formed on the ventral side of the axial furrow. The position of this ridge in *Eurekia* determines the angle of inclination of the hypostome. In Ordovician asaphids such as *Stegnopsis* (Fig.
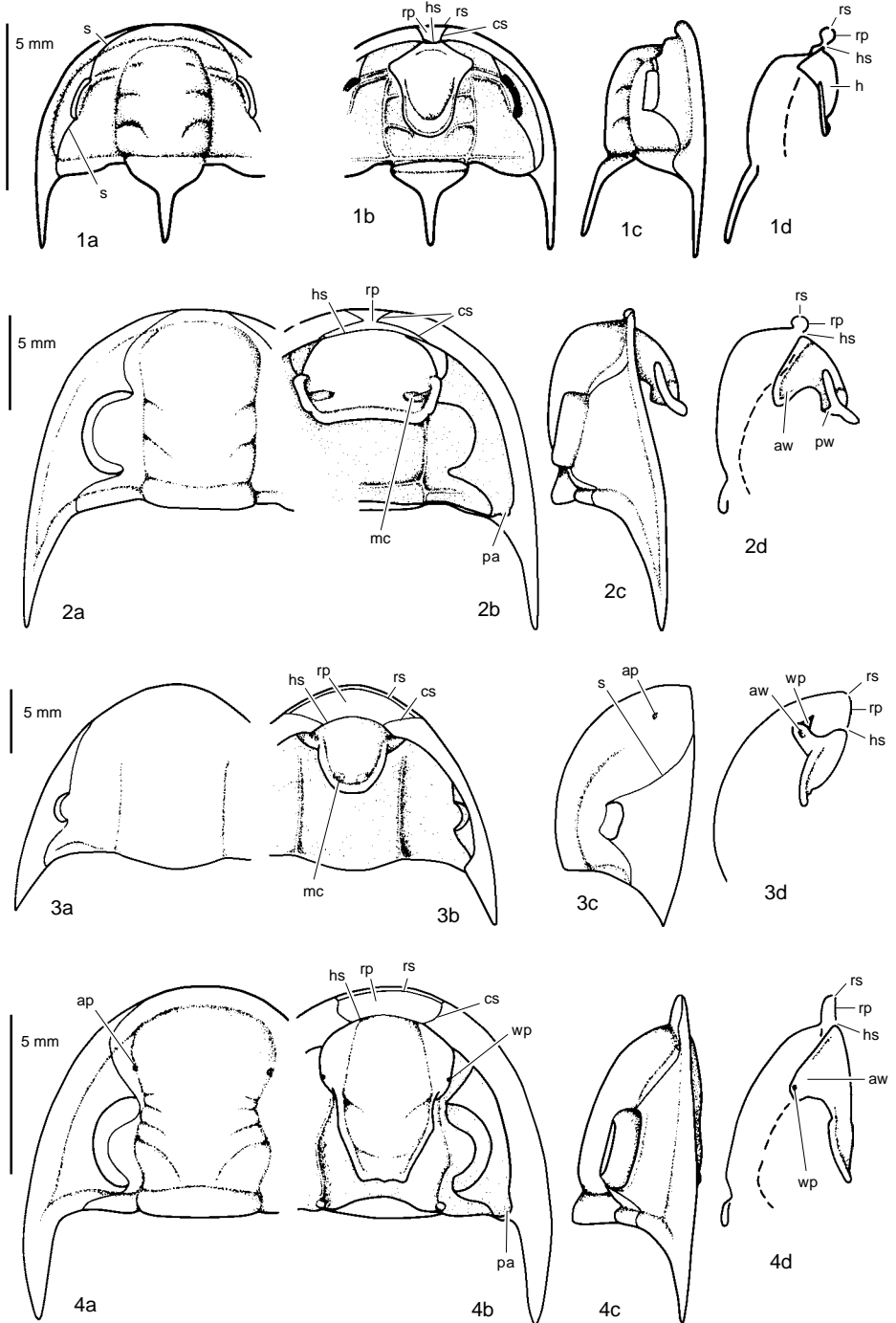
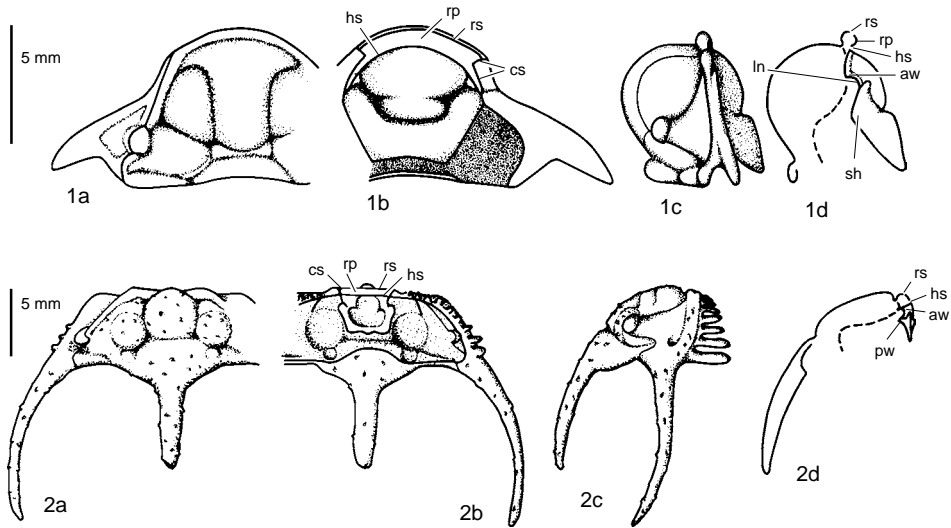FIG. 31. *For explanation, see facing page.*

FIG. 32. Cephala with a conterminant hypostome and rostral plate. *1, Acanthopyge* sp., Silurian to Devonian (Whittington, 1988b, fig. 25). *2, Acidaspis* sp., Ordovician to Devonian (Whittington, 1988b, fig. 26). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral and hypostomal suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 for list of abbreviations.

35.3) the arrangement is similar, but the hypostomal suture is wider (tr.) and runs in a curve along the upturned doublure, so that the close fit is not in a single plane. In *Remopleurides* (Fig. 35.4) the suture also has this curved course, and a long wing process extends to the pit in the fossular apodeme and to the tip of the process formed by the pit in the anterior doublure. Peculiar to remopleuridids is the oval area that occupies much of the middle body, over which the exoskeleton is thinner and is either smooth externally or bears raised lines.

FORTEY and CHATTERTON (1988) included in the Asaphida the Anomacaroidea, a super-family that includes *Auritama.* In one species

of this genus, ÖPIK (1967, fig. 75) described the marginal rostral suture, from each end of which a connective suture is directed inward, the two meeting to isolate a small triangular plate on the anterior edge of the doublure, the **rostellum**. From the posterior tip of this plate a median suture traverses the cephalic doublure. The rostellum is also known in a species of *Pterocephalia* (CHATTERTON & others, 1994, fig. 6.6).

In *Symphysurus* (FORTEY, 1986) and *Nileus* (Fig. 36.1) the hypostome is attached and braced by a long, upwardly directed anterior wing, but the cephalic doublure is not crossed by a median or connective sutures. This latter condition is thought to be

FIG. 31. Cephala with a conterminant hypostome and rostral plate. *1, Welleraspis swartzi* (TASCH), Upper Cambrian (Whittington, 1988a, fig. 18). *2, Bathyurus* sp., Middle Ordovician (Whittington, 1988b, fig. 10). *3, Dysplanus* sp., Ordovician (Whittington, 1988b, fig. 8). *4, Paladin* sp., Carboniferous to Permian (Whittington, 1988b, fig. 12). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral or hypostomal suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.
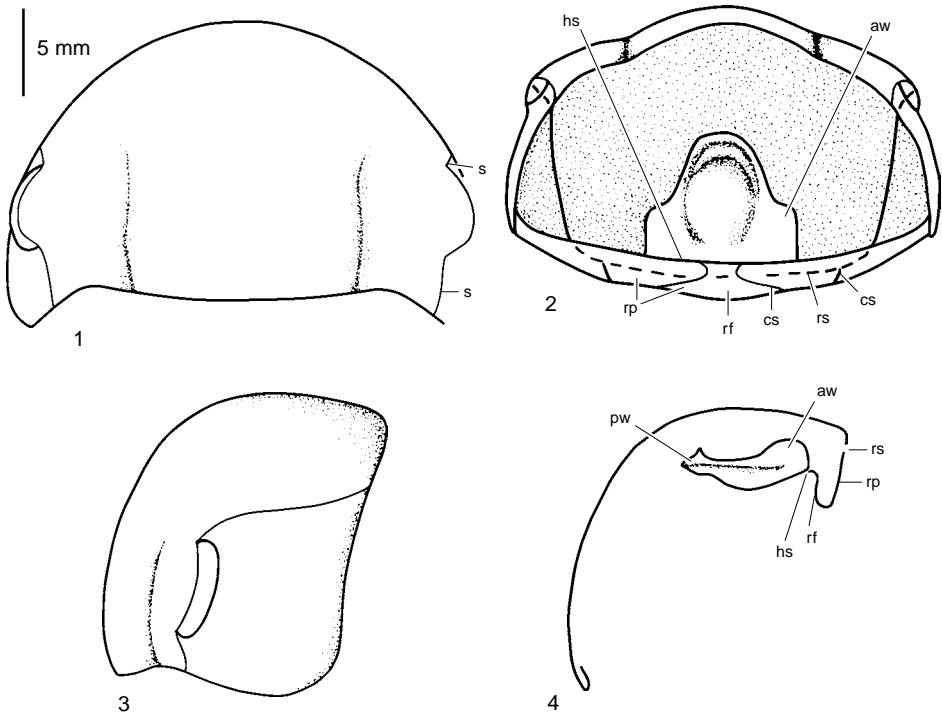
FIG. 33. Cephalon of Ordovician *Illaenus* sp.; the hypostome is conterminant and held at an unusual angle; *1,* partial dorsal view; *2,* posteroventral view, *dashed line* showing course of suture where hidden; *3,* right lateral view; *4,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome; position of rostral and hypostomal sutures shown by a gap in the section (Whittington, 1988b, fig. 7). See Figure 27 (p. 30) for list of abbreviations.

secondary in nileids, *Platypeltoides* (FORTEY & OWENS in OWENS & others, 1982) having a median suture. In *Phacops* (Fig. 36.2) the hypostome is attached and braced by a large anterior wing bearing a small wing process, and the cephalic doublure is entire. In early Phacopina (HENRY, 1980a) the condition of the doublure is similar, so the lack of median or connective sutures may be a cardinal character of this group. JAANUSSON (1975), however, described the Early Ordovician genus *Gyrometopus,* which is phacopid in appearance but has the cephalic doublure divided by a rostral plate. He pointed out that this species fulfills the requirements of an immediate ancestor of Phacopina but that the presence of a rostral plate might be considered to exclude it from that group.

A special case of the conterminant condition of the hypostome is fusion with the rostral plate, so far known only in Cambrian trilobites. In *Paradoxides* (Fig. 37.1) this condition is considered to be a diagnostic character of the genus, and it also obtains in *Oryctocephalus* (SHERGOLD, 1969, pl. 1, fig. 4, pl. 2, fig. 4) and many genera of corynexochoids. In *Fieldaspis* (Fig. 37.2), a corynexochoid, a long, steeply inclined anterior wing extends dorsally so that the tip lies beneath the axial furrow immediately in front of the eye ridge. In *Paradoxides* there is a similar arrangement, the wide (tr.), inflated, middle body lying beneath the expanded anterior portion of the glabella. Thus the **rostral-hypostomal plate** in these genera is rigidly braced against the rest of the cephalic exoskeleton.

The ventral cephalic sutures in the Lower Cambrian *Bathynotus* (Fig. 37.3) are unique, in that they diverge at about 100° from the
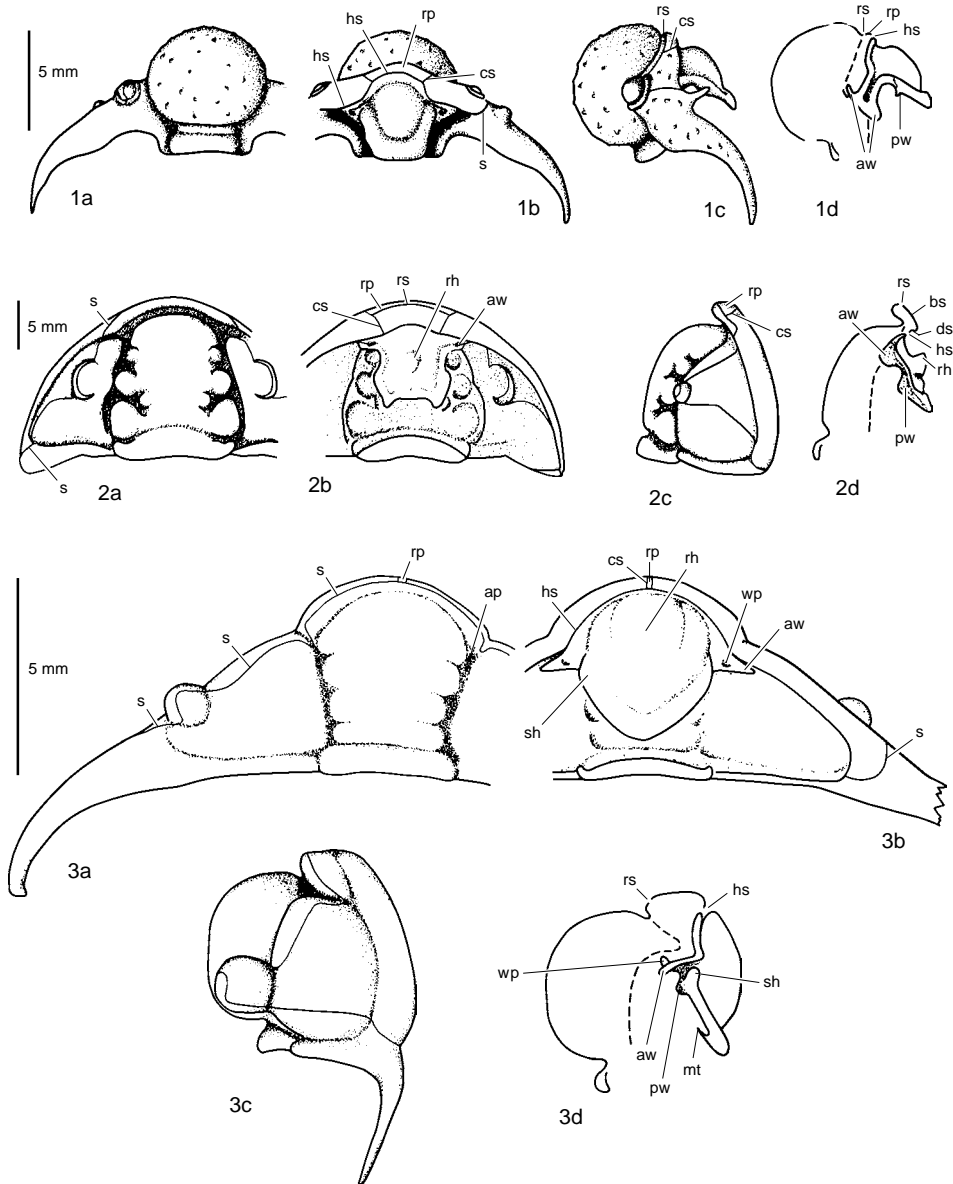
FIG. 34. Cephala with a conterminant hypostome and rostral plate. *1, Deiphon* sp., Silurian (Whittington, 1988b, fig. 19). *2, Calymene* sp., Silurian to Devonian (Whittington, 1988b, fig. 23). *3, Encrinuroides* sp., Ordovician to ?Silurian (Whittington, 1988b, fig. 20). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral and hypostomal suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

midpoint of the anterior edge of the doublure to isolate a hypostome that is pentagonal in outline. Whether these two sutures are sections of the hypostomal suture or whether they should be regarded as connective sutures is uncertain. If the latter, the supposed hypostome is composed of the true hypostome fused with a triangular rostral plate.
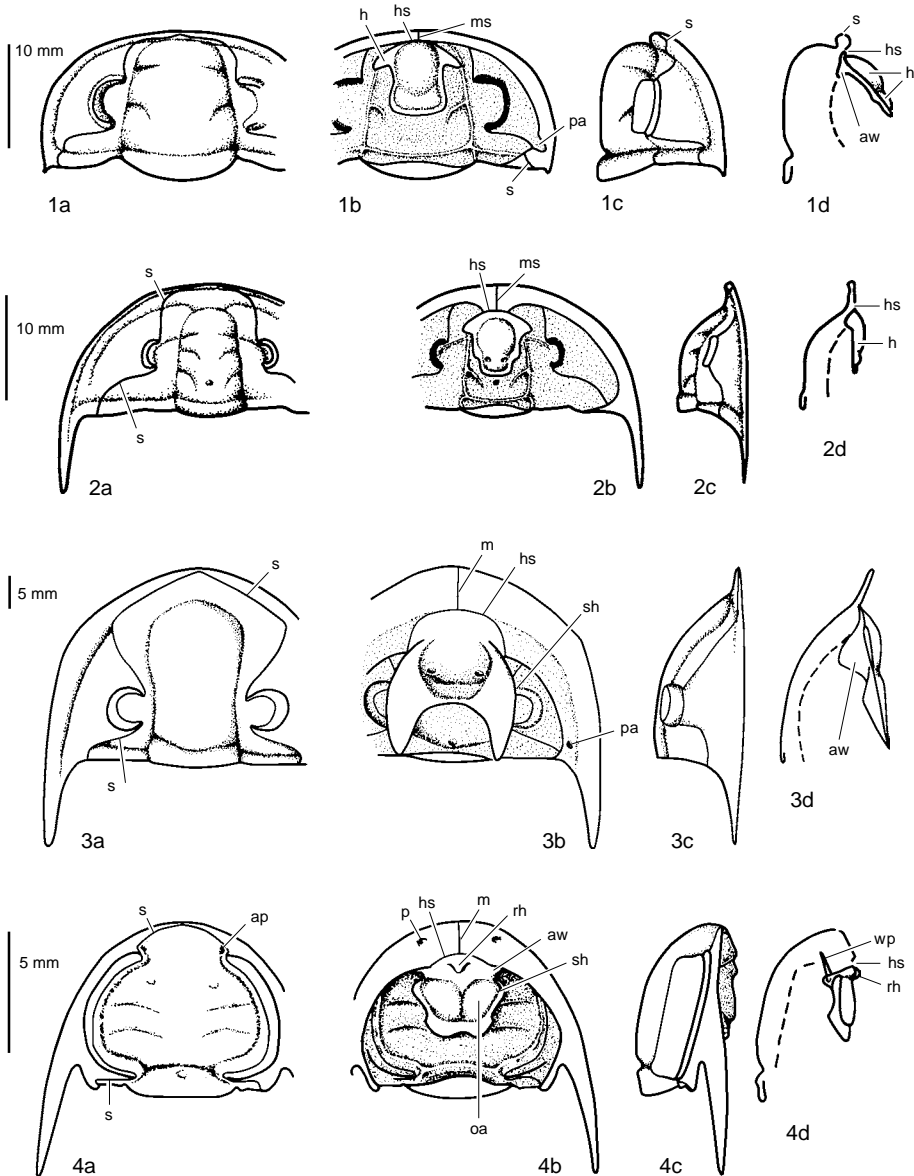
FIG. 35. Cephala with a conterminant hypostome, the doublure crossed by a median suture. *1, Eurekia ulrichi* (RASETTI), Upper Cambrian (Whittington, 1988a, fig. 20). *2, Proceratopyge* sp., Middle to Upper Cambrian, Tremadoc (Whittington, 1988a, fig. 16). *3, Stegnopsis* sp., Ordovician (Whittington, 1988b, fig. 3). *4, Remopleurides* sp., Ordovician (Whittington, 1988b, fig. 6). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of a suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

No other species is known with such a ventral structure or with a triangular rostral plate in which the apex of the triangle is directed forward.

FORTEY and CHATTERTON (1988, p. 178, fig. 5) proposed the term **impendent** for a condition seen, for example, in *Nileus* (Fig. 36.1), *Remopleurides* (Fig. 35.4), *Dysplanus*

Fig. 36. Cephala with a conterminant hypostome, but lacking a connective or a median suture. *1, Nileus* sp., Ordovician (Whittington, 1988b, fig. 5). *2, Phacops* sp., Devonian (Whittington, 1988b, fig. 21). Both *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of a 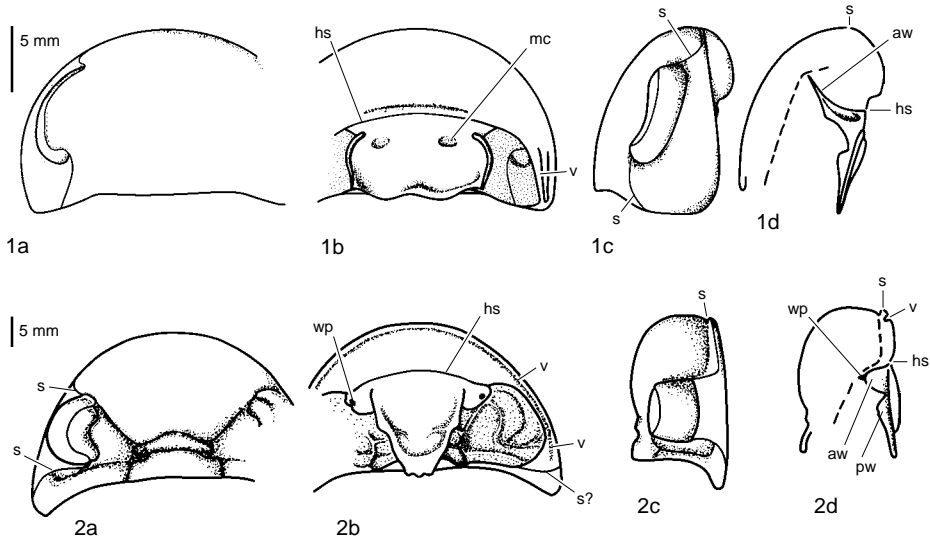suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

(Fig. 31.3), and *Phacops* (Fig. 36.2). Here the direct relationship between the hypostomal position and the glabella is supposedly lost. As may be seen, the connection between the fossular apodeme and anterior wing process is retained in these forms, as it is in other species with the conterminant hypostome. What is different is that the glabella and presumed preglabellar area or field are merged into a continuous slope, which becomes vertical, overhangs the anterior margin, or, in the case of *Phacops,* overhangs an extremely short (sag.) anterior border. The doublure is relatively broad (sag. and exs.) so that the anterior margin of the hypostome appears to lie farther posteriorly and is not approximately beneath the preglabellar furrow in *Phacops,* for example. The impendent condition appears to reflect an expansion of the anterior glabellar lobe (possibly related to an expansion of the anterior portion of the alimentary canal) at the expense of the anterior border, with the basic relationship of hypostomal wing and fossula being retained.

The foregoing account has shown that the position of the tip of the anterior wing of the hypostome, close beneath the fossula or equivalent position in the axial furrow, was homologous in all trilobites (cf. FORTEY, 1990a, p. 531). This arrangement appears to have been maintained, whatever the hypostomal attachment condition may have been.

MOVEMENT OF THE HYPOSTOME

The possibility of such movement has long been discussed (e.g., SCHEVILL, 1936; ELDREDGE, 1971; WHITTINGTON, 1988a, 1988b). In trilobites having a conterminant hypostome (and especially in those having a fused rostral-hypostomal plate), the hypostome was held rigidly in relation to the remainder of the cephalic exoskeleton. The anterior wing resting against the fossula or inner surface of the axial furrow braced the hypostome and determined its attitude, as the lateral views and sagittal sections of Figures 30 through 37 illustrate. The
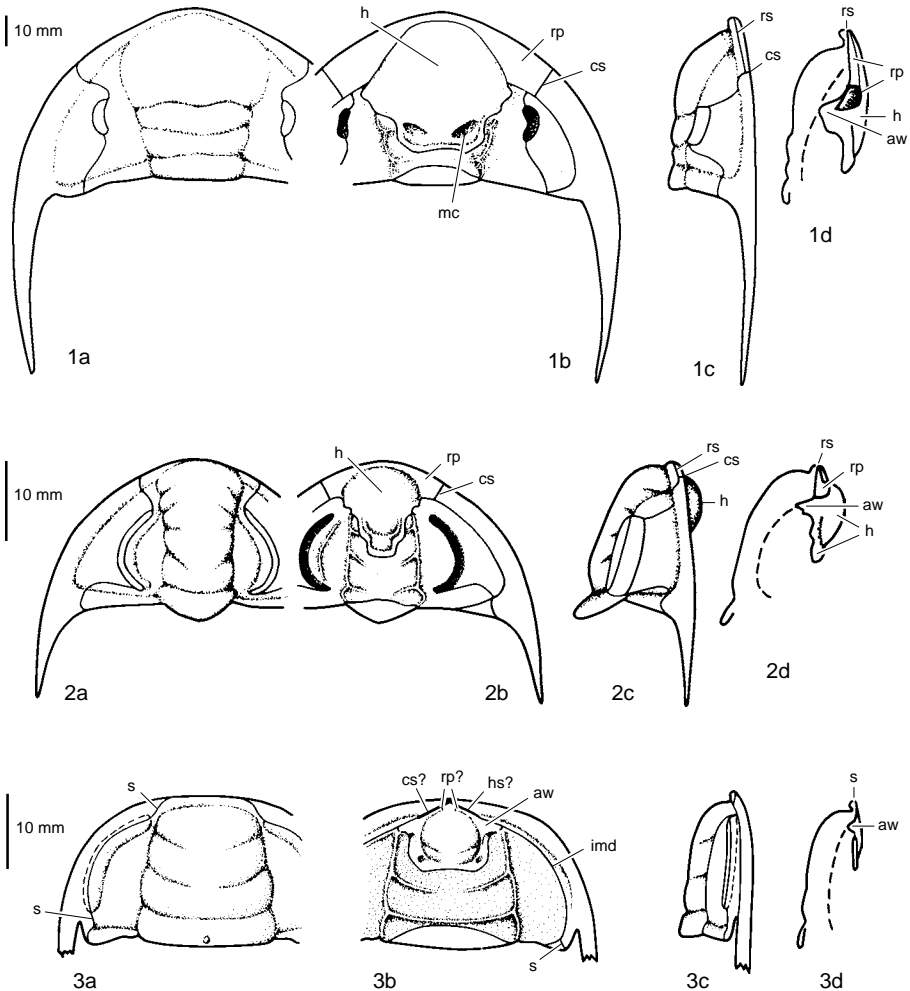
FIG. 37. Cephala in which rostral plate and hypostome are fused (possibly so in *Bathynotus*). *1, Paradoxides davidis* SALTER, Middle Cambrian (Whittington, 1988a, fig. 8). *2, Fieldaspis celer* (WALCOTT), Middle Cambrian (Whittington, 1988a, fig. 10). *3, Bathynotus holopygus* (HALL), Lower Cambrian (Whittington, 1988a, fig. 5). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral or facial suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 for list of abbreviations.

hypostome hence formed part of a capsule in the axial region of the exoskeleton, which enclosed the U-shaped anterior portion of the alimentary canal. In trilobites that had a natant hypostome (Fig. 27–29), the relationship was less rigid. Any movement of the natant hypostome would have depended upon musculature, the flexibility of the ventral integument into which it was inserted,

and the nature of the link between anterior wing and fossular apodeme.

THORAX

The thoracic region of the trilobite body consists of a number of similar somites that articulate with one another and with the fused somites of the cephalic and pygidial

regions. The thorax (Fig. 2) is the exoskeleton of this region, including the doublure, and the exoskeleton of each somite is referred to as a segment. Each segment consists of the **axial ring**, the exoskeleton of the axis, and the **pleura**, that of the pleural region. The number of segments in the thorax may be 2 (Agnostina) or 3 (Eodiscina), whereas in most other trilobites the number is between approximately 6 and 15. This generalization led JAEKEL (1909) to propose the terms Miomera for trilobites with 2 or 3 thoracic segments and Polymera for trilobites with 6 or more such segments. Thus Miomera could be used as an inclusive term for Agnostida and Polymera for all other trilobites. However, it is known that these other trilobites include species that had 2, 3, or 4 thoracic segments (e.g., ROBISON & CAMPBELL, 1974; W. ZHANG, 1980; FORTEY & RUSHTON, 1980); and Miomera is a junior synonym of Agnostida (MOORE, 1959, p. 172). Hence these terms cannot be used for formal taxonomic categories, but only informally as adjectives (**miomerid** and **polymerid**) to describe trilobites with few or many segments (cf. ROBISON & CAMPBELL, 1974, p. 281). In some groups of trilobites other than Agnostina and eodiscoids, a specific number of thoracic segments may be present in most if not all species, such as 6 in trinucleids, 8 in asaphids, or 13 in calymenids. In other groups the number may vary to a greater extent between species of closely related genera or species of one genus as, for example, in the 17 to 32 segments in the thorax of species attributed to *Alokistocare* (ROBISON, 1971).

The maximum number of segments known in any species appears to be 61, in an emuellid (POCOCK, 1970). The specimen on which the oft-quoted figure of 40 is based is the original of WALCOTT (1916a, pl. 26, fig. 4b,c) of *Menomonia calymenoides.* In this specimen the convex thorax of many segments narrows backward gradually, and more than 40 axial rings may be counted. Preservation is poor; it is uncertain whether the thorax is complete anteriorly, and the boundary between thorax and pygidium cannot be ascertained. This difficulty of determining, in a series of similar segments diminishing progressively backward in width (tr.) and length, where thorax ends and pygidium begins applies also to specimens of hapalopleurids (HARRINGTON & LEANZA, 1957, p. 203–205). In *Seleneceme,* a similar problem has been solved by examining new material (KENNEDY, 1989). BURLING (1916) claimed that the specimen of *Olenellus robsonensis* exhibited 44 thoracic segments, but a re-examination (WHITTINGTON, 1989) suggests that the number does not exceed 40. The pygidium is not preserved, so that the original total number of segments in the thorax is unknown. Specimens of the emuellids described by POCOCK (1970) show much of the pleural region posteriorly and the minute pygidium, so that the basis for a maximum number of 61 thoracic segments appears to be sound.

The axial ring of the thorax is separated from the pleura by the axial furrow (Fig. 2). The depth of this furrow and the transverse convexity of the axial ring vary; the transverse profile of the axial ring may be evenly curved and subtend an arc of up to 180° or may be flattened medially. The ring may be flat or convex in longitudinal (sag. and exs.) profile, the slope being steepest posteriorly; it slopes anteriorly into the transverse **articulating furrow** (Fig. 38–39) and has an anterior extension, the **articulating half ring**, the anterior edge of which curves in an arc so that the half ring is longest sagittally. This half ring projects forward beneath the similarly shaped doublure of the next ring in front (Fig. 38.2, 39) or of the occipital ring of the cephalon (Fig. 26). It acted as a guide during flexure of the thorax and covered the gap that opened between adjacent axial rings during flexure. It was absent only from the first thoracic segment of almost all species of Agnostina. In silicified examples of remopleuridids (CHATTERTON & CAMPBELL, 1993, p. 121), a small, transverse plate along the anteromedian margin of the articulating half ring is isolated by a suture. The lateral
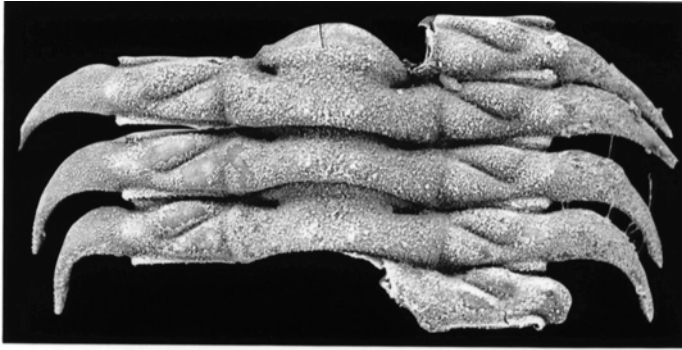
Fig. 38. *Ceraurus whittingtoni* Evitt, Middle Ordovician, Virginia, USA. *1,* Dorsal view of portions of 5 thoracic segments, ×4.5 (new). *2,* Ventral view of portions of 5 segments and the pygidium, ×4.5 (Whittington, 1960b, fig. 1g).

extremity of the articulating furrow may deepen into an **apodemal pit**, which varies in depth and projects into the body as an **apodeme**. Such apodemes form a graded morphological series with those of the cephalon (Fig. 26.1) and pygidium (Fig. 38.2, 39.2) (Ludvigsen & Chatterton, 1982, pl. 6; Chatterton & Perry, 1983, pl. 1, 13). In some species the axial ring is divided (Fig. 40.2) by an intra-annular furrow into the smaller **preannulus** and a larger **postannulus.** The axial ring may bear a tubercle or **axial spine,** which may be median and borne by some or all the segments of the thorax in a size series or by only one segment. The long

axial spine on the 15th segment of *Olenellus* (see Fig. 45) is well known, but equally conspicuous are the spines on the 13th segment of the Ordovician *Balnibarbi* (Fortey, 1974b, fig. 4), on the 10th segment of the Silurian *Encrinurus* (Ramsköld, 1986, pl. 39, fig. 1), and on the 6th segment of the Devonian *Otarion* (Morzadec, 1983, pl. 3, fig. 3). Axial spines or tubercles may be paired close to the midline, and additional pairs may occur. In some trilobites the lateral extremity of the axial ring may be inflated and rounded distally, in some sufficiently so as to form a **lateral axial lobe** that may be separated from the rest of the ring by a shal-
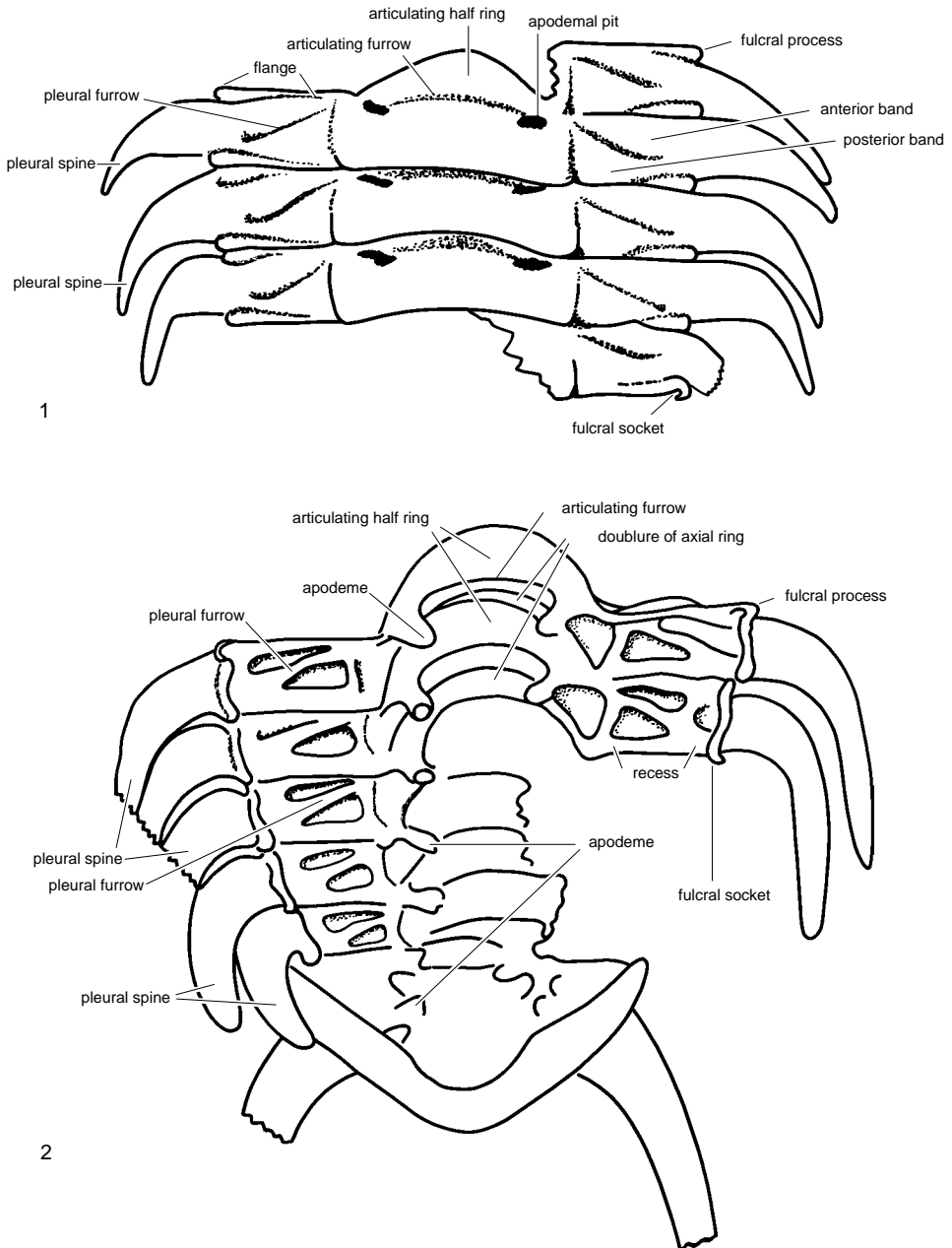
FIG. 39. Diagrammatic representation of Figure 38 to show terminology of thoracic features (new).

low furrow. A serial homology between axial rings is shown in many trilobites by their duplication of the form of the axial spine or tubercle and lateral lobes of the occipital ring. On the other hand, RAMSKÖLD (1985, p. 36) has noted that in some species of *Dalmanites* the lateral axial lobe is more prominent on particular segments.

The pleura of the segment extends outward from the axial furrow, and in most
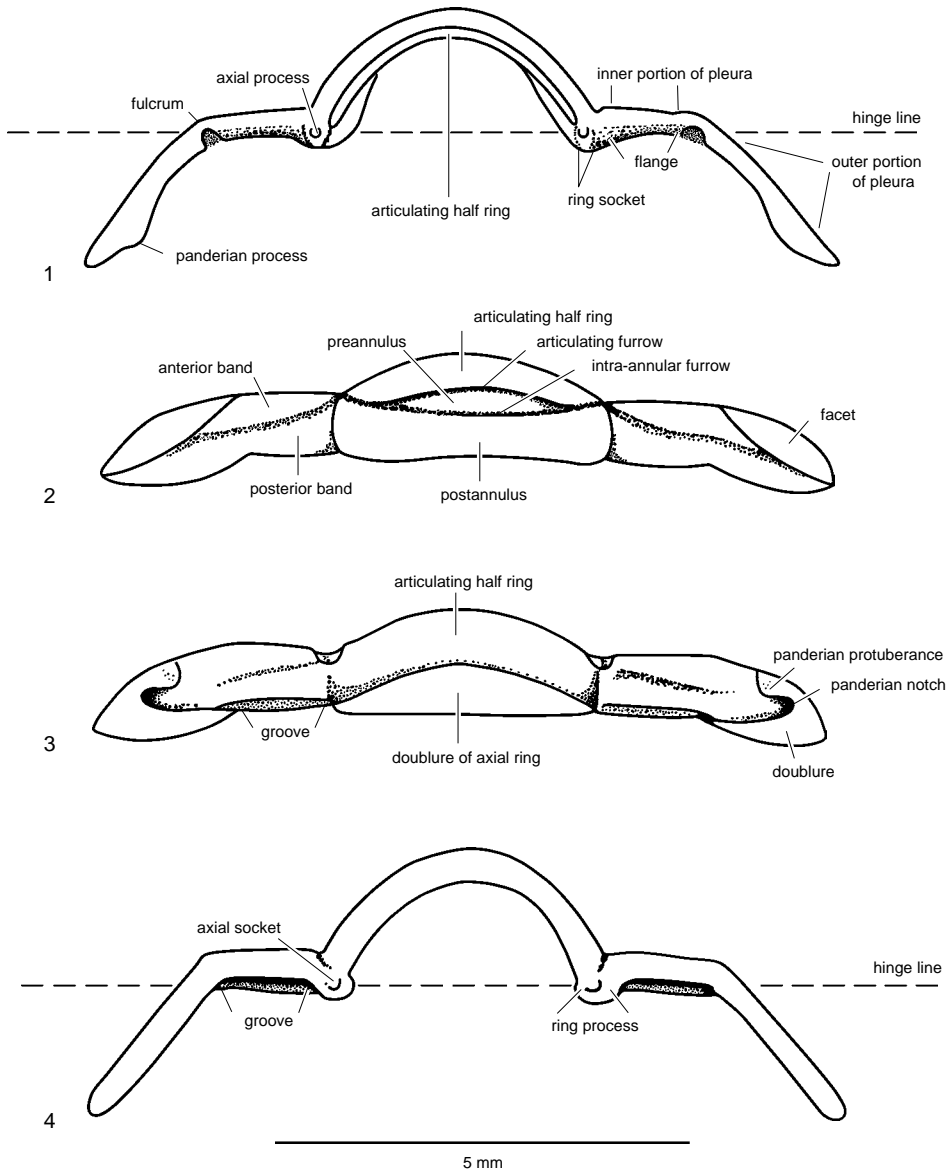
FIG. 40. Thoracic segment of *Proetus pluteus* WHITTINGTON & CAMPBELL. *1–4,* Anterior, dorsal, ventral, and posterior views, respectively, showing terminology and mode of articulation (adapted from Whittington & Campbell, 1967, pl. 2, fig. 14, 25, 31–32).

trilobites (as seen in anterior or posterior views, Fig. 40.1,4) is divided at the **fulcrum** into an **inner portion** that is horizontal and an **outer portion** that slopes downward outside the fulcrum. The same division obtains in *Ceraurus* (Fig. 38–39) at the fulcral process and socket between the inner, horizon-

tal portion and the downwardly directed pleural spine. In contrast, in *Olenoides* the inner portion of the pleura is not horizontal (Fig. 41.5); but, after ascending from the axial furrow, it curves to slope gently downward and outward and there is no fulcrum. In *Olenellus* the pleura was similarly curved

FIG. 41. Restoration of left halves of two midthoracic segments of *Olenoides serratus* (ROMINGER). *1,2,* Dorsal and left lateral views of extended position; *3,4,* dorsal and left lateral views of flexed position; *5,* posterior view. *Dashed line* and *x* indicate position of hinge line; *coarse stipple* indicates portions of flange and articulating half ring exposed by flexure; *dotted line* on left side of anterior segment in part 1 indicates position of inner margin of doublure (Whittington, 1980a, fig. 3).

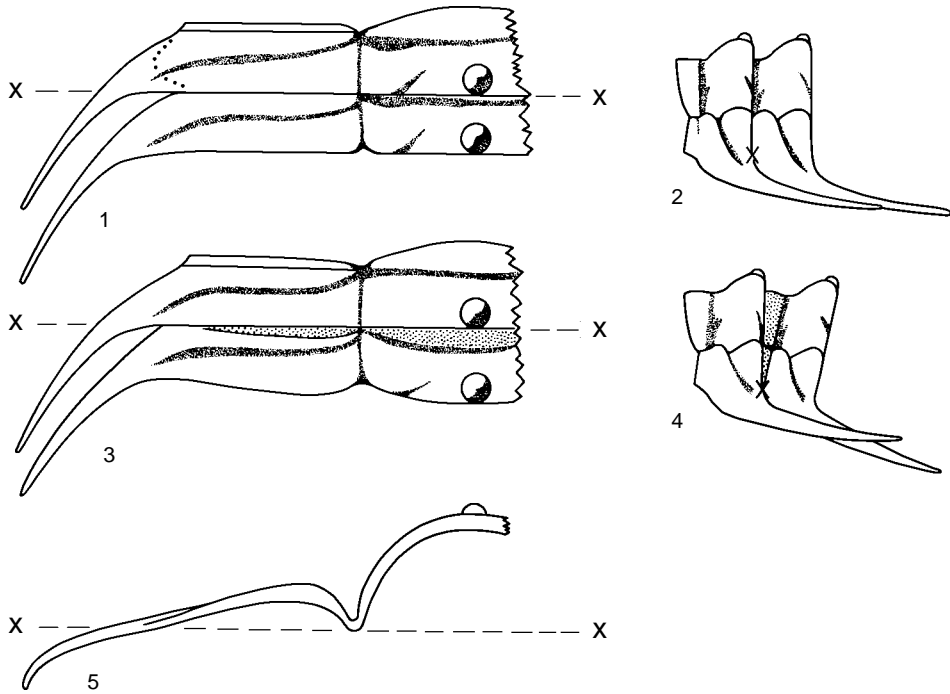and lacked the fulcrum (see Fig. 45.4). In *Remopleurides* (CHATTERTON & LUDVIGSEN, 1976, pl. 1) the fulcrum is adjacent to the axial furrow so that most of the pleura represents the outer portion; in *Cybantyx* the horizontal inner portion of the pleura is absent and the pleura continues the slope of the axial ring (see Fig. 47).

A **pleural furrow** (Fig. 39) commences at the axial furrow, opposite the outer end of the articulating furrow, and is directed outward and slightly backward across the pleura, dividing it into **anterior** and **posterior bands**. The depth and slope of the sides of this furrow vary, and the pleura may be almost flat or inflated to differing degrees. Thus the pleural furrow may be flanked by slightly inflated areas (or by ridges as in odontopleurids) or may be broad and shallow and occupy much of the dorsal area of the pleura. The pleural furrow may be absent

or may be replaced by a row of pits, as in certain cheirurids (LANE, 1971, p. 44; C. P. HUGHES, 1969, pl. 8, fig. 4–5). In trilobites in which the outer portions of the pleurae overlap during enrollment (Fig. 2, 40), the anterolateral surface of this outer part is bevelled to form an articulating **facet**. The surface of this facet is gently concave (a section of a cone), to enable it to glide closely beneath the doublure in front of it. The pleural furrow may continue for a short distance on the outer portion and die out, or it may continue behind the facet (**postfacetal** condition), as in asaphids such as *Isotelus* and in the proetid *Proetus* (Fig. 40.2). In phacopids and calymenids (HAMMANN, 1983, pl. 2; CHATTERTON & CAMPBELL, 1993, fig. 1d, 1h, 2f), for example, the pleural furrow crosses the posterior margin of the facet and continues on the facet—the **epifacetal** condition. The doublure extends

inward beneath the outer portion of the pleura to a varying distance; for example, in *Proetus* it extends a short distance inside the posterior and distal margins (Fig. 40), but in *Ceraurus,* in which the outer portion is a pleural spine, it extends to the fulcrum (Fig. 39). In trilobites in which the pleurae are facetted and slide closely one over another in enrollment, the doublure may carry a device to limit the amount of overlap. This device may be in the form of a notch in the narrow doublure, the **panderian notch,** the anterior side of which is raised to form a stop, the **panderian protuberance,** as in *Proetus* (Fig. 40.3) and in the Early Cambrian *Crassifimbra* (PALMER, 1958, fig. 5) or the Ordovician *Dimeropyge*. In trilobites with a wider (tr.) doublure, the stop may take the form of a sharp, raised fold directed outward and backward, as in *Symphysurus* or *Nileus.* In asaphids there may be a similar fold or a notch with a raised margin, the panderian protuberance, so called because of the small elliptical or circular opening, the **panderian opening**, immediately anterior to it. These structures have been studied by SIEGFRIED (1936) and HUPÉ (1955b) and illustrated in work on silicified (CHATTERTON & LUDVIGSEN, 1976) and other specimens (BALASHOVA, 1976; HAMMANN, 1983, p. 38, pl. 22; CHATTERTON & CAMPBELL, 1993).

The distal tip of the outer portion of the pleura may be rounded as in *Isotelus* (Fig. 2) or bluntly pointed as in *Proetus* (Fig. 41); the doublure of the outer portion of the pleura is either a narrow band around the tip and along the posterior edge or is more extensive. In forms in which the entire outer portion of the pleura forms a spine as in *Ceraurus* (Fig. 39), *Olenellus,* or *Remopleurides,* the doublure extends beneath the hollow spine to the fulcrum (or its equivalent). In encrinurids and odontopleurids (Fig. 42–43), each band of the pleura is extended into a spine, the major spine being on the longer (exs.) posterior band. The minor spine on the anterior band may be forwardly or upwardly directed or, in *Dicranurus,* vertically downward. It is apparently rare for the major spine

to arise from the anterior pleural band as it does in *Dorypyge* (WESTERGÅRD, 1948, pl. 2, fig. 4; W. ZHANG & JELL, 1987, pl. 12, fig. 5).

The pleural or major pleural spines may form a graded size series, progressively more strongly backwardly directed posteriorly. Odontopleurids illustrate this well; for example, in *Miraspis mira mira* (BRUTON, 1968b, pl. 7, fig. 3), *Ceratocephala vesiculosa* (BRUTON, 1968b, pl. 8, fig. 5–6), and *Dicranurus monstrosus* (Fig. 42) the series of major pleural spines is graded in direction and length. In such trilobites as *Dicranurus hamatus elegantus* (Fig. 43), the series of major spines is not evenly graded in length, there being long major spines on segments 4, 6, and 7 but a much reduced major spine on the fifth segment. Different lengths of major spines are also shown by species of *Leonaspis,* for example, in *L. tuberculatus* (WHITTINGTON, 1956b, pl. 57, fig. 8) the series is graded but is longest anteriorly, in *L. jaanussoni* (CHATTERTON & PERRY, 1983, fig. 19) it is graded but longest posteriorly, and in *L. brittanica* (MORZADEC, 1983, pl. 32, fig. 1) the major spines on pleurae 5, 6, and 7 are much longer than others. A single, conspicuously longer spine is termed **macropleural**. In odontopleurids and *Cybeloides* (INGHAM, 1968) it is the spine, the outer portion of the pleura, that is long and stout. The inner portion of the pleura is not enlarged relative to the adjacent segments. This contrasts with the condition in *Olenellus* (see Fig. 45.1), in which the inner portion of the pleura becomes longer (exs.) abaxially. *Emuella* (POCOCK, 1970) and the olenellid *Biceratops* (Fig. 44) provide additional examples of such macropleurae, showing how the shape of the inner portions of adjacent segments are modified to accommodate the macropleura and also illustrating the great length and thickness of the outer spine compared to those of other segments. Examples of macropleurae in which the inner portion of the pleura is enlarged are rare in post-Early Cambrian trilobites, but one is the anterior thoracic segment in the raphiophorid
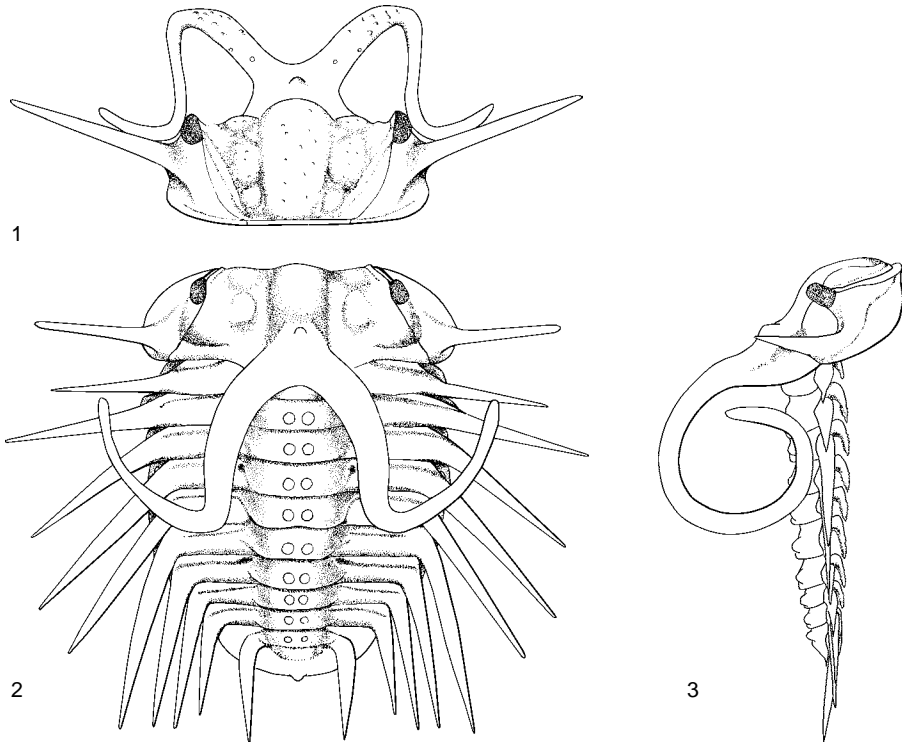
Fig. 42. *Dicranurus monstrosus* (Barrande), Devonian, Bohemia. *1,* Anterior view of cephalon; *2,* dorsal view of exoskeleton; *3,* right lateral view of exoskeleton, ×1 (Whittington, 1956d, fig. 18).

Cnemidopyge (C. P. Hughes, 1969). It may be noted that the enlargement of the inner portion of the pleura in the macropleura takes place from the axial furrow outward, the axial ring being one of a graded series and not enlarged (e.g., *Olenellus* or *Biceratops*). In trilobites that lack a macropleura, thoracic segments may form a graded series, diminishing posteriorly, in length (sag.) of the axial ring and length (exs.) of the inner portion of the pleura. This is not invariably so, as was shown by Ramsköld (1991b, fig. 8) in odontopleurids. His measurements of the original of Figure 43, for example, show an increase in the lengths of segments 1 to 6 (segment 5 is slightly shorter than 4 and 6) and a decrease in the lengths of 6 to 9. Such a size gradation is characteristic of one subfamily, the Selenopeltinae.

Olenellus (Fig. 45) illustrates another type of change that may take place in the series of pleurae. The long, spinose pleura of the 14th segment is directed exsagittally backward, so that the pleurae of the 15th and succeeding segments must necessarily be narrow (tr.) and the pleural spine short, to fit between the 14th pleural spines. A similar abrupt change in size of the pleurae takes place in the same position in the thorax in other species of *Olenellus,* in which the pleural spines of the 14th segment are less strongly backwardly directed. In other Olenellina a change in form of the pleurae may occur much less abruptly or not at all (Whittington, 1989). This change in the form of the thorax in Olenellina was discussed by Walcott (1910, p. 244–245), Hupé (1953a, p. 117–118, footnote; p. 122–123), and Pocock (1970, p. 551–552), Hupé having introduced the terms **prothorax** and post-thorax (=**opisthothorax**) for the two portions. Hupé considered that the first segment of the

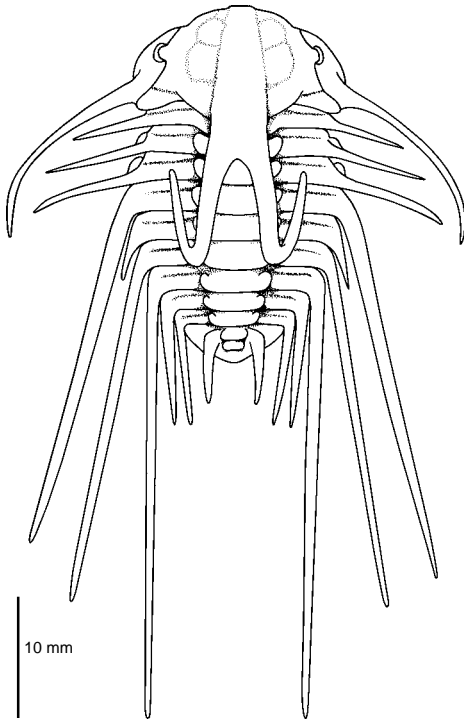FIG. 43. Dorsal view of exoskeleton of *Dicranurus hamatus elegantus* CAMPBELL, Devonian, Oklahoma (adapted from Campbell, 1977, 1982).

opisthothorax of *Olenellus,* bearing the long median spine, was the 15th and that in this portion of the thorax the pleurae were reduced or absent. The opisthothorax in Olenellina is not well known (WHITTING-TON, 1989), but pleurae, though reduced in size, are present. A subdivision of the thorax is also well displayed by emuellids (POCOCK, 1970), the prothorax having 6 segments, the last two of which are fused, and the 6th being macropleural. The opisthothorax has from 42 to 55 segments and, as in Olenellina, has the axial rings diminishing posteriorly in a graded continuum with those of the prothorax. The pleura of the anterior opisthothoracic segment is much reduced compared to the macropleura, behind this first segment the opisthopleurae show a continuum in reduction posteriorly. Thus some Lower Cambrian trilobites show an abrupt change in the form of the entire pleura rather than the characteristic graded series of changes.

Articulation of the segments with one another and with the cephalon and pygidium is characteristic of trilobites, enabling flexure of the thorax in the vertical plane and partial or complete enrollment. Segments differ in form and convexity and in the way in which the form is modified along the thorax of a particular species to facilitate articulation, enrollment, and the close fit of coaptational devices. A thoracic segment of *Proetus* (Fig. 40) from the midportion of the thorax illustrates the mode of articulation, termed **fulcrate** (ÖPIK, 1970b, p. 4), that is most widespread in trilobites. The hinge line between segments runs through the ring and axial processes and sockets in the axial furrow and along the horizontal edge of the inner portion of the pleura to the fulcrum. The rounded, anterior edge of this inner portion forms a flange, which fits into a groove below the posterior edge of the inner portion of the pleura next in front. The articulating half ring fits below the doublure of the axial ring of this next segment; corresponding structures are present on the posterior margin of the cephalon and the anterior margin of the pygidium. On enrollment, the outer portion of each pleura slides below the one in front; the facet enables this, and the raised anterior edge (panderian protuberance) of the (panderian) notch in the doublure limits the amount of overlap. The articulation devices in hystricurids (WHITTINGTON & EVITT, 1954, fig. 10) and otarionids (WHITTINGTON & CAMPBELL, 1967) are like those of proetids, and similar structures are present in the Lower Cambrian *Crassifimbra* (PALMER, 1958) and probably in most Middle (e.g., ROBISON, 1964, pl. 87, fig. 16, pl. 89, fig. 8–9) and Upper Cambrian trilobites (e.g., STITT, 1976, 1983; LUDVIGSEN, 1982, fig. 49). Many post-Cambrian trilobites, such as calymenids (CAMPBELL, 1967; HAMMANN, 1983), phacopids (MILLER, 1976), and dalmanitids (CAMPBELL, 1977; HOLLOWAY, 1981; MORZADEC, 1983), have essentially

similar segments, but a **fulcral process** and **socket** (Fig. 39) may be developed at the abaxial end of the flange as an additional aid in articulation.

A different type of articulation was first recognized by Öpik (1970b, p. 3–4) in *Redlichia* and is referred to as **nonfulcrate**. It is known also in other Cambrian trilobites such as *Olenoides* (Fig. 41), *Olenellus* (Fig. 45) and other Olenellina, and *Paradoxides* (Whittington, 1990). In these trilobites the pleura curves downward and outward and lacks the inner horizontal portion and fulcrum. The details of the structure need further investigation, but in species of *Paradoxides* (Fig. 46) there is an axial articulating process and socket, and a concave flange on the anterior margin of the pleura fits beneath a narrow strip of doublure along the posterior margin of the sclerite in front. A projection at the distal corner of the flange acted as a guide in articulation (the pleural guide of Öpik, 1970b, or the marginal connective device of Bergström, 1973a, p. 13). These devices are similar to those in *Olenellus* (Fig. 45), *Olenoides* (Fig. 41), and *Redlichia* (Öpik, 1970b) and appear to have allowed flexure of the body without the precision of the straight, horizontal hinge-line of the fulcrate form. In his study of xystridurids, Öpik (1975a, p. 23) pointed out that, while species of *Xystridura* had the nonfulcrate type of exoskeleton, that of *Galahetes* was fulcrate. Similarly in corynexochoids, *Olenoides* is nonfulcrate but *Ogygopsis* is fulcrate, and some redlichioids (for example, species of dolerolenids, Jell in Bengtson & others, 1990, p. 272, 292) were fulcrate.

In the trinucleids, raphiophorids, and harpetids (Whittington, 1959a; Campbell, 1975; Chatterton & Ludvigsen, 1976), most of the width (tr.) of the pleura is the horizontal inner portion, the outer portion being narrow (tr.) and sloping. Articulation along the wide (tr.), straight hinge line is by a flange and grooved recess that extends from the axial process or socket to the fulcrum. The outer portion of the pleura has a narrow
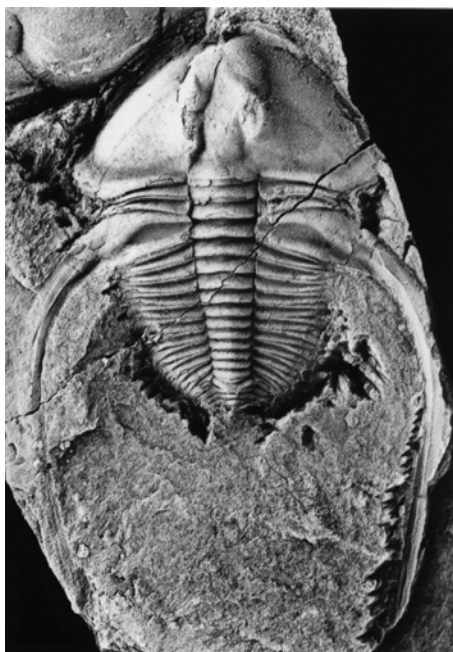

FIG. 44. *Biceratops nevadensis* Pack & Gale, Lower Cambrian, Nevada; dorsal view of paratype, ×3 (Whittington, 1989, fig. 11).

doublure and panderian notch in *Cryptolithus* and *Dolichoharpes,* a process projecting forward from the anterolateral tip fitted into a recess in the doublure of the segment in front, serving to limit enrollment (Chatterton & Campbell, 1993, fig 8h).

Characteristic of asaphids (Siegfried, 1936; Jaanusson, 1953a, 1953b; Balashova, 1976; Chatterton & Ludvigsen, 1976; Chatterton & Campbell, 1993, fig. 8d) is the relatively wide (tr.), steeply sloping outer portion of the pleura that is broadly facetted and has the doublure extending far inward, cut off along an exsagittal line anteriorly, posteriorly extending up to the fulcrum. This outer portion of the pleura is thus shaped like a pocket and has a panderian opening or notch and protuberance; these flattened outer portions overlap on enrollment. The horizontal inner portion of the pleura (present in most genera) articulates by an anterior flange and posterior recess, and there are axial and ring processes and sockets.
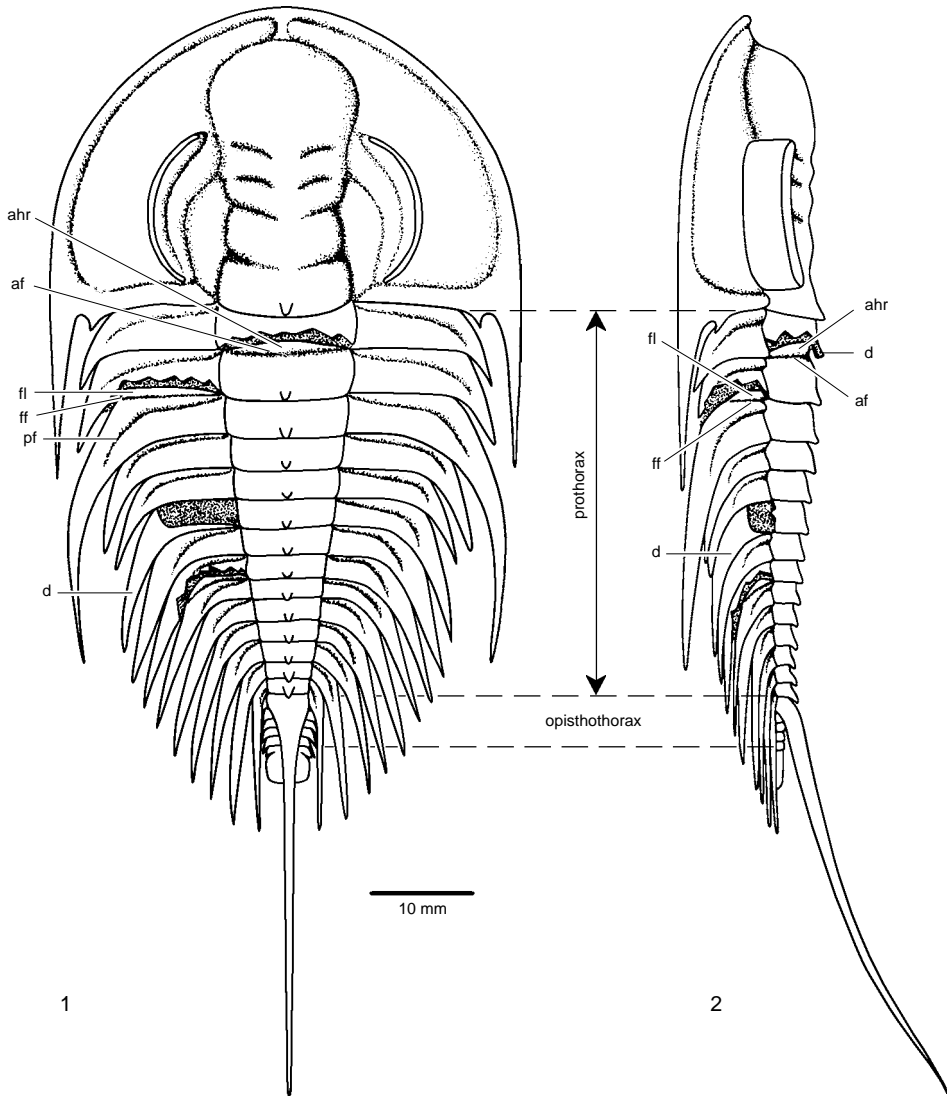
FIG. 45. Restoration of exoskeleton of *Olenellus thompsoni* (HALL), Lower Cambrian, eastern United States. *1,2,* Dorsal and left lateral views, with portions of exoskeleton cut away to show articulating half ring (*ahr*), articulating furrow (*af*), flange furrow (*ff*) and flange (*fl*), pleural furrow (*pf*), and doublure of thoracic segment (*d*); subdivisions of thorax shown; *3,* left lateral view, partly enrolled, with segments 5 and 10 numbered (*solid circles* showing position of axis of rotation between segments); *4,* posterior view, partly enrolled (Whittington, 1989, fig. 1–2).

In the related nileids (WHITTINGTON, 1965; FORTEY, 1986) the inner portion of the pleura is narrow (tr.) with large processes and sockets at the fulcrum, and the outer portion is formed like that of asaphids, a fold (directed transversely) in the doublure acting to limit enrollment. The facet in asaphids (see

Fig. 74) and the nileid *Symphysurus* is relatively broad (exs.) and bears terrace ridges; it has been described as **petaloid** by FORTEY (1986) and FORTEY and CHATTERTON (1988, p. 178, fig. 13). In remopleuridids the structure of the pleura (WHITTINGTON, 1959a; CHATTERTON & LUDVIGSEN, 1976; CHAT-
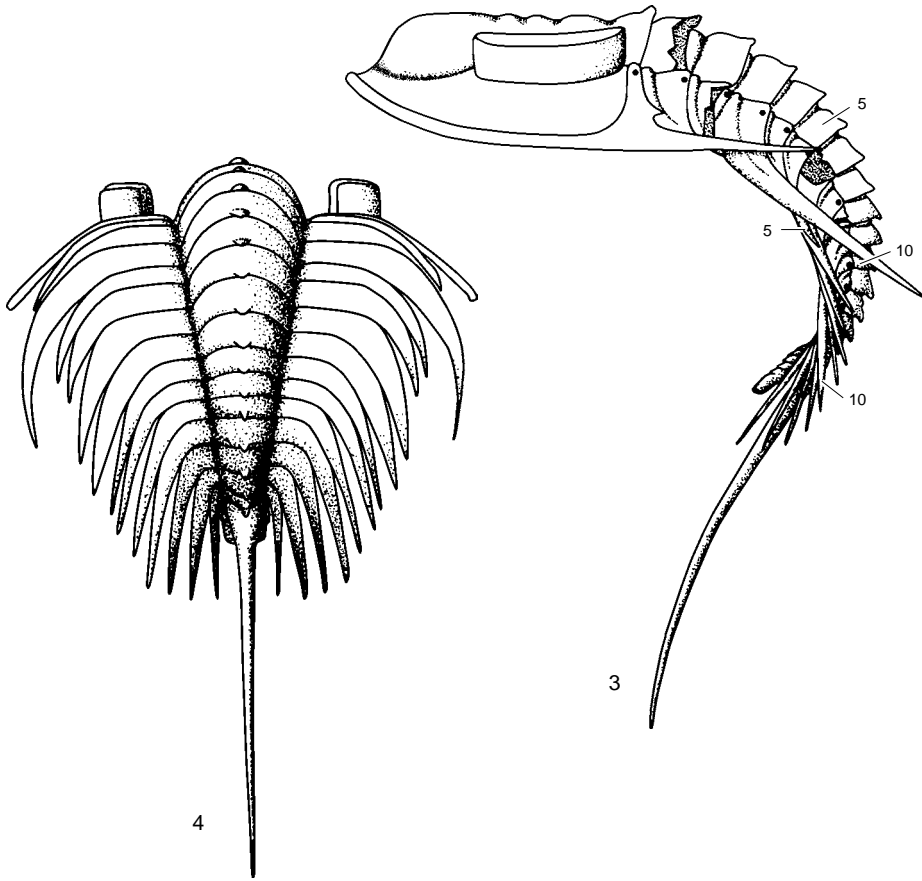
FIG. 45 (continued). *For explanation, see facing page.*

TERTON & CAMPBELL, 1993) is similar—the inner portion extremely narrow (tr.), the fulcral process and socket prominent, the doublure extending in to the fulcrum—and enrollment of the falcate outer portions is limited by a transverse fold in the doublure and the way the anterior edge of the following pleura fits into it.

In Cyclopygidae the bent-down, facetted, outer portions of the pleurae become successively wider (tr.) posteriorly, giving a thorax that is widest (tr.) across the last segment. This form of the thorax is related to the manner in which the tips of the pleurae fit into the vincular notches beneath the cephalon when enrolled (MAREK, 1961, pl. 4, fig. 3–4; HAN, 1978).

The thoracic segments of cheirurids (e.g., *Ceraurus,* Fig. 39) are known in detail from silicified specimens (WHITTINGTON & EVITT, 1954; CHATTERTON & LUDVIGSEN, 1976; HOLLOWAY, 1980; CHATTERTON & PERRY, 1984). The inner portion of the pleura is horizontal with an anterior flange and posterior recess; the outer portion is a spine, the doublure curved in beneath the fulcral process and socket to form a ventral flange in *Deiphon* (HOLLOWAY, 1980, fig. 7). The pleural spines (usually a single spine, in some species two) may be shaped and directed so that they pass one behind the other in enrollment; in *Sphaerexochus* the blunt, thick spines may have projections and corresponding recesses to give a close fit when enrolled.
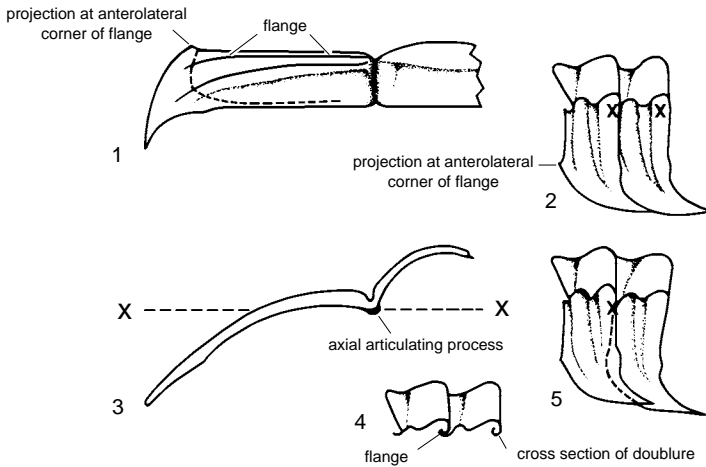
FIG. 46. *Paradoxides (Hydrocephalus) carens* BARRANDE, Middle Cambrian, Bohemia, showing articulation devices in the thorax of a nonfulcrate trilobite; *x* is the axis of rotation. *1,* Dorsal view of left half of segment (*dashed line* shows position of inner edge of doublure); *2,* left lateral view of two segments in the extended position; *3,* posterior view of left half of segment; *4,* left lateral view of two axial rings in the extended position, with inner portion of pleura shown in cross section; *5,* left lateral view of two segments in flexed position (*dashed line* shows anterior edge of pleura) (Whittington, 1990, fig. 21).

The preannulus (Fig. 40.2) has been observed in the axial ring of some species.

Thoracic segments of odontopleurids (WHITTINGTON & EVITT, 1954; BRUTON, 1966; CHATTERTON & LUDVIGSEN, 1976; CHATTERTON & PERRY, 1983) resemble in some respects those of cheirurids, particularly in the flat inner portion of the pleura, the spines (two) forming the outer portion, and the narrow doublure beneath their bases with the fulcral process and socket. A flange on the anterior edge of the inner portion of the pleura articulates with a groove on the posterior edge of the segment in front; the fulcral process and socket act as guides and limit enrollment. In such odontopleurids as *Ceratocephala* the pleural furrow is shallow and indistinct. In others, however, the pleural furrow separates an anterior and posterior ridge, the latter passing in to the base of the principal pleural spine; the ridge may be inflated into a **fulcral swelling** at the base of the spine. So far only known in *Ceratocephala* (WHITTINGTON, 1956d, p. 240; THOMAS, 1981, p. 96; CHATTERTON & PERRY, 1983, p. 48) is a peculiar posterior thoracic segment, in which anterior and posterior pleural spines are alike, and a curved suture traverses (exs.) the inner portion of the pleura. In silicified specimens this outer portion of the pleura occurs in isolation, the axial portion remains undetected. Unusual also is the **fenestra** in the exoskelton of *Laethoprusia* (RAMSKÖLD, 1991a); these openings occur in the segmental boundaries of the pleural region, from the posterior cephalic margin to within the pygidium. The exoskeleton is curved downwards (ventrally) around the margin of the ovate fenestra, and each edge projects beside an intervening trough, a form like that of the edge of the articulating flange. Less well preserved but seemingly similar structures are the unmineralized slitlike areas between the inner portions of the pleurae in the thorax of species of asteropyginids (MORZADEC, 1983; SMEENK, 1983).

The encrinurid pleura (WHITTINGTON & CAMPBELL, 1967; EVITT & TRIPP, 1977; RAMSKÖLD, 1986) has a horizontal inner portion and steeply down-curved outer portion and is characterized by the prominent posterior pleural ridge that continues into the spinose tip. WHITTINGTON and CAMPBELL
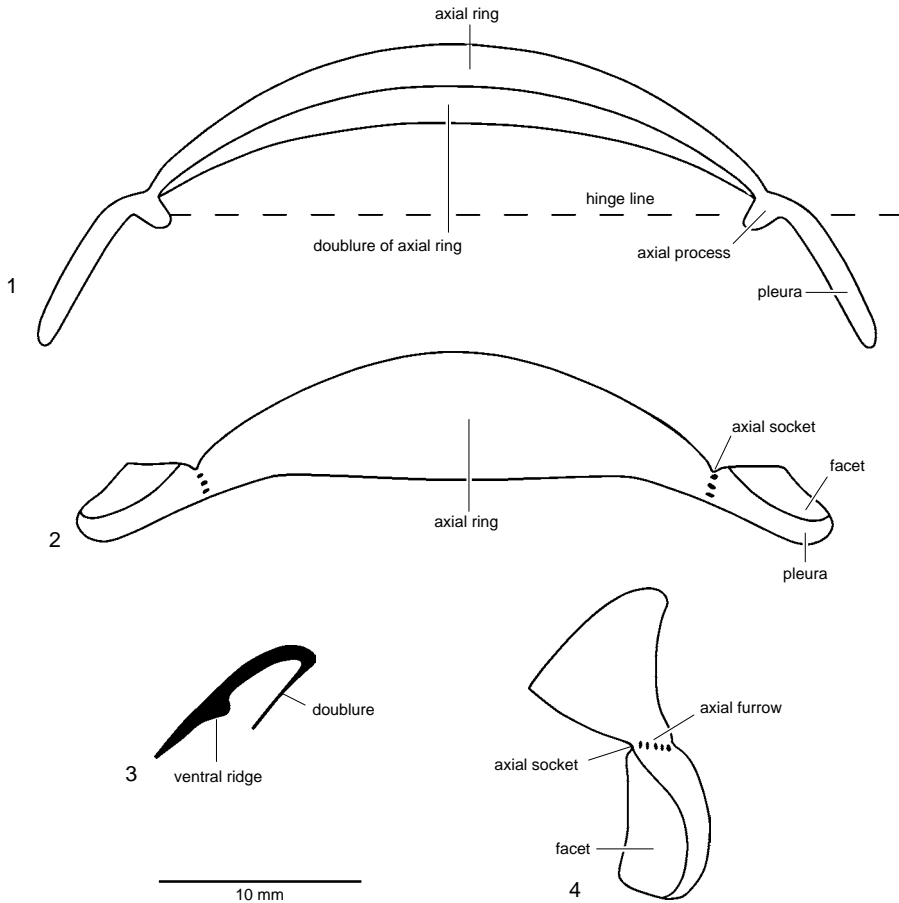
FIG. 47. Thoracic segment of *Cybantyx anaglyptos* Lane & Thomas in Thomas. *1,2,4,* Posterior, dorsal, and left lateral views; *3,* sagittal section of axial ring, showing thick dorsal exoskeleton and ventral ridge (new).

(1967, p. 470–471) and Campbell (1967, p. 22) drew attention to the exceptional thickness of the exoskeleton along the posterior pleural ridge and the median, internal row of canals that apparently did not traverse the outermost layers of the exoskeleton. The much lower anterior pleural ridge dies out distally. The posterior pleural ridge with its fulcral swelling is so shaped on the outer portion that it acts to limit enrollment. An anterior flange and axial processes and sockets aid in articulation; the doublure extends only to the base of the spine at the tip of the outer portion of the pleura.

Articulation in the thorax of *Phacops* was described in detail by Miller (1976), and

Campbell (1977) illustrated the doublure of other phacopids with its raised stop and the form of the pleural tips that fitted into vincular sockets in the cephalon (see also Lespérance, 1991; Bruton & Haas, 1997). Campbell (1977) and Speyer (1988) have noted that the pleural furrow is postfacetal in dalmanitids, not epifacetal as in phacopids, and that details of the articulation and the fit of the pygidium and cephalon are different in the two groups.

In the Silurian *Cybantyx* (Fig. 47), the axis is broad (tr.), the pleura narrow and curving down in a continuation of the slope of the distal portion of the axial ring; the fulcrum is absent. The axial ring, longest sagittally,

curves downward and forward and is not interrupted by the downfold of an articulating furrow; the doublure has a similar downward curvature. Exfoliated specimens show that on the inner surface of the anterior portion of the ring there is a transverse ridge, steep on the posterior side, extending between the shallow axial furrows. An axial articulating process projects ventrally at the posterior edge of the ring and fits into a socket at the anterior edge of the following ring. The outer surface of the pleura is largely occupied by the facet, which has a gently concave surface. The doublure has a U-shaped inner margin, the edges of which extend in to the axial furrow. In many Ordovician species of illaenids (WHITTINGTON, 1997), the axial region of the thorax is relatively narrow (sag.), the axial ring and articulating process similar to that of *Cybantyx* and having the transverse ventral ridge. The pleura is relatively broader (sag.), fulcrate, the inner portion lacks a pleural furrow, the outer portion similar in form to that of *Cybantyx.* In contrast to the Illaenidae, the thorax of Styginidae and Scutelluidae (ŠNAJDR, 1960; CHATTERTON & CAMPBELL, 1980; ARCHINAL, 1994) has the axial ring (in many species shortest sagittally) descending to an articulating half ring that extends forward almost horizontally and underlies the almost horizontal doublure of the ring in front. The fulcrate pleura has an articulating flange on the inner portion, a fulcral articulating process and socket, and the outer portion is a spine that has the doublure extending in to the fulcrum.

The fulcrate form of articulation is seen in Agnostina and eodiscoids (WHITTINGTON, 1963, 1965; HUNT, 1967; MÜLLER & WALOSSEK, 1987; JELL, 1975a), the inner portion of the pleura horizontal, the outer portion narrow (tr.), bent down, and shaped so that the close fit enables complete enrollment (Fig. 48.3). This close fit is edge to edge; the outer portion lacks a facet, and there is no overlap between adjacent sclerites. A unique feature of Agnostina is the absence of the articulating half ring on the first tho-

racic segment throughout ontogeny (ROBISON, 1964, p. 515). It is present on the second segment and the pygidium. Hence, when the exoskeleton is enrolled, an elliptical opening appears in a median portion of the axial region, the **cephalothoracic aperture,** between the narrow (tr.), convex occipital band of the cephalon and a slight recess in the anterior margin of the first thoracic segment (Fig. 48; ROBISON, 1964, fig. 3). This aperture appears to be common to Agnostina, the only exception being the presence of an articulating half ring on the first segment of a species of *Leiagnostus* (PEK & SMOLA, 1989). In eodiscoids the articulating half ring is present on all segments and the pygidium.

In discussing the articulation of the pygidium of Agnostina, ÖPIK (1963, p. 31; 1967, p. 53) commented on the form of the articulating half ring and articulating furrow in different subfamilies. In the common or basic type the half ring has the shape of a segment of a circle, and the furrow is narrow (sag. and exs.). In glyptagnostoids the half ring is a narrow ridge curved forward, the furrow a wide (sag.), elliptical depression. In the clavagnostid *Aspidagnostus* the articulating half ring arched backwards, a form he termed *agnostoid* and regarded as distinct from that in glyptagnostoids. These distinctions have been used as diagnostic by SHERGOLD, LAURIE, and SUN (1990). In his later discussion of articulation in Agnostina, ÖPIK (1979, p. 25–28, 32–34) concentrated on the structures at the fulcrum, which he termed *prongs.* External prongs are short projections or spines directed backward from the posterior cephalic border and the abaxial posterior margin of each segment and are visible in dorsal view. Similar prongs may also project forward from the facet of the pygidium and the abaxial anterior margin of each segment but are concealed beneath the external prongs in dorsal view. ÖPIK considered that these fulcral prongs were the points about which the sclerites of the exoskeleton hinged. Earlier, ÖPIK (1967, p. 55) referred to the concavity of the facet of the pygidium
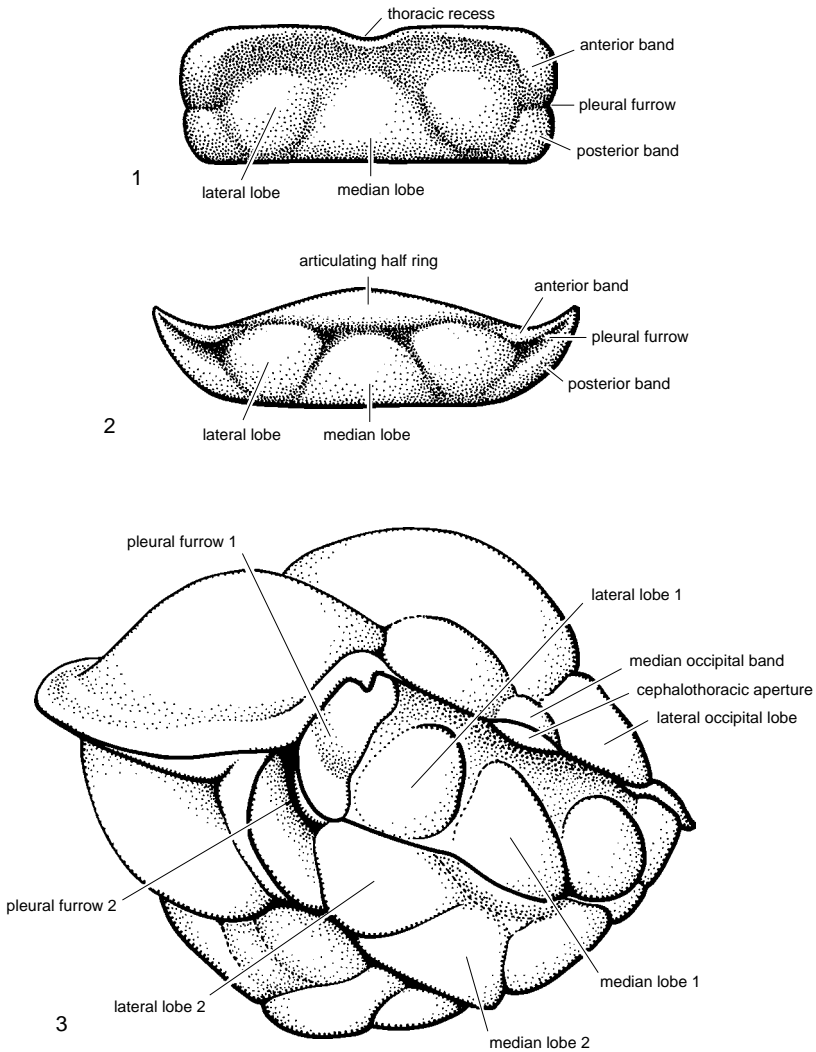
FIG. 48. *Geragnostus clusus* WHITTINGTON, Ordovician, Newfoundland. *1,2,* Dorsal views of first and second thoracic segments, showing thoracic recess, the posterior margin of the cephalothoracic aperture, and articulating half ring of second segment; axial ring of segment divided into median and lateral lobes; pleura divided by pleural furrow into anterior and posterior bands; *3,* posterolateral view of enrolled exoskeleton, to show segments, coaptation, and cephalothoracic aperture; occipital ring divided into lateral lobes and median occipital band, ×36 (Whittington, 1963, fig. 3).

in certain Agnostina in which a fulcral prong was present. Possibly this concavity fitted against the ventral side of the external prong of the second thoracic segment.

The thoracic segment of the Silurian illaenid *Cybantyx* (Fig. 47) lacks the inner, horizontal portion of the pleura and the fulcrum; the pleura continues the slope of the axial ring. This nonfulcrate form of segment differs from that of the Cambrian species described above in that the axial region is wide (tr.) and the pleural region narrow. These segments articulate with each other, and with the cephalon and pygidium, about the deep axial process. A like form of segment occurs also in the unrelated Silurian

and Devonian homalonotids, in which the pleura continues the lateral slope of the broad axial ring and has no horizontal inner portion. These Silurian and Devonian homalonotids also have, as in older species, the straight, outward and backwardly directed lateral margin of the axial ring (and occipital ring), which gives a zigzag course to the axial furrow (HENRY, 1980b, p. 357; 1996), and the deep, narrow articulating furrow that is continuous across the axial furrow with the pleural furrow and dies out on the broad facet (WOLFART, 1968, pl. 1–2; THOMAS, 1977, pl. 24, fig. 12; MORZADEC, 1983, pl. 4, fig. 1; WENNDORF, 1990, pl. 15, fig. 3). The articulating half ring formed a continuous structure with the anterior band of the pleura and is relatively long (sag. and exs.). THOMAS and LANE (1984) suggested that this gave an unusual amount of dorsoventral flexibility to the thorax. The great depth of the pleural furrow and the ridge it formed on the visceral surface were shown in a Devonian example by HAAS (1981, fig. 4), and both BRASSEL and BERGSTRÖM (1978) and THOMAS and LANE (1984) regarded this ridge as a device to limit enrollment. The ridge is present in the Silurian homalonotid *Trimerus* (WHITTINGTON, 1993b) but cannot have acted to limit enrollment.

In trilobites the segments were articulated with one another and with the cephalon and pygidium so that flexure of the exoskeleton and (with rare exceptions) enrollment were possible. The straight hinge line afforded by the horizontal inner portion of the pleura (Fig. 40), the abaxial fulcrum, and the facet on the outer portion of the pleura were the most widespread articulatory devices but were not universal (Fig. 41). Back-arching of the thorax, so that it was concavely flexed dorsally, was possible to a limited extent by many trilobites, depending on the form of the axial ring. Such back-arching was facilitated if the ring had the anterior face forwardly concave in profile (as seen in dorsal view) and in longitudinal section sloped forward on the anterior side and backward on

the posterior side (cf. HAMMANN, 1985). This allowed the axial rings, which were situated above the axis of articulation, to be rotated close to each other. At the same time the outer parts of the pleurae, lying below the axis, were fanned out to cover the sides of the body. CHATTERTON and PERRY (1983, p. 17) suggested that the function of the preannulus (Fig. 40) was to allow concave-dorsal flexure in odontopleurids, cheirurids, and proetids, by allowing the axial ring of the segment in front to rotate back over it. The unusual structure of the axial ring in illaenids (Fig. 47) means that dorsoventral movement between them—and between thorax, cephalon, and pygidium—is not limited, so that the maximum amount of back-arching is possible (WHITTINGTON, in press). Rarely, the flexure of the thorax appears to have been limited (e.g., in the remopleuridid *Hypodicranotus* WHITTINGTON, 1952b) by the exceptionally long fork of the hypostome. I argued (WHITTINGTON, 1981, p. 598–599) that in the Upper Cambrian *Schmalenseeia* the exoskeleton may not have hinged between the thoracic segments but may have been a rigid shield. Further studies (WHITTINGTON, 1994) have led me to rescind this argument and to consider that the burlingiid exoskeleton was articulated and had some flexibility.

The external surface of the axial ring and inner portion of the pleura of the thorax is similar in form and sculpture to the occipital ring and furrow and the posterior border and furrow of the cephalon. This is well shown, for example, by Agnostina (HUNT, 1967; ÖPIK, 1979), asaphids and nileids (HENNINGSMOEN, 1960; WHITTINGTON, 1965; SCHRANK, 1972b), and calymenids (CAMPBELL, 1967) and by the arrangement of spines in odontopleurids (CHATTERTON & PERRY, 1983). These similarities apply to the lateral lobes, smooth areas, apodemes, and course of terrace ridges. On the outer portions of the pleura and on the doublure, particular arrangements of terrace ridges are recorded, as for example in asaphids and

Symphysurus (Siegfried, 1936; Hupé, 1955b; Fortey, 1986). Granulation on the articulating facet of a calymenid was described by Chatterton and Campbell (1993, fig. 3f–h); the facet of a homalonotid (Whittington, 1993b, fig. 4g) is also granulose. Öpik (1961a) described the faint, transversely directed ridge on each band of the thoracic pleura in *Redlichia, Papyriaspsis,* and *Centropleura* and the branches from it. Such ridges have been observed in *Paradoxides* (Bergström & Levi-Setti, 1978, p. 9) but not in the thorax of other trilobites.

PYGIDIUM

This posterior region of the body consists of a number of fused somites, and the **pygidium** is the exoskeleton of this region (Fig. 2). Almost all pygidia have a convex axial region that is separated from the lateral pleural region by the axial furrow; the axial furrows merge at the terminus of the axis, and the pleural region extends behind the axis. The somites of the pygidium and thorax were similar, judging by the similarity in morphology between thoracic segments and the fused segments forming the pygidium. Like the thoracic segments, the anterior pygidial segment may have a horizontal inner portion of the pleural region, a sloping outer portion outside the fulcral line (Fig. 2), and a facet. Distally the exoskeleton extends beneath the outer portion of the pleural region as a doublure. This doublure is (in most cases) continuous behind the axis; it varies in width (tr. and sag.) and convexity and may form a tubular or flattened structure with the lateral and posterior border. The latter may be convex and defined on the inner side by a border furrow or lacking in independent convexity, not defined by a border furrow nor crossed by pleural or interpleural furrows. When the exoskeleton is sharply flexed at the margin, the border may be flattened or concave. Fenestrae, oval or slitlike areas in the interpleural furrows that are not mineralized are known in asteropyginids (Mor-

zadec, 1983; Smeenk, 1983), and well-preserved ones have been described in an odontopleurid (Ramsköld, 1991a).

In Agnostina the axis may be subdivided by the anterior two axial rings, whereas the remainder of the axis is not divided by inter-ring furrows (Fig. 6.2). This has led to the distinction of the two rings as the **anteroaxis** and the remainder as the **posteroaxis**. A notation of M for the axial ring and F for the inter-ring furrow, numbered from the anterior ring posteriorly, is used by some authors. Agnostina having the axial lobe unmodified (Fig. 6.2) are termed **axiolobate** (Öpik, 1967, p. 53). In Pseudagnostinae, for example, the posteroaxis is expanded, defined laterally by the **accessory furrow** (Fig. 11.2) and posteriorly by the border furrow. It thus includes both axial and pleural areas, and this composite lobe is the **deuterolobe** (Öpik, 1963, p. 31). In Eodiscina the axis may be divided by many inter-ring furrows, and the terminology used in Agnostina is not applicable.

The pygidium in Olenellina (Whittington, 1989; Fritz, 1995) is formed of two to five or six fused segments with a convex axis. The pleural region in *Olenellus* is narrow (tr.) (Fig. 45), in association with the backwardly directed pleurae of the 14th thoracic segment. In *Wanneria* (Fig. 49) the posterior thoracic pleurae are more outwardly directed, so that the pleural region was relatively wider (tr.). The posterolateral margin of the pleural region was bilobed or prolonged as one or more pairs of spines, as in *Judomia* (Fig. 50). The doublure in both of these genera extended in toward the tip of the axis. The view that the pygidium in Olenellina was not like that of other trilobites but was "a true telson or caudal piece" (Harrington in Moore, 1959, p. 73) is considered to be without foundation. The small pygidium of *Redlichia* (Öpik, 1958; W. Zhang, Lu, & others, 1980, fig. 56) has three axial rings, and the pleura of the first segment extends into a short spine. Öpik described two types of pygidia as belonging to one species, which was therefore
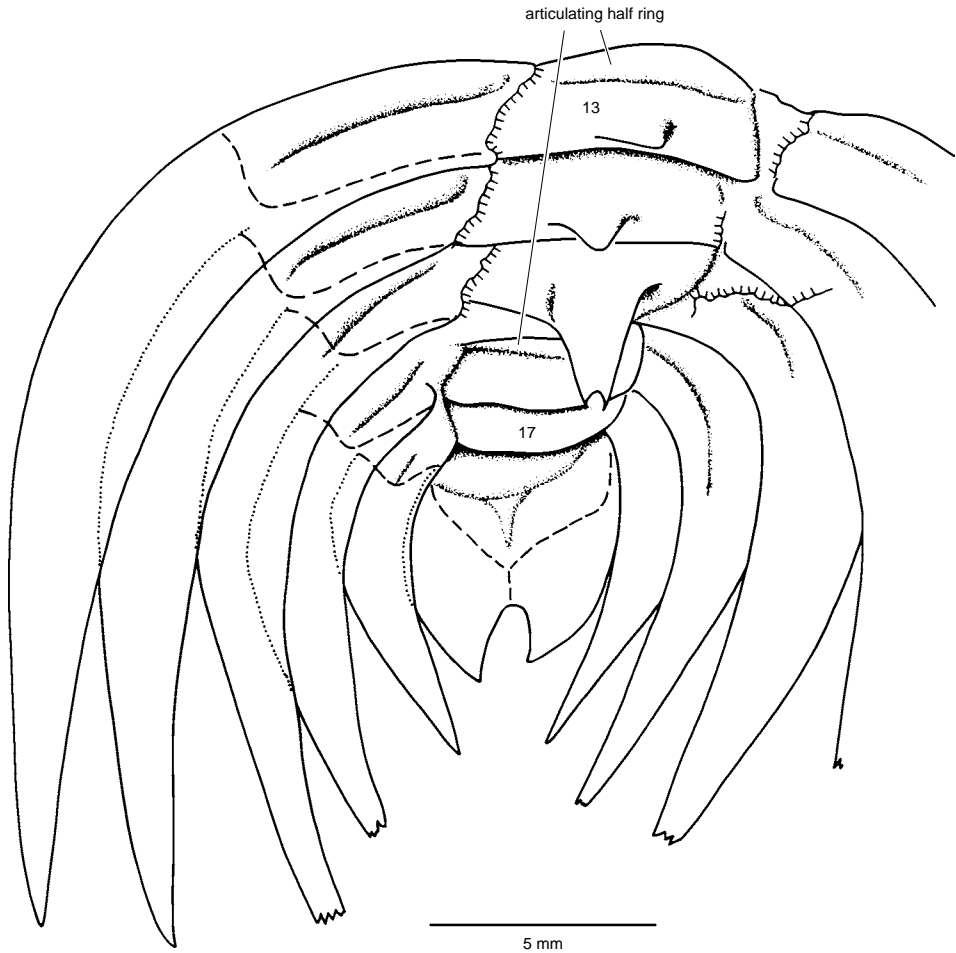
Fig. 49. Thoracic segments 13 through 17 and pygidium of *Wanneria walcottanus* (Wanner), Lower Cambrian, Pennsylvania. *Dashed line* indicates margin of doublure; *dotted line* indicates anterior margin of articulating flange; *hachures* indicate fractures in exoskeleton (Whittington, 1989, fig. 28).

dimorphic. In one type the doublure is absent along the posterior margin. The occurrence of these two types of pygidia is said by W. Zhang and Jell (1987, p. 48) to characterize species of *Redlichia,* whereas in species of dolerolenids (Jell in Bengtson & others, 1990, p. 287, 292) the doublure is lacking posteriorly in all examples. Sdzuy (1959, p. 402–404) described a pygidium of *Saukianda* as also lacking the doublure medially but did not see this as having great taxonomic significance. *Paradoxides* (Bergström & Levi-Setti, 1978; Dean in Martin & Dean, 1988) also has a small pygidium, which

shows the axis and one or two rings and may be partially or completely fused to the last thoracic segment, as is the case with some species of *Redlichia*. The last thoracic segment has been termed the **semi-ankylosed segment** (W. Zhang, Lu, & others, 1980, fig. 55) because in some individual specimens it may be fused to the pygidium, in others not.

Among stratigraphically younger trilobites, many rings may occur in the pygidial axis. The Ordovician *Dionide* (Whittington, 1952a) has 20. Up to 45 have been noted in a Silurian encrinurid (Temple &

TRIPP, 1979, p. 233) and 27 or 28 in Permian proetids (OWENS, 1983, p. 28–29). In the Ordovician *Hypodicranotus* (LUDVIGSEN & CHATTERTON, 1991), however, the axis is not defined, the pleural region is unfurrowed, there is a small pair of posterior marginal spines, and the doublure extends far forward so that the axis must have been extremely short (sag.). It is thought that this pygidium was derived from that of ancestral remopleuridids, in which the axis was defined and bore inter-ring furrows and in which pleural furrows were present. Presumably in the pygidium each axial ring (or pair of apodemes or muscle scars) indicates one somite. In *Olenoides* (WHITTINGTON, 1975, p. 128) a maximum of six pairs of appendages are known in the pygidial region, the axis having five rings and the terminal axial piece. In *Triarthrus* (WHITTINGTON & ALMOND, 1987) there are up to 12 pairs of limbs in the pygidial region, but the axis has only four rings and the terminal piece. Thus, the number of axial rings in the pygidium may be taken only as an indication of the minimum number of somites in the pygidial region.

In Olenellina, some Redlichiina, and paradoxidoids the pygidium is much smaller than the cephalon, and the exoskeleton may be described as **micropygous**. In most other Cambrian trilobites and in stratigraphically younger groups, the pygidum is relatively larger but not as wide (tr.) or long as the cephalon. The Agnostida are characterized by a pygidium similar in size to the cephalon, a condition described as **isopygous**. In many species of asaphids (Fig. 2) and scutelluids the exoskeleton approaches the isopygous condition. The term **macropygous** describes trilobites in which the pygidium is larger than the cephalon. Exactly what is meant by smaller or larger than the cephalon has not been defined, nor did KOBAYASHI (1942a, p. 145) define size in introducing the terms heteropygous and parapygous as stages intermediate between micropygous and isopygous. It is suggested here (see glossary, p. 314) that micropygous be taken to refer to a pygidium considerably shorter (sag. and exs.) and narrower (tr.) than
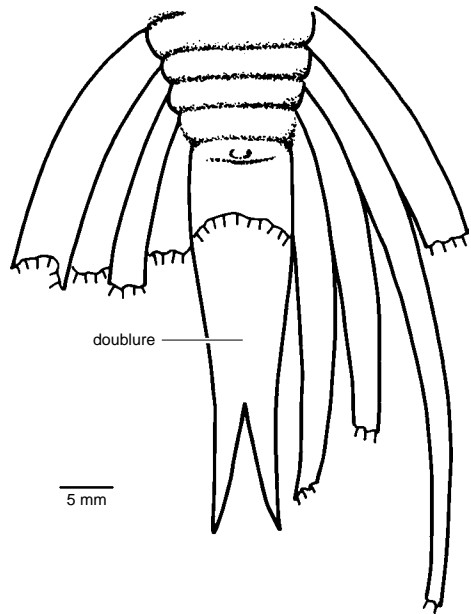

doublure

5 mm

FIG. 50. Posterior four thoracic segments and pygidium of *Judomia tera* LAZARENKO, Lower Cambrian, Siberia; *hachures* indicate edge of exoskeleton (Whittington, 1989, fig. 54b).

the cephalon, while isopygous implies similarity in both maximum width (tr.) and length (sag. and exs.) of cephalon and pygidium. These terms are thus generalized, and to attempt to define intermediates between them appears unprofitable. Macropygous is taken to imply a pygidium greater in maximum width (tr.) than the cephalon. This means that in *Macropyge* (LU & QIAN, 1983), while the pygidium is longer (sag.) than the cephalon, it is considerably narrower (tr.), so that this form is not considered to be an example of a macropygous trilobite.

The axis of the pygidium, defined by its convexity independent of the pleural regions and by the axial furrow, may be short (sag.) or long relative to the length of the pygidium, the relative width being likewise variable, and may extend back as far as the border furrow or so that the tip lies above the inner edge of the doublure. In *Bumastus* (Fig. 1) and some homalonotids, in which the convexity of the axis is continuous with that

of the pleural region and the axial furrow is effaced, the position of the axis is indicated only by the articulating furrow and articulating half ring. Characteristically the axis is divided by **inter-ring furrows** into a series of rings, the anterior ring usually defined and closely resembling those of the thorax. Thus, the special features of the thoracic axial rings—preannulus, apodemal pit, apodeme, lateral lobe, length (sag. and exs.) and form of the articulating half ring, etc.—are duplicated in the first ring of the pygidium. Succeeding rings become less convex and shorter (sag. and exs.) posteriorly, and the inter-ring furrows (and apodemal pits) become successively shallower and the apodeme lower. An undivided posterior portion of the axis is referred to as the **terminal axial piece** (see Fig. 53). In the axis of Agnostina, muscle scars may be preserved (as in the cephalic axis) as smooth areas on the external surface or as impressions, ridges, or grooves in the internal mold (SHERGOLD, 1975, pl. 4, 10) (Fig. 10.3, 11.2). In raphiophorids similar paired areas may be raised on the parietal surface of the axis or be discernible as dark patches (Fig. 51).

The pleural region (Fig. 52) may be divided by the **border furrow** into an inner **pleural field** and **border**. The border may be convex, flattened, concave upward, or sloping vertically; and the definition and depth of the border furrow differs. The border may merely be the outer, unfurrowed portion of the pleural region, lacking independent convexity or the definition of a border furrow. Dependent on the relative length (sag.) of the axis to that of the pygidium is the length (sag. and exs.) of the pleural region posteriorly. Anteriorly the pleural region conforms to the form of the thoracic segments; if the inner portion of the thoracic pleura is horizontal, so is the pleural region, and the anterior margin is straight and transverse. Outside the fulcrum the margin is directed outward and backward, and the anterolateral corner is facetted.

Behind the anterior portion the pleural region in most trilobites is reduced in width

(tr.) and convexity, the outline narrowing backward. Characteristic of the pleural region (Fig. 53) is the subdivision by furrows that are successively more strongly backwardly directed. The most anterior and most prominent of these **pleural furrows** is that which extends outward and backward from the articulating furrow; successive pleural furrows originate at the axial furrow opposite the inter-ring furrow. The anterior portion of the pleural region of the pygidium is thus equivalent to the anterior band of a thoracic segment. It not only carries the facet, but there may also be a narrow (exs.) flange along the margin, similar to that on the segment.

The second series of furrows in the pleural region are **interpleural furrows**, successively arising opposite inter-ring furrows of the axis, each directed outward and less strongly backward than the pleural furrow immediately in front of it. The relation between the articulating or inter-ring furrow and the pleural and interpleural furrow of the same segment is usually clear on the first segment of the pygidium, but it may be obscured or lost posteriorly, especially when the number of axial rings greatly exceeds that of pleura. For example, in *Olenoides* (see Fig. 83) the relationship of ring and pleura is unequivocal. At the other extreme, however, is the encrinurid *Cybeloides* (Fig. 54), having some 30 axial rings but only 4 pleurae (the count of 30 axial rings being based on the assumption that the incomplete furrows on the axis behind the first axial ring are inter-ring furrows). Pleural and interpleural furrows may become less deep posteriorly and may die out on the pleural field before reaching the border furrow, or they may extend on to the border. As in the thoracic pleurae, the two pleural bands may be convex and ridgelike, the posterior band being more prominent. OWENS (1973, p. 5) observed that in proetids the anterior and posterior pleural bands differ in convexity (as seen in exsagittal profile), depending on the relative depths of pleural and interpleural furrows; three distinctive profiles were recognized. In other trilobites one convex band may occupy
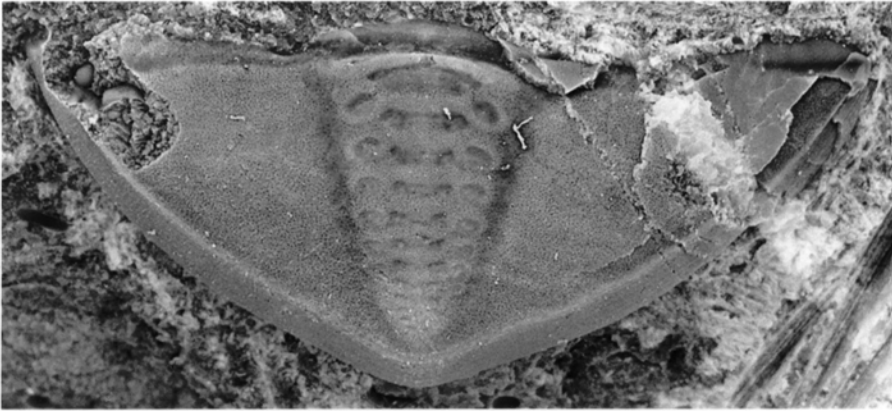
1a
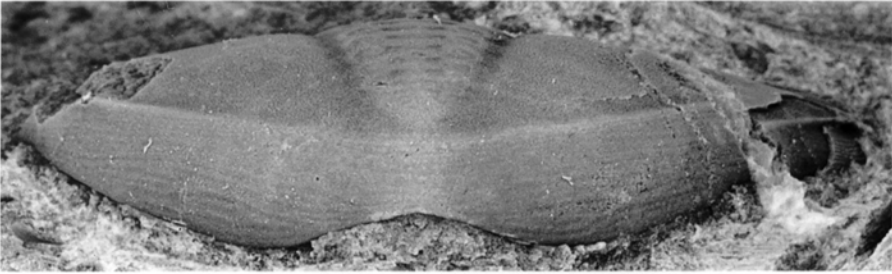
1b
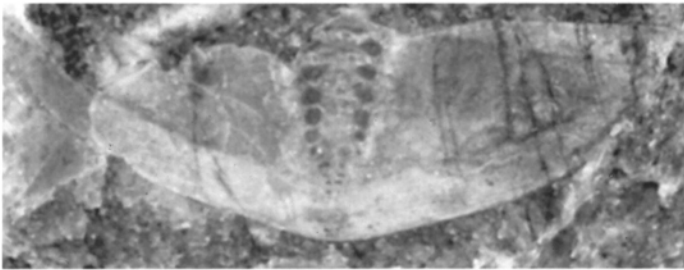
2

Fig. 51. *1a,b, Lonchodomas clavulus* Whittington, Ordovician, Newfoundland. Internal mold of pygidium showing impressions of raised areas on parietal surface of axis of exoskeleton and posterior embayment in outer portion of pleural region; *a,* dorsal and *b,* posterior views, ×4.5 (Whittington, 1965, pl. 11, fig. 4, 6). *2, Ampyxoides semicostatus* (Billings), Ordovician, Newfoundland. Incomplete pygidium, photographed under alcohol, showing dark patches on axis, ×9 (Whittington, 1965, pl. 12, fig. 18).

the whole length (exs.) between pleural furrows as a **pleural rib** (Fig. 52), the interpleural furrow being absent. Such ribs are characteristic of scutelluids, in which the axis is short (sag.) and the ribs more and more strongly backwardly directed, the last pair of which may merge wholly or partly to form a median posterior rib on the terminal area (Fig. 55). Ramsköld (1985, p. 36) has noted convex oval areas on the posterior pleural band or bands of species of *Dalmanites*; the inner surface bears numerous minute perforations. The pleural region may also lack pleural furrows except for a shallow
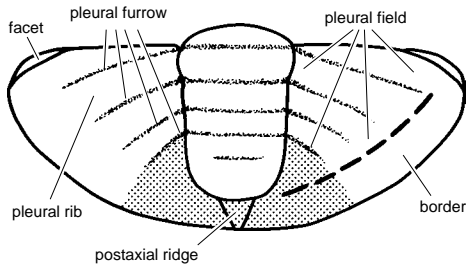
F<small>IG</small>. 52. Diagram to explain terminology of the pleural region of the pygidium. *Shaded portion* is the terminal area, which lies behind the posterior pair of pleural furrows; *dashed line* on right side indicates position of inner margin of doublure (new).

anterior furrow adjacent to the fulcrum; an extreme example is *Bumastus* (Fig. 1), in which pleural region and axis merge into a continuous convexity and there is no border. Most unusual is the inflated pleural field in the Upper Cambrian *Pemphigaspis* (P<small>ALMER</small>, 1951), which bulges up above the axis and outward and backward over the narrow, vertical, lateral and posterior border. In the pygidium of Agnostina the pleural region has a

well-defined border, the area within the border furrow being referred to as the **acrolobe**, an area that includes the axial region in effaced species (Fig. 13). In species in which the anteroaxis is defined, an **accessory furrow** may be directed outward and backward from the second inter-ring furrow (Fig. 11). This accessory furrow may extend to the border furrow and the pair thus enclose the **deuterolobe**, an area that may include part of the pleural field as well as the posteroaxis. The axis of the eodiscoid pygidium may have many similar rings and extend back close to the border furrow; the pleural field may have many pleural furrows or lack such furrows. Eodiscoid species with a faint or effaced axis are known. Various trilobites have a **postaxial ridge** behind the axis in the midline of the pygidium (Fig. 52, 54), and in Agnostina a **postaxial furrow** may be present (Fig. 6).

Tubercles and spines may be developed on the pygidium as they are on the thorax. On the axial rings a single median or pair of prominent tubercles, spines, or nodes like those of the thorax, may be present on the
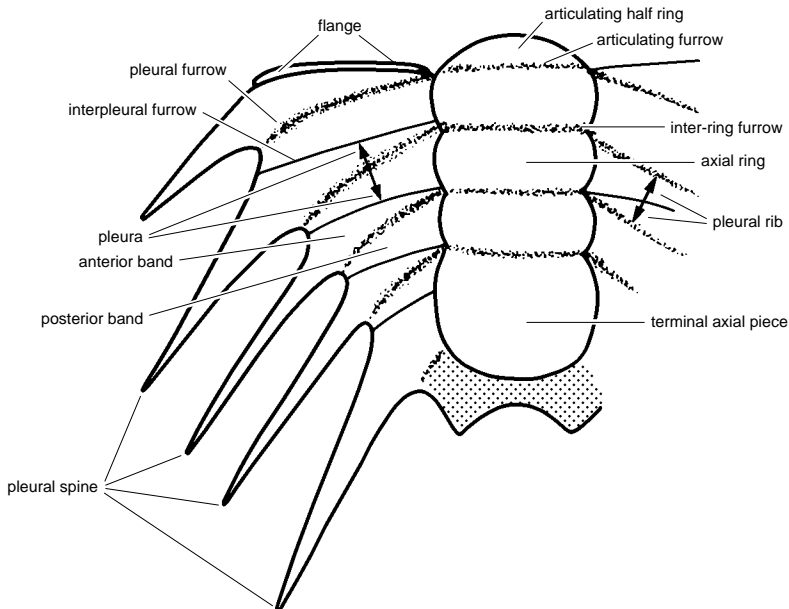

F<small>IG</small>. 53. *Dorypyge* sp., generalized diagram to explain terminology; terminal area shaded (adapted from Kushan, 1973).
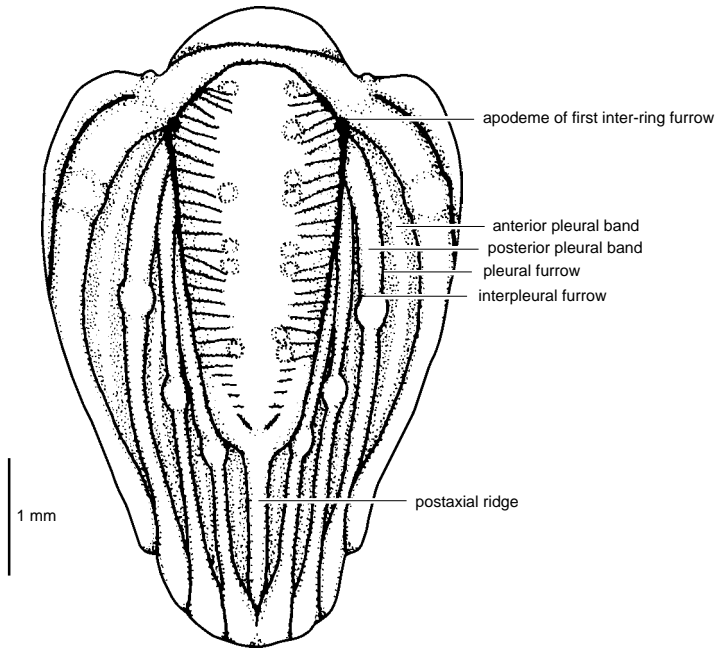
FIG. 54. Dorsal view of pygidium of *Cybeloides virginiensis virginiensis* COOPER, Ordovician, Virginia (Evitt & Tripp, 1977, fig. 15).

first few rings, diminishing posteriorly and disappearing. A single prominent spine may be present on the axis, as in some eodiscoids (RASETTI, 1966a, pl. 2), or as a **terminal axial spine** (Fig. 56). In *Encrinurus* (Fig. 57) a median tubercle occurs on particular axial rings, a smooth sagittal band surrounding and extending between these tubercles; no such structures are present on the thorax. Some species of *Encrinurus* bear a posterior spine or **mucro** that projects from the border behind the axis; similar spines are developed in asaphids and dalmanitids. The lateral margin of the pygidium may be entire or bear spines. These spines are formed in the same way as those of the thoracic pleurae, that is, as projections from both bands of the pleura, as in the dalmanitid *Greenops* (Fig. 58) or lichids; from the posterior band of the pleura as in the major spine of odontopleurids (Fig. 42–43) and many other trilobites; from the pleural rib as in scutelluids (Fig. 55); and less commonly from the anterior band of the pleura (Fig. 53). These spines are therefore termed **pleural spines;**

they have also been referred to as border spines when a border is developed on the pygidium or as marginal spines when a border is not present. In the latter instance, if the margin is sharply flexed, they may be flattened in cross section and blade shaped in
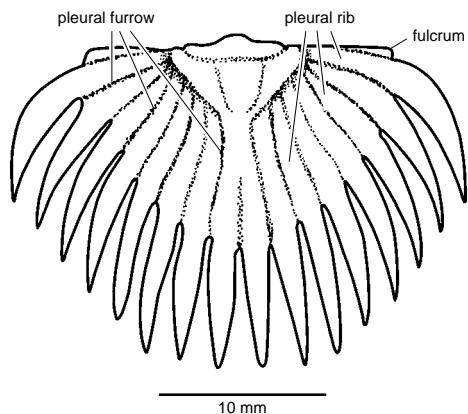
FIG. 55. Dorsal view of pygidium of *Weberopeltis* aff. *arcticum* (WEBER), Devonian, Arctic Canada (adapted from Ormiston, 1967, pl. 4, fig. 1).
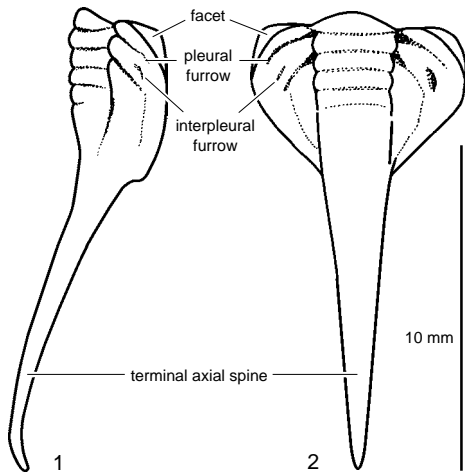
FIG. 56. *Acidiphorus spinifer* RAYMOND, Ordovician, Canada. *1,2,* Right lateral and dorsal views of pygidium (adapted from Whittington, 1965, pl. 44, fig. 4, 6, 12, 14).

outline rather than elongated-conical in form. Pleural spines of the pygidium may be graded in size, or one or more spines may be larger than those adjacent. In odontopleurids the base of the large spine may be continued by a pleural ridge across the pleural field to the axis. In the cheirurid *Holia* (WHITTINGTON & EVITT, 1954) a similar ridge forms the majority of the pleural region. In the styginid *Ancyropyge* (ORMISTON, 1967) the pleural region is largely formed of long, curved pleural spines. Some pygidia bear a single pair of large pleural spines, as in *Proceratopyge* (Fig. 59) or the redlichioid *Yinites* (W. ZHANG, LU, & others, 1980). Such spines appear to belong either to one particular segment of the pygidium (not in all examples the anterior) or, when the base is broad, to more than one segment. A postaxial ridge, extending back sagittally from the tip of the axis towards the margin, may be developed with or independently of any posterior spine (Fig. 52, 54). In addition to axial and pleural spines, large spines may arise from the pleural field, as in the odontopleurid *Apianurus* (WHITTINGTON, 1956b); these spines are upwardly directed and curve backward, rather than being outwardly directed as were pleural spines. A

pattern of anastomosing ridges, similar to the genal caeca, has been described on the pleural field of Cambrian trilobites (ÖPIK, 1961a) and in one example of a styginid (Fig. 60). In this example the ridges commence at the axial furrow, and the pattern is related to segmentation, there being a major branch commencing opposite each inter-ring furrow.

The doublure of the pygidium in most trilobites is narrow (tr.), convex ventrally, and curled beneath the border. Cross sections (e.g., OSMÓLSKA, 1975, pl. 2) show that the exoskeleton thins toward the inner margin. The doublure does not extend beneath the axis but may extend beneath the pleural field, as in some asaphids (Fig. 61) and scutellluids (ŠNAJDR, 1960). In illaenids the doublure may extend in toward the tip of the axis to surround it in a scalloped (Fig. 9.4, 62) or pointed projection, or the inner margin may follow the curve of the pygidial margin (JAANUSSON, 1954). In the asaphids *Ogygiocaris* (HENNINGSMOEN, 1960) and *Gog* (FORTEY, 1975b), the inner edge of the doublure has a distinctive, scalloped outline related to the pleural furrows. Silicified material has shown the structure of the
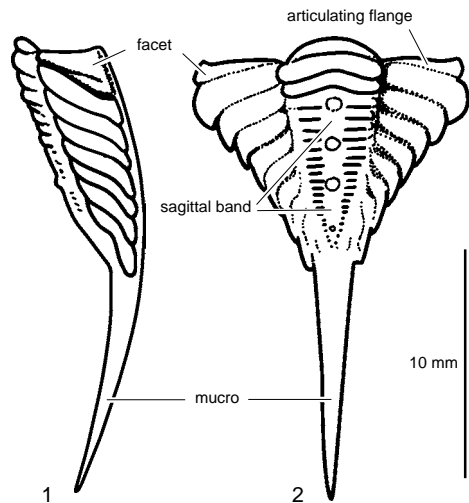

FIG. 57. *Encrinurus (Encrinurus) intersitus* RAMSKÖLD, Silurian, Sweden. *1,2,* Right lateral and dorsal views (adapted from Ramsköld, 1986, pl. 39, fig. 8a,b).
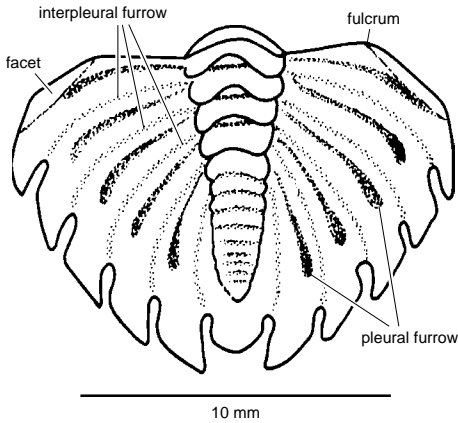
Fig. 58. Dorsal view of pygidum of *Greenops struvei* Morzadec, Devonian, France (adapted from Morzadec, 1983, fig. 7).

doublure posteriorly: in cheirurids (Whittington & Evitt, 1954; Chatterton & Perry, 1984), for example, the profile of the ventral margin of the doublure in posterior view has a median arch, and there is a small, rounded projection on the inner margin of the doublure at the tip of the axis. Many other groups of trilobites (e.g., Chatterton & Ludvigsen, 1976) show a depression in the doublure behind the axis in ventral view or an arch in posterior view. In trinucleids and raphiophorids (Fig. 51.2), in which the inner, horizontal portion of the thoracic pleurae is wide (tr.) and the outer portion narrow and steeply inclined, the outer portion of the pygidium likewise slopes steeply, and this border has a median arch in posterior view, and has an extremely narrow doublure. In Agnostina (Robison, 1964) a groove in the pygidial doublure, the **fibular furrow**, is a vincular structure into which the inner edge of the cephalic doublure fitted at complete enrollment. In some eodiscoids Rushton (1966) and Rasetti (1966b, 1967) have described vertical spines on the border of the pygidium, the tips of which on enrollment fitted beneath tubercles on the cephalic border. In *Isotelus* (Chatterton & Ludvigsen, 1976), *Annamitella* (Fortey & Shergold, 1984), and *Symphysurus* (Fortey, 1986) a process projecting from the antero-

lateral margin of the doublure fitted on enrollment into a depression in the cephalic doublure.

ENROLLMENT AND COAPTATIVE STRUCTURES

E. N. K. Clarkson and
H. B. Whittington

Articulation of the thoracic segments with one another and with the cephalon and pygidium enabled enrollment in trilobites. Such enrollment is complete when a posterior portion of the thorax or the pygidium was brought into contact with the ventrally or inwardly facing inner surfaces of the cephalic doublure.

Complete enrollment is exhibited by trilobites throughout their history, from the Lower Cambrian Agnostida to Permian proetoids. Such complete enrollment is characteristic of trilobites that had a fulcrate exoskeleton, the straight, horizontal hinge-line having given a precision of movement in articulation. In such familiar examples as Agnostida (Fig. 48.3), *Calymene* (Chatterton & Campbell, 1993, fig. 2a–c, e–g), and the phacopid *Acernaspis* (Chatterton & Campbell, 1993, fig. 1a,b), the exoskeleton fitted together to give a closed capsule. In some forms with a fulcrate thorax and spinose pleurae, however, the exoskeleton was not closed laterally at full enrollment,
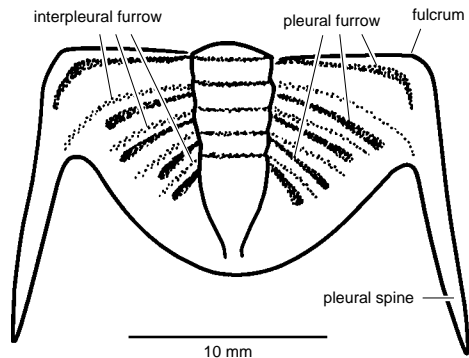

Fig. 59. *Proceratopyge* sp., Cambrian. Dorsal view of pygidium (adapted from Westergård, 1947, and Jago, 1987).
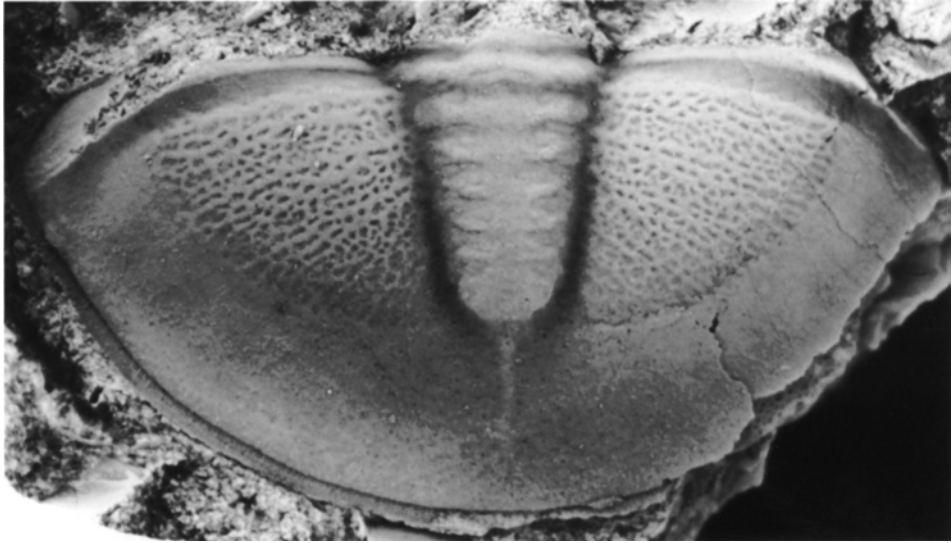
Fig. 60. *Raymondaspis reticulatus* Whittington, Ordovician, Newfoundland. Dorsal view of internal mold of pygidium, showing inter-ring furrows and lateral impressions from parietal surface of exoskeleton and caeca on pleural field, ×12 (Whittington, 1965, pl. 57, fig. 13).

the spines projecting around a lateral gap, as in *Remopleurides* (Nikolaisen, 1983, pl. 5; Chatterton & Campbell, 1993, fig. 4), *Selenopeltis* (Hammann & Rabano, 1987), and some cheirurids (Chatterton & Campbell, 1993, fig. 3a–c). The nonfulcrate exoskeleton is known only in Cambrian trilobites, and the amount of movement possible between sclerites suggests that complete enrollment may have been possible for some, if not all, species (Whittington, 1989, 1990). No close fit would have occurred in a completely enrolled paradoxidid, with its many thoracic segments, long pleural spines, and small pygidium, an example of which has long been known (Pompeckj, 1896, pl. 16, fig. 1). Bergström (1973a, p. 14, fig. 8b, pl. 1, fig. 6) used the term *cylindrical* for this type of enrollment with a lateral gap, exemplifying it by the Olenellina *Fallotaspis*. This term would apply to both fulcrate and nonfulcrate forms. Other terms purporting to characterize different types of enrollment (Harrington in Moore, 1959; Bergström, 1973a; Chatterton & Campbell, 1993) have been coined, but as Bergström remarked almost any number could be added.

The basic types he recognized are broadly drawn, and hence their use is limited. Bergström (1973a) employed the manner of enrollment as a character in high-level classification. Fortey and Owens (1979), however, made a strong case that the exact manner of enrollment may vary between species of one genus and was not a character to be considered fundamental in classification.

Coaptative structures are complementary morphological features that ensured close interlocking of opposing surfaces (i.e., **coaptation**) when enrollment was complete. Alignment of the cephalon and pygidium in such enrollment was facilitated by the straight hinge-line of fulcrate trilobites, together with the axial and fulcral processes and sockets (Fig. 38). The facet on the outer portion of the pleura fits closely beneath the edge of the next pleura in front, and a raised stop (the panderian protuberance) limits the amount of overlap (Fig. 40). Such devices are well known in post-Cambrian trilobites (Chatterton & Campbell, 1993) but were present in the Lower Cambrian *Crassifimbra* (Palmer, 1958), in Lower and Middle Cam-
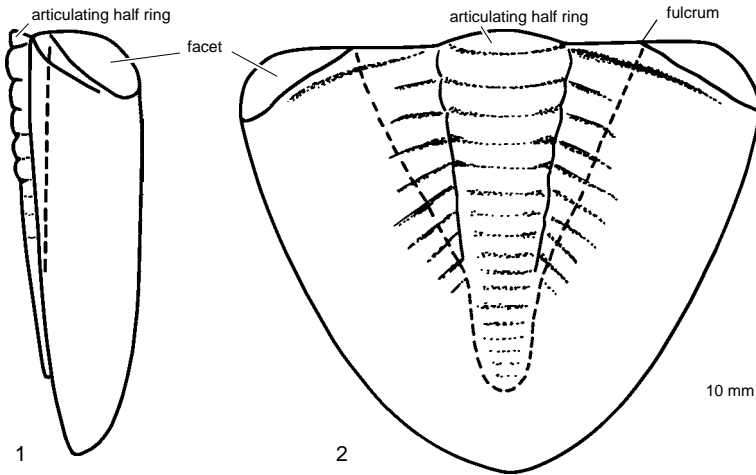
FIG. 61. *Pseudasaphus aciculatus* (ANGELIN), Ordovician, Sweden. *1,2,* Right lateral and dorsal views of pygidium, with *dashed line* showing position of inner edge of doublure (adapted from Jaanusson, 1953a, pl. 4, fig. 2, 4, 7).

brian ellipsocephalids (GEYER, 1990b, p. 55–58), in the Middle Cambrian *Bolaspidella* (ROBISON, 1964, pl. 89, fig. 8–10), and in Upper Cambrian species described by STITT (1983). In some of these Cambrian examples the width (tr.) and form of the segments and the outline of the pygidium enabled their extremities to fit closely against the inner edge of the rolled cephalic doublure; in others the posterior few thoracic segments and pygidium fitted beneath the cephalon (spiral enrollment). In the Upper Cambrian damesellinid *Stephanocare,* ÖPIK (1967) described vincular notches on the outer and ventral sides of the anterior and lateral cephalic borders. These notches received the tips of the pygidial and thoracic pleural spines on en-

rollment. In Agnostina the close fit of the enrolled exoskeleton is characteristic, the flat doublures of cephalon and pygidium being brought into contact and the tips of the thoracic pleurae being specially shaped to tuck in beneath the doublure of the posterior cephalic border (Fig. 48.3). HUNT (1967, pl. 22, fig. 47) illustrated a vincular notch in the posterolateral cephalic border, developed in the holaspis, into which a projection of the pygidial doublure fitted. ROBISON (in PEEL, 1988, p. 40) regarded the inflated postero-axis of *Oidalagnostus trispinifer* as a coaptative structure to accommodate the hypostome on enrollment. In eodiscoids (JELL, 1975a) the close fit of the completely enrolled exoskeleton is well known. RUSHTON
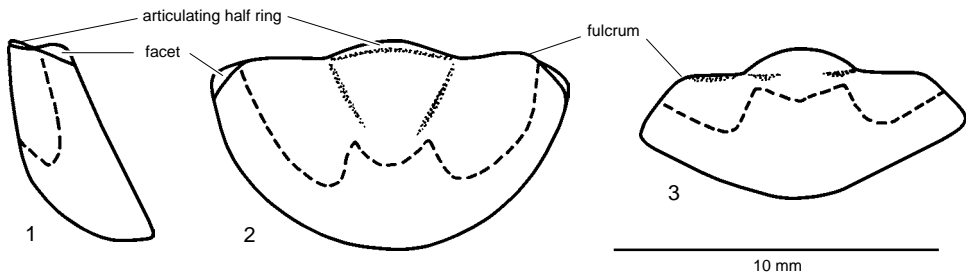

FIG. 62. Pygidium of *Illaenus tumidifrons* BILLINGS, Ordovician, Newfoundland. *1–3,* Pygidium, right lateral, dorsal, and posterior views, respectively, with *dashed line* showing position of inner edge of doublure (adapted from Whittington, 1965, pl. 15, fig. 12–13; pl. 16, fig. 14, 16).

(1966) showed that in *Serrodiscus* ventral spines on the pygidial doublure fitted beneath nodes on the cephalic border in a coaptative device and that in *Chelidiscus* the pygidial doublure fitted inside the rolled cephalic doublure in complete enrollment, the tip of the pleura of the first thoracic segment fitting beneath the posterior fixigenal cephalic spine.

In such post-Cambrian trilobites as trinucleids, coaptative structures are relatively simple, the slight projection of the pygidium behind the axis fitting into a shallow embayment in the inner edge of the lower lamella of the fringe (e.g., WHITTINGTON, 1959a, pl. 20, fig. 1, pl. 20, fig. 11). C. P. HUGHES, INGHAM, and ADDISON (1975, fig. 5) showed that there are also vincular notches on the flange of the lower lamella into which the tips of the thoracic pleurae fitted. Similar notches in the lateral or posterolateral portions of the cephalic doublure are known in such diverse trilobites as *Symphysurina* (ROSS, 1951b; HINTZE, 1953) and *Phacops* (CAMPBELL, 1967). Analogous are the ridge and groove in the cephalic doublure of some asaphids—*Kirkella* (ROSS, 1951b) and *Isotelus* (CHATTERTON & LUDVIGSEN, 1976)—although in the latter genus this structure engages with one in the doublure of the pygidium.

Coaptative devices in Ordovician and Silurian trilobites, including both lateral and median vincular structures, have been described in detail (CLARKSON & HENRY, 1973; HENRY & CLARKSON, 1975; HENRY, 1980a, 1985). Enrollment and coaptative structures in Devonian *Phacops* and *Greenops* have been compared and contrasted by SPEYER (1988). In the Ordovician dalmanitid *Crozonaspis* (Fig. 63), CLARKSON and HENRY (1973) described the lateral vincular groove in the cephalic doublure and the median anterior projection of the cephalic border, which upon complete enrollment fitted into a notch beneath the base of the posterior pygidial spine. They emphasized how constant are the vincular structures in a single species and showed how the median projection and

notch increased in size with time as the species evolved. In contrast to *Crozonaspis,* in the calymenoid *Colpocoryphe* (CLARKSON & HENRY, 1973; HAMMANN, 1985) a projection on the axis of the pygidium and a vincular furrow on the pleural region fit on enrollment into a deep anterior notch in the cephalon (Fig. 64). In *Flexicalymene* (ROSS, 1967; HAMMANN, 1985) the tip of the pygidial axis does not fit so closely into the anterior arch of the cephalon. By virtue of the sharp dorsal flexure of the inner portion of the cephalic doublure (including the doublure sector of the rostral plate), the posterior margin of the pygidium fitted against this cephalic doublure, the pygidial doublure coming to rest against the flat anterior border of the hypostome. A ridge along the posterior margin of the facet of each thoracic segment and a panderian projection and notch (HAMMANN, 1985, fig. 4e) also limited enrollment. Similar features are exhibited by the Silurian *Calymene* (CHATTERTON & CAMPBELL, 1993, fig. 2a–c, e–g).

In the Silurian *Encrinurus variolaris* (CLARKSON & HENRY, 1973; TRIPP, TEMPLE, & GASS, 1977) the pygidial and cephalic contours are identical so that the two fitted neatly when the animal was enrolled (Fig. 65.1–2). The contact surface between the two is twisted and changes in form from front to rear. Thus the pygidial doublure slopes ventrally towards its inner margin. In an enrolled specimen with the lateral part of the cephalon removed (Fig. 65.3–4), this pygidial doublure (since it is upside down) shows an outward and downward inclination, while in the thoracic doublures (which fit beneath the lateral cephalic border) the surface becomes increasingly concave and inwardly inclined. From the outer edge of the thoracic doublure arise small, flat pleural spines that fit in a groove on the cephalic doublure. The internal surfaces of these spines contacted a narrow vertical flange on the inner side of the cephalic doublural groove. The contact surface was thus twisted through some 90° from pygidial tip to genal angle, and coaptation was reinforced by the
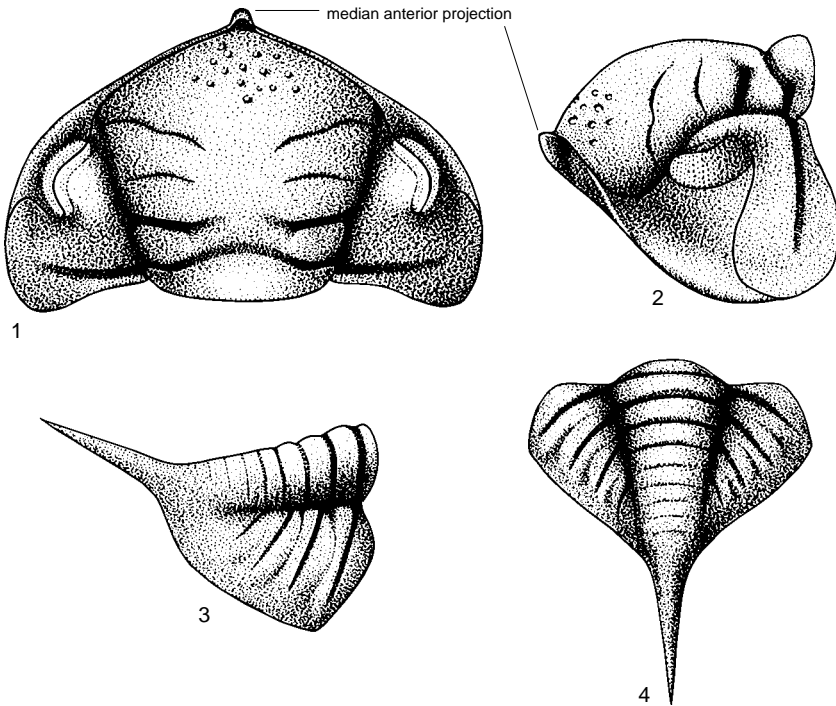
median anterior projection

1

2

3

4

FIG. 63. *Crozonaspis dujardini* (ROUAULT), Ordovician, Brittany. *1,2,* Dorsal and left lateral views of cephalon, ×3 (approximately); *3,4,* right lateral and dorsal views of pygidium, ×3 (approximately) (Clarkson & Henry, 1973, fig. 8).

small pleural spines interlocking with the cephalic groove. In *E. tuberculatus* (CLARKSON & HENRY, 1973; TRIPP, 1962) the arrangement was similar, but the pygidium was long and mucronate, and the tip and spine projected well beyond the cephalon. CLARKSON and HENRY claimed that a gap was left where the median posterior pygidial doublure was not in contact with the cephalon. They did not, however, draw attention to the prominent rhynchos on the hypostome, which must have fitted against the inner, posterior edge of the pygidial doublure. This doublure also had a median ventral projection, and it appears at least possible that these complementary projections closed the exoskeletal capsule anteriorly. The rhynchos was also prominent in *Calymene* (CAMPBELL, 1977), and upon complete enrollment the pygidial border and doublure must have fitted closely between the doublure sector of the rostral plate and the rhynchos (Fig. 34.2). The latter appears to have been a coaptative device in these groups. In the Devonian Homalonotinae *Digonus* and *Burmeisterella,* a forwardly and downwardly directed projection on the rostral plate was coaptative, fitting against the upturned inner edge of the posterior pygidial doublure on complete enrollment (WENNDORF, 1990, fig. 13).

The Devonian *Phacops* had a single, continuous vincular furrow on the cephalic doublure, extending almost all around but becoming crenulated to form vincular notches posterolaterally; similar structures are present in many phacopids (Fig. 66) (see also CHLUPÁČ, 1977; CAMPBELL, 1977; SPEYER, 1988). On enrollment, these structures interlocked with the pygidial margin as a tongue-and-groove coupling, the vincular notches receiving the imbricated pleural tips. The different forms of vincular furrows in
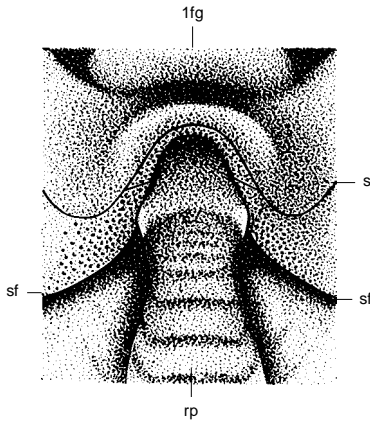
FIG. 64. *Colpocoryphe rouaulti* HENRY, Ordovician, Brittany. Anterior view showing how the axis of the pygidium fit into an anterior notch in the cephalon on complete enrollment, ×4 (approximately). Abbreviations: *1fg,* frontal lobe of glabella; *s,* facial suture; *sf,* vincular furrow of pygidium; *rp,* axis of pygidium (Clarkson & Henry, 1973, fig. 11).

phacopids and their significance in systematics were brought out by Zhiqiang ZHOU and CAMPBELL (1990) and LESPÉRANCE (1991); much new information is given by BRUTON and HAAS (1997). MILLER (1976) observed the microstructure of *Phacops rana* and noted that the vincular furrow lacked socket pits for tactile microtrichs. The pygidial margin, however, bore such pits as well as macrotrich canals, and these presumably relayed information to the central nervous system when enrollment was completed.

As mentioned above, in Ordovician dalmanitids such as *Crozonaspis,* the enrolled exoskeleton formed a closed capsule. While it may be that in some younger dalmanitoids the pygidial and cephalic doublures were everywhere in contact on enrollment, in some Silurian (Fig. 67) and Early Devonian (CAMPBELL, 1977) species this was not so. The outline of the pygidium was such that the posterior portion projected beyond the anterior border of the cephalon on enrollment and left an anterior gap in the enrolled capsule. This gap was subdivided by the median flexure in the cephalic doublure (as seen in anterior view) or partially covered by the frontal process or cephalic border spines.

A similar type of anterior opening in the enrolled capsule of species of the proetid *Gerastos* was described by ŠNAJDR (1980, p. 27).

Thus complete closure of the exoskeletal capsule on enrollment was characteristic of many different groups of trilobites, but within such groups some species may have had an anterior gap. A lateral gap, between the tips of the overlapping pleurae, appears to have been present in a species of *Remopleurides* (NIKOLAISEN, 1983, pl. 5), as well as coaptative devices—a projection of the cephalic doublure fitting between the posterior pair of pygidial spines. Whether there was a similar lateral gap in trilobites with outwardly directed pleural spines when enrolled is less certain. For example, in the odontopleurid *Ceratocephala* (BRUTON, 1968b, pl. 8, fig. 1–3) there were vertical as well as outwardly directed pleural spines. The vertical spines may well have overlapped on enrollment to give lateral closure. On the other hand, in *Selenopeltis* (HAMMANN & RABANO, 1987) the flanks of the animal were open when enrolled, protected by the long, outwardly projecting spines. FORTEY (1986) showed that when the nileid *Symphysurus* is closely enrolled with the aid of coaptative devices, the arrangement of terrace ridges on the overlapping pleurae is such that minute passages to the exterior are open. Thus the exoskeletal capsule is not completely closed to the exterior. The prevalence of such devices in apparently closed capsules remains to be explored (e.g., FORTEY & CHATTERTON, 1988, fig. 13).

The fossil record suggests that new types of coaptative structures arose abruptly. Once established, however, there may have been further and more gradual evolutionary development on a smaller scale, a kind of fine-tuning process leading to an apparent improvement of the coaptative mechanism as a whole. One such example (Fig. 68) showing an evident evolutionary trend is in the Lower Silurian phacopid *Acernaspis* from northern Europe. *A. elliptifrons* (Fig. 68.1), the earliest species, has nine, narrow vincular notches deeply indenting the flat surface of the
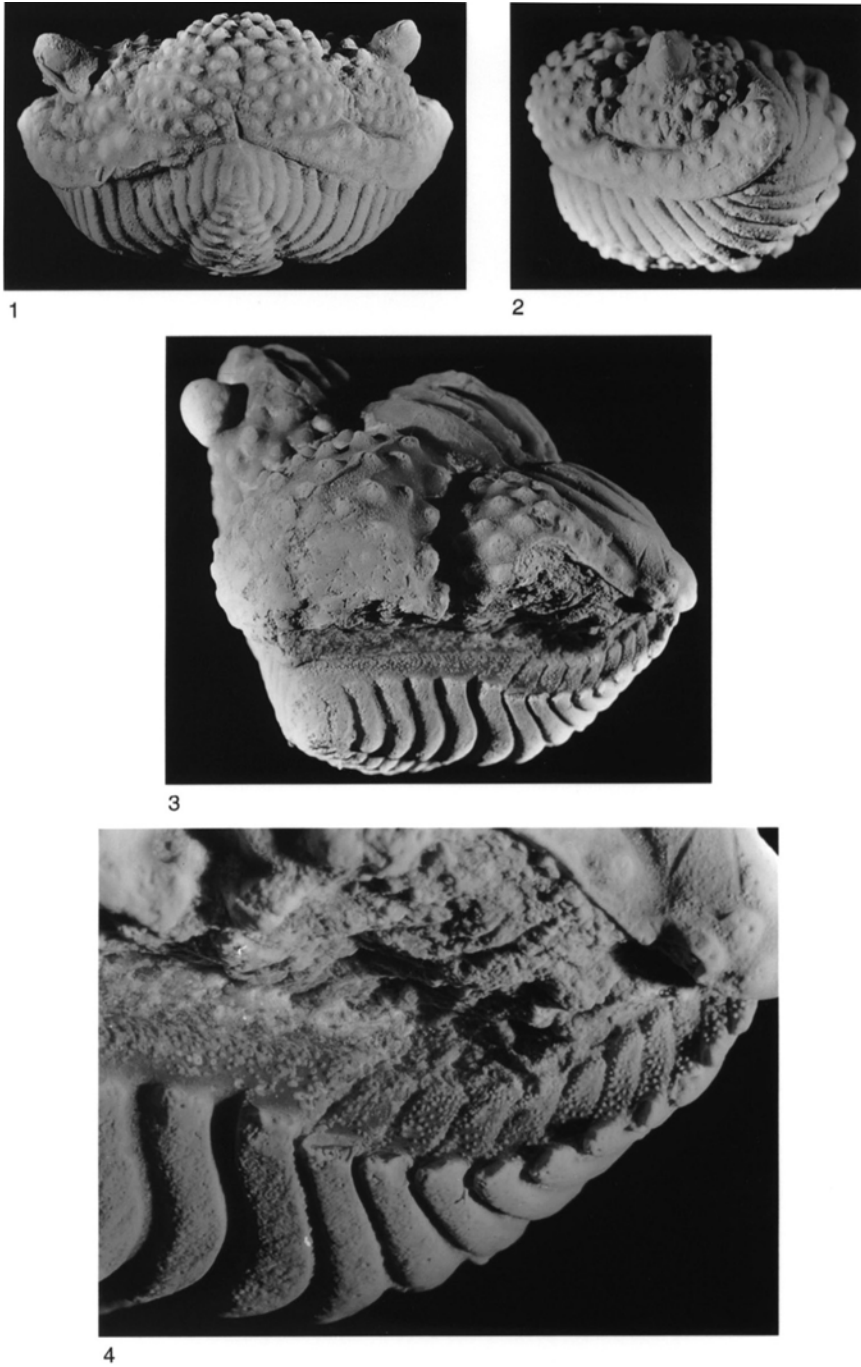
FIG. 65. *Encrinurus variolaris* (BRONGNIART), Wenlock, Silurian, England. *1,2,* Anterior and left lateral views of an enrolled specimen, ×4; *3,4,* anterolateral view of an enrolled specimen, the left librigena missing, exposing the doublure of pygidium and thorax; *3,* entire, ×3.5; *4,* detail of thoracic doublure, ×10 (Clarkson & Henry, 1973, fig. 13a,b, 14a,b).
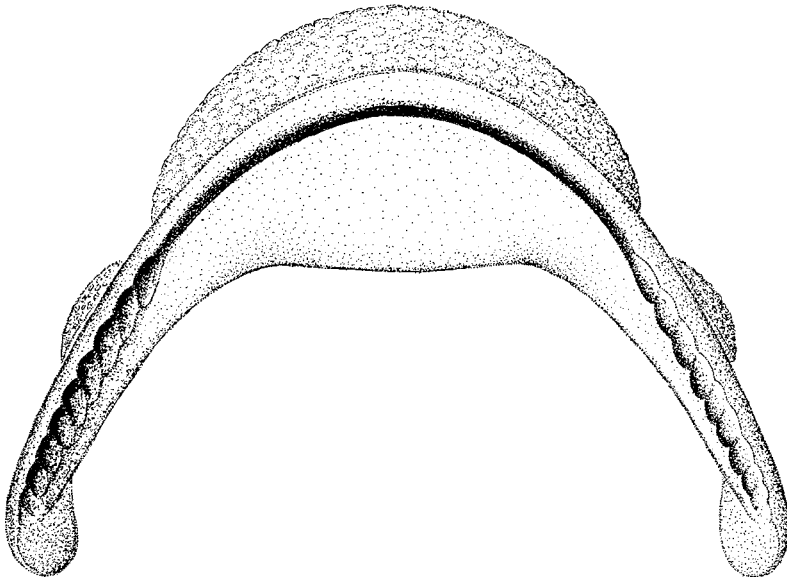
F𝐢ɢ. 66. *Paciphacops (Paciphacops) raymondi* (D𝐞ʟᴏ), Lower Devonian, Oklahoma. Ventral view of doublure of cephalon, showing vincular furrow and lateral vincular notches (adapted from Campbell, 1977, pl. 10).

cephalic doublure, the anteriormost notch running into a deep vincular furrow. Behind this the doublure forms a flat shelf. In Scotland, the later, successive species *A. (Eskaspis) woodburnensis* and *A. (E.) sufferta* show a progressive effacement of the vincular furrow (Fig. 68.2–3), but at the same time the vincular notches broaden and deepen posteriorly and become more obliquely set. Moreover, the two doublure ridges on either side of the vincular notches become oblique to each other as seen in lateral view. The coaptative anatomy of these three stratigraphically successive Scottish species shows a clear morphological trend, and a parallel development seems to have taken place in contemporaneous Estonian species also (C𝐥ᴀʀᴋsᴏɴ, E𝐥ᴅʀᴇᴅɢᴇ, & H𝐞ɴʀʏ, 1977).

A second case is illustrated by the Ordovician genus *Placoparia*. The outer and ventral border of the librigena bears depressions into which the distal ends of the posterior thoracic pleurae and the tip of the first pygidial spine fits during enrollment. The coaptative surfaces follow a sinuous course (H𝐞ɴʀʏ, 1985). In the three successive species, *P. (Coplacoparia) cambriensis, P. (C.) tourne-* *mini,* and *P. (C.) borni,* which form a stratigraphical series in the Llanvirn and Llandeilo of the Massif Armoricain, France, additional depressions appear on the anterior cephalic border (Fig. 69). These receive the tips of the posterior pygidial spines during enrollment and become increasingly pronounced through time. Contemporaneous species of *Placoparia* in Bohemia, however, show no such modification of the anterior cephalic border, and the two species groups presumably evolved in isolation (H𝐞ɴʀʏ & C𝐥ᴀʀᴋsᴏɴ, 1975; H𝐞ɴʀʏ, 1985).

MICROSTRUCTURE AND SCULPTURE OF THE EXOSKELETAL CUTICLE

H. B. W𝐇𝐢𝐭𝐭𝐢ɴɢᴛᴏɴ and N. V. W𝐢ʟᴍᴏᴛ

Studies of the cuticle since 1960 have used the scanning electron microscope, etching, and other techniques to supplement optical examinations of thin sections. Because well-preserved material in limestone is available, attention has concentrated on the Devonian *Phacops,* Ordovician species including
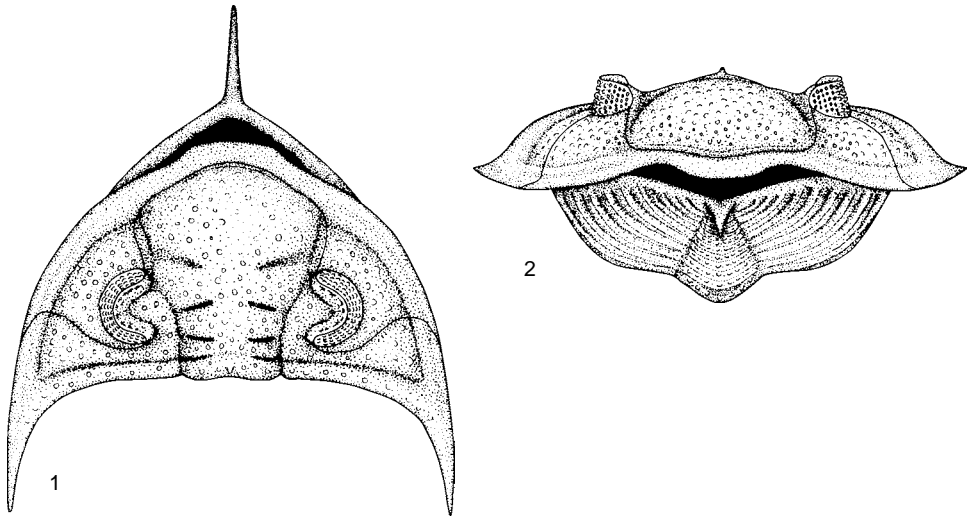
FIG. 67. *Glyptambon verrucosus* (HALL), Wenlock, Indiana, USA. *1,2,* Dorsal and anterior views of a completely enrolled individual, showing gap between cephalon and pygidium (Holloway, 1981, fig. 1).

Asaphus, and recently (DALINGWATER & others, 1993b) Silurian calymenids. The cuticular structure of the Middle Cambrian *Ellipsocephalus* has also been studied (DALINGWATER & others, 1991); otherwise few Cambrian specimens have been commented on. Uncertainties in understanding the effects of diagenesis and contradictory interpretations of what is seen in thin section show the importance of investigating primary and diagenetic microstructures (MCALLISTER & BRAND, 1989; WILMOT, 1990b). The cuticles of Lower Ordovician trilobites (FORTEY & WILMOT, 1991) show a range of thicknesses from 8 to 350 μm, 70 to 100 μm being an average range, with considerable variation in thickness shown by single species. In Devonian phacopids OSMÓLSKA (1975) has recorded a range of thicknesses from 120 to 500 μm, some proetids having a thinner cuticle, 10 to 60 μm thick; MILLER (1976) recorded cuticle as thick as 1 mm. FORTEY and WILMOT (1991) measured cuticle thickness in a sample of species across an onshore to offshore gradient, noting that greater thicknesses characterized inshore sites. Thickness does not appear to be related to size, some large species having a thin cuticle. It has been stated that the cuticle con-

tained significant amounts of phosphate, and the outer layer in *Ellipsocephalus* appears to be composed of calcium phosphate (DALINGWATER & others, 1991). The data of WILMOT and FALLICK (1989) suggest that the exoskeleton originally had a low-magnesium calcite mineralogy. Other recent work (DALINGWATER, 1973; TEIGLER & TOWE, 1975; OSMÓLSKA, 1975) has shown that the calcite crystals have a preferred orientation of the *c* axis more or less at right angles to the surface. Decalcification of the cuticle (TEIGLER & TOWE, 1975, p. 139, pl. 5; DALINGWATER & MILLER, 1977, p. 29) leaves a delicate residue, the remains of the organic framework of the cuticle. Distinct layers (Fig. 70.1) have been recognized in the cuticle (STØRMER, 1930), and DALINGWATER (1973) considered that there is a thin, outer, prismatic layer (Fig. 70.2) one-tenth to one-thirtieth of the total thickness that overlies a principal layer. WILMOT (1990a) has shown that in some Agnostina the cuticle is only 5 to 15 μm thick and constructed like the prismatic layer.

Whether lamination is present, as seen in cross sections of modern arthropod cuticle, has been argued. A study by MUTVEI (1981) of the cuticle of a calymenid (probably
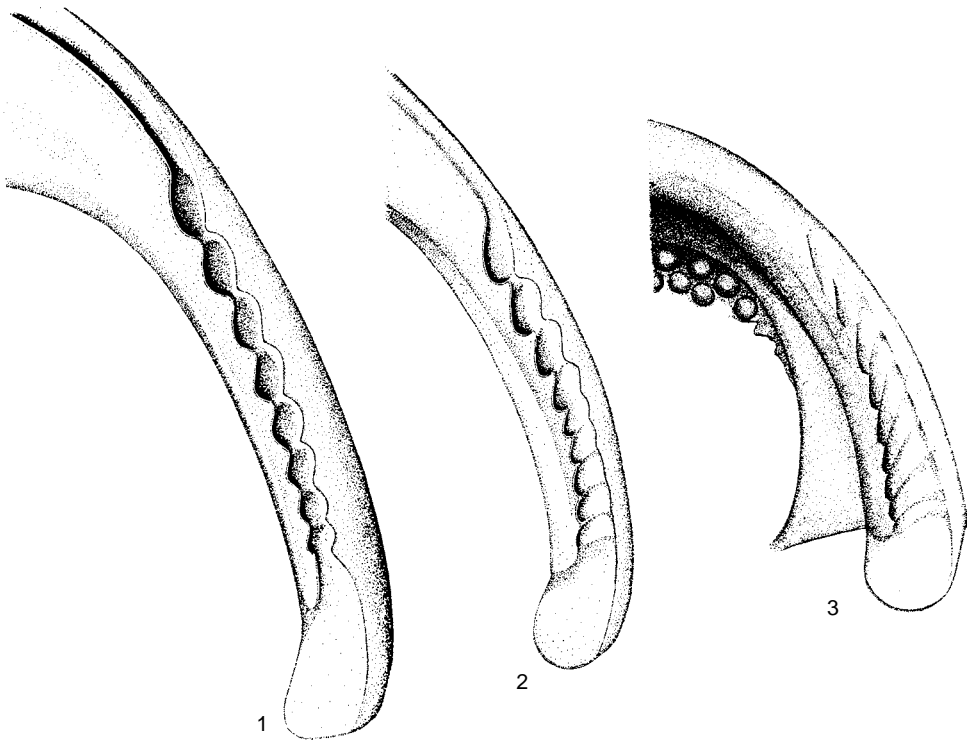
FIG. 68. Left lateral portion of the doublure of the phacopinid *Acernaspis,* showing vincular structures. *1, A. (A.) elliptifrons* (ESMARK), Llandovery, Scotland; *2, A. (Eskaspis) woodburnensis* CLARKSON, ELDREDGE, & HENRY, Llandovery, Scotland; *3, A. (E.) sufferta* (LAMONT), Llandovery, Scotland; all ×14 (Clarkson, Eldredge, & Henry, 1977, fig. 3).

Thelecalymene, see WHITTINGTON, 1971) showed an outer layer that is one-fifth in thickness of the total and horizontally laminated (compare Fig. 70.3). DALINGWATER and MILLER (1977) investigated the cuticle of *Asaphus raniceps* after breaking and etching it with EDTA (disodium salt); they distinguished three zones in the principal layer—an outer and an inner, finely laminated zone separating a much thicker, widely-laminated central zone. Using the same methods, MILLER (1976) and MILLER and CLARKSON (1980) distinguished the same zones in the principal layer of the cuticle of *Phacops rana.* The cuticle of *Ellipsocephalus* (DALINGWATER & others, 1991) appears to have a very thin outermost epicuticle, an outer laminated layer, and a principal layer. In *Tapinocalymene* (DALINGWATER & others, 1993b) the

outermost layer was less than 1 μm thick; the outer layer was finely laminated, 10 to 35 μm thick; the finely foliated principal layer was 200 to 400 μm thick; and there was a very thin (about 1 μm) innermost layer. These same authors (DALINGWATER & others, 1993a) concluded that the mineralization mechanism of trilobites was similar to that of living decapod crustaceans, in contrast to TEIGLER and TOWE (1975), who compared trilobite cuticle with that of ostracodes (cf. TOWE, 1978).

The cuticle may be pierced by canals perpendicular to the surface (Fig. 70.4–5); larger diameter canals have long been recognized in thin section or in exceptionally preserved material. In silicified specimens (EVITT & WHITTINGTON, 1953, pl. 9, fig. 12–19), where the inner and outer surfaces

of the exoskeleton are each represented by a thin layer, these canals may be preserved as hollow pillars connecting the two layers. Such structures and pyrite fillings of canals seen in thin section (HAMMANN, 1983, pl. 25) show that these canals passed through the entire thickness of the exoskeleton. These canals are considered to have been integumental glands or setal ducts (CAMPBELL, 1977, p. 41–42; HAAS, 1981), and their concentration around the margins of the exoskeleton is characteristic. Very numerous, narrow canals (about 1 μm in diameter) occur in all regions of the cuticle studied (Fig. 70.6) and were considered by DALINGWATER and MILLER (1977) to be similar to the pore canals in living arthropod cuticle. These authors considered that the term pore canal should be restricted to such narrow canals and not applied to canals of wider diameter, as TEIGLER and TOWE (1975) advocated. OSMÓLSKA (1975, p. 203) drew attention to small, shallow pits (12 to 15 μm in diameter) distributed more or less evenly over the surface of the phacopid exoskeleton. MILLER (1976, p. 349) observed similar pits in *Phacops,* judging them to be artifacts produced by tangential sectioning of pits that led into ducts. STØRMER (1980, p. 256–259) termed these pits "Osmólska cavities" and thought that they were infilled cavities lying immediately below the outer prismatic layer of the cuticle. New studies (WILMOT, 1990b) show that these cavities lie within the prismatic layer and appear to be connected to fine, vertical canals through the exoskeleton (Fig. 71.1–2). Similar cavities in the outer layer of *Ellipsocephalus* (DALINGWATER & others, 1991) are connected to canals, 3 μm in diameter, in the principal layer that extend to the inner surface of the cuticle.

The outer surface of the exoskeleton is smooth in the troughs of furrows, in pits, and in the areas of the axial region regarded as areas of muscle attachment. Elsewhere the surface may be sculptured in pustules of varied size and distribution, pitted, or covered by raised symmetrical or asymmetrical ridges arranged in various ways. Such surface sculp-
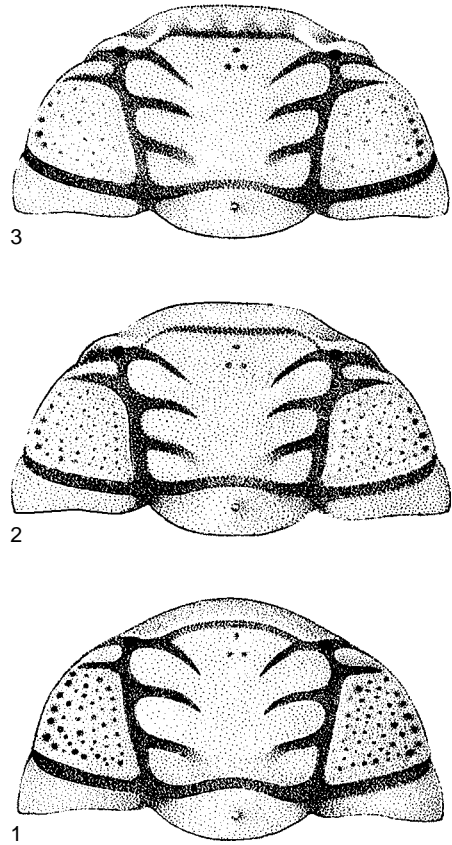

FIG. 69. Dorsal views of cranidia of *Placoparia* from the Ordovician of Brittany. *1, P. (Coplacoparia) cambriensis* HICKS, ×6; *2, P. (C.) tournemini* (ROUAULT), ×5; *3, P. (C.) borni* HAMMANN, ×4.5 (Henry & Clarkson, 1975, fig. 3).

ture is frequently referred to as *ornament,* but as GILL (1949) argued in proposing to call it *prosopon*, ornament is a general word that gives an erroneous impression of mere decoration, whereas surface **sculpture** has biological significance. The sculpture (or prosopon) embraces small features, not large genal, pleural, or axial spines that are hollow extensions of the entire cuticle. MILLER (1976) showed that tubercles, prominences on the external surface, were of different types when seen in cross sections of the cuticle: a **dome** (Fig. 71.3) when the cuticle bulged upward and thinned at the apex of the bulge, a structure that projected from the surface and had
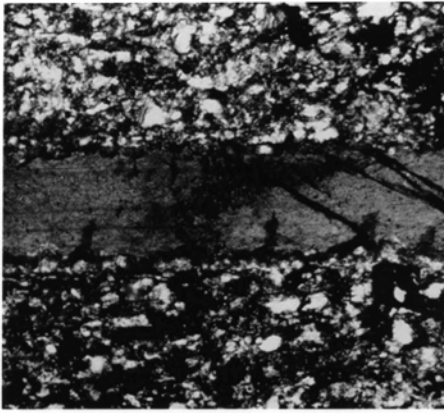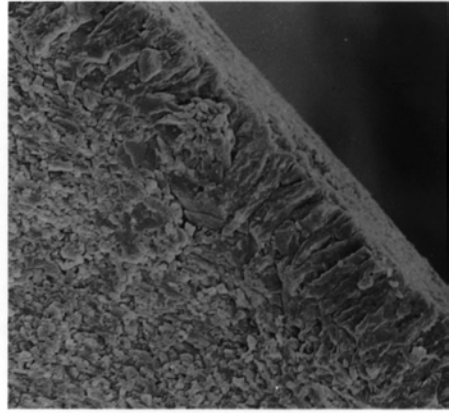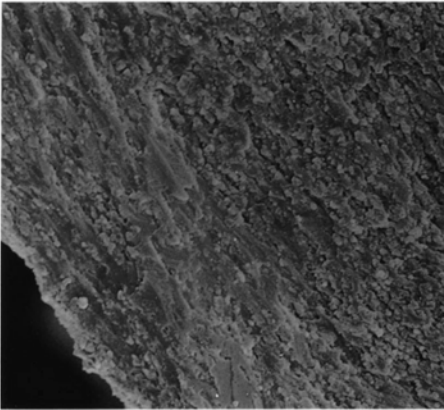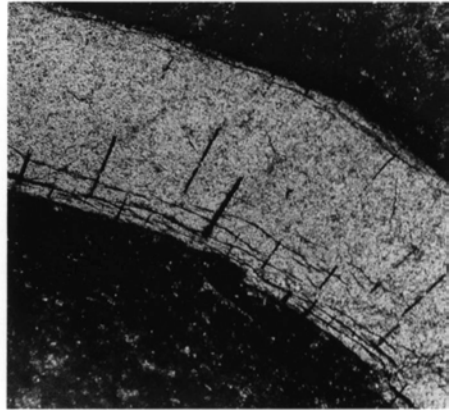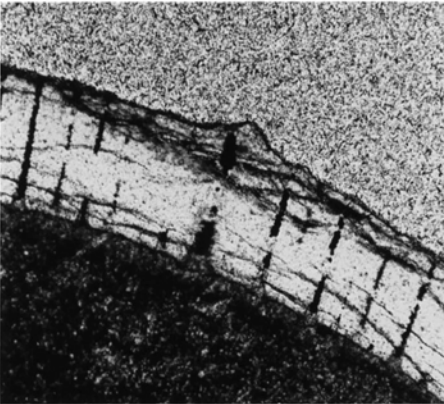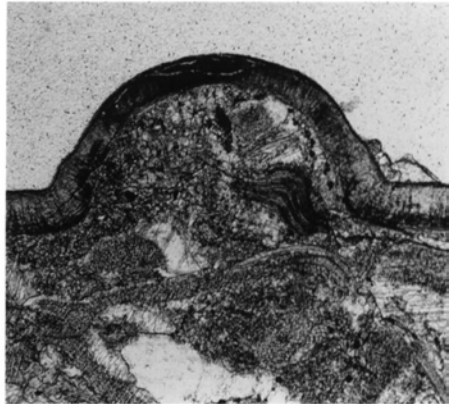
FIG. 70. Thin sections of trilobite cuticle. *1, Asaphus* sp., Asaphus Limestone, Norway, Ordovician, NMW 88.22G.16. Stained thin section revealing primary horizontal laminations within the principal layer. Large borings (30 μm diameter) are present on the visceral surface (the lower in the photograph) of the exoskeleton. The irregular external surface indicates dissolution of the cuticle, ×40 (Wilmot, 1990b, fig. 1c). *2, Phacops rana crassituberculata* STUMM, Silica Shale, Silica, Ohio, Middle Devonian, NMW 88.22G.41. SEM of prismatic layer with calcite crys- *(Continued on facing page.)*

an apical pore (Fig. 71.4), or a more complex projection that he termed a *pseudotubercle* (Fig. 71.5). STØRMER's (1980) investigation of phacopoid tubercles and their internal structures showed a range of types from smooth tubercles with no central opening, to domed and spiniform tubercles that had a central canal, to large composite tubercles or *pseudotubercles.* His illustrations include not only cross sections but the external surface and mold of the internal surface of the exoskeleton as well as diagrams of his interpretations of the effects of incomplete preservation and abrasion on the appearance of these features. Granulation is not invariably confined to the outer surface of the exoskeleton but has been recorded on the inner surface in illaenids (WHITTINGTON, 1965, pl. 46, fig. 19, pl. 51, fig. 11; OWEN & BRUTON, 1980, pl. 4, fig. 2, 6).

Studies of silicified specimens, including growth stages, have shown that thornlike pustules, spines rather than tubercles, may be prominent in meraspid growth stages but reduced later (WHITTINGTON, 1941, 1956b; CHATTERTON, 1980; WHITTINGTON & EVITT, 1954). Such spines may be in pairs along the axial region, reflecting segmentation, and in odontopleurids pairs of spines on the pleural regions form rows with axial pairs and may be recognizable in holaspid stages. In encrinurids paired spines or tubercles in rows on the glabella and on the fixigena are similarly recognizable during ontogeny (EVITT & TRIPP, 1977). Openings at the tips of such spines or tubercles have been described, particularly in those along the border or the distal portion of an occipital, genal, or pleural spine (WHITTINGTON & EVITT, 1954). The opening may be single or multiple (Fig. 72.1), or in encrinurids (EVITT & TRIPP, 1977, p. 118) may lie between the granules at the tips of axial and pleural spines.

A median occipital spine or tubercle occurs on many trilobites, and in certain odontopleurids (Fig. 72.2) and styginids (WHITTINGTON, 1965, p. 297) such a tubercle has been shown to bear at the summit four tiny pits arranged in a square. A median glabellar tubercle in front of the occipital ring is present in asaphids, nileids, and illaenids (FORTEY & CLARKSON, 1976). In asaphids the structure appears to be a dome, whereas in nileids and illaenids only a depression in the inner surface of the exoskeleton is visible (as a low mound in the mold of that surface) and is an area over which the exoskeleton is thinned. In the median occipital node of *Proetus,* the cuticle thins at the apex so that only the prismatic layer remains, whereas in *Harpidella* there is a central canal (WILMOT, 1991). In the cyclopygids *Pricyclopyge* and *Symphysops* (MAREK, 1961; FORTEY & OWENS, 1987, p. 180) a pair of structures appears that on molds are either domes or pits with a raised rim and are considered to have been formed within the cuticle.

Raised ridges are another type of sculpture, the asymmetrical **terrace ridges** (Fig. 73–74) being characteristic of the outer portions of the pleural region, the border and doublure, and the hypostome. The steep slope of the ridge faces abaxially, and the ridges are strongest, long and continuous, occasionally anastomosing, on the border and doublure, running subparallel to the margin. On the dorsal side, inside the

Fig. 70. *Explanation continued from facing page.*

tals (1 × 10 µm) oriented with their c-axes perpendicular to the surface, ×1000 (Wilmot, 1990b, fig. 1a). *3, Phacops rana crassituberculata* STUMM, Silica Shale, Silica, Ohio, Middle Devonian, NE4.C, NMW 88.22G. SEM of the principal layer with calcite crystals aligned parallel to the surface, ×1000 (courtesy of N. V. Wilmot). *4, Calymene* sp., Mulde Beds, Gotland, Silurian (Wenlock), NMW 88.22G.12. Thin section through the pygidium, the canals infilled by micrite, ×30 (Wilmot, 1990b, fig. 1f). *5, Calymene* sp., Mulde Beds, Gotland, Silurian (Wenlock), NMW 88.22G.11. Thin section through the cranidium, revealing canals infilled by pyrite, ×30 (Wilmot, 1990b, fig. 1d). *6, Proetus (Proetus) concinnus* (DALMAN), Silurian (Wenlock), PRO 12, NMW 88.22G, locality 64 of THOMAS (1978). Transverse section through pygidium revealing numerous fine canals (1µm diameter), ×30 (courtesy of N. V. Wilmot).
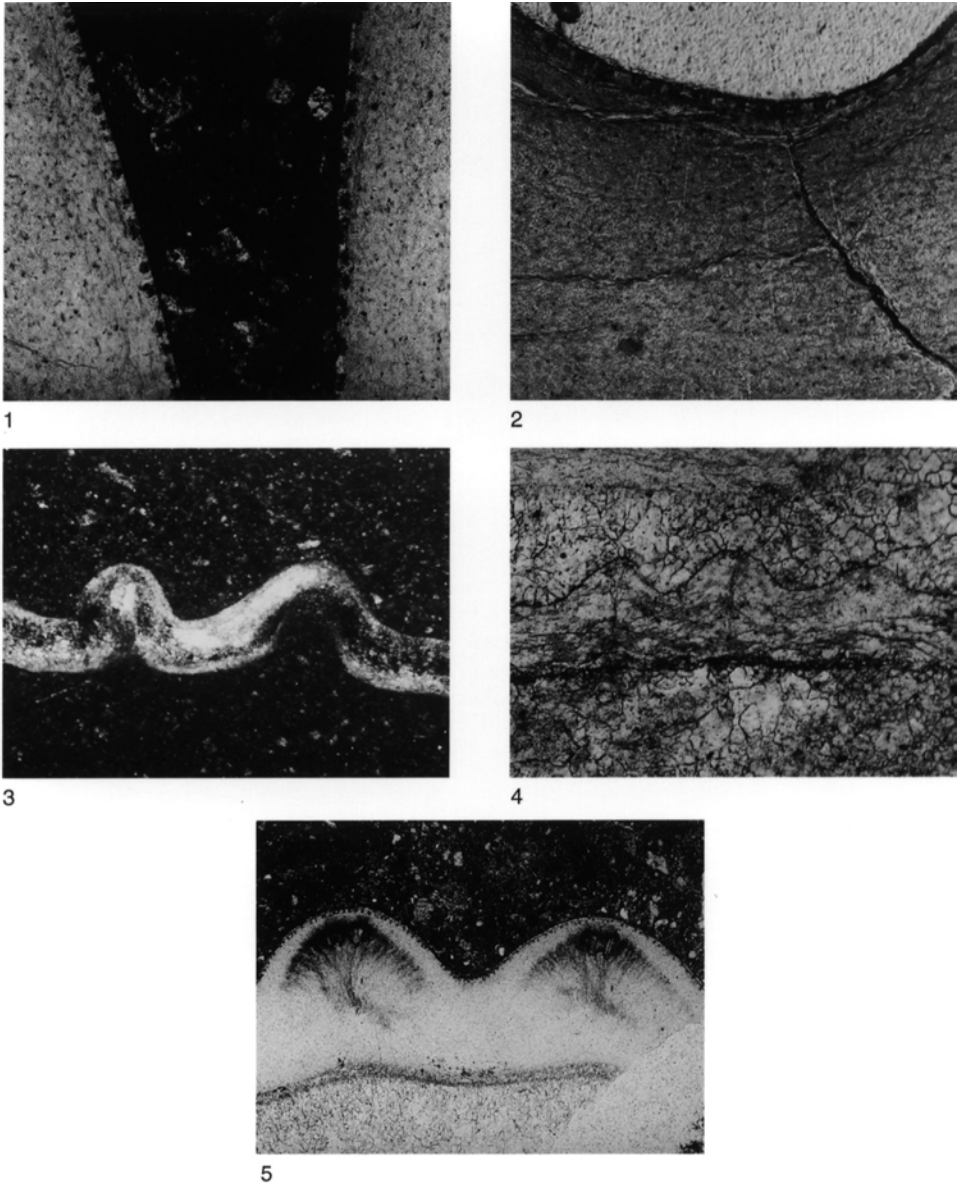
FIG. 71. Thin sections of trilobite cuticle. *1, Phacops rana crassituberculata* STUMM, Silica Shale, Silica, Ohio, Middle Devonian, NMW 88.22G.6. Longitudinal section through thoracic segments, showing Osmólska cavities within the prismatic layer, ×100 (Wilmot, 1990b, fig. 5c). *2, Phacops rana crassituberculata* STUMM, Silica Shale, Silica, Ohio, Middle Devonian, NMW 88.22G.8. Transverse section through the cephalon, showing Osmólska cavities within the prismatic layer connected to fine canals within the principal layer, ×50 (Wilmot, 1990b, fig. 5b). *3, Hemiarges bucklandii* (MILNE EDWARDS), Much Wenlock Limestone Formation, Wren's Nest, Dudley, Silurian (Wenlock), D33.3, NMW 88.22G. Longitudinal section through domes in the cranidium, ×40 (courtesy of N. V. Wilmot). *4, Cyphoproetus depressus* (BARRANDE), Dolyhir and Nash Scar Limestone Formation, near Dolyhir Bridge S0 2403 5825, Silurian (Wenlock), NW10.1, NMW 88.22G. Stained thin section through a cranidium containing tubercles with central canals, ×50 (courtesy of N. V. Wilmot). *5, Phacops granulatus* (MÜNSTER), Poland, Devonian, P.M.O A38817.1. Thin section through pseudotubercles, which contain internal tubules and show Osmólska cavities in the outer, prismatic layer, ×30 (Størmer, 1980, pl. 30, fig. 1a).
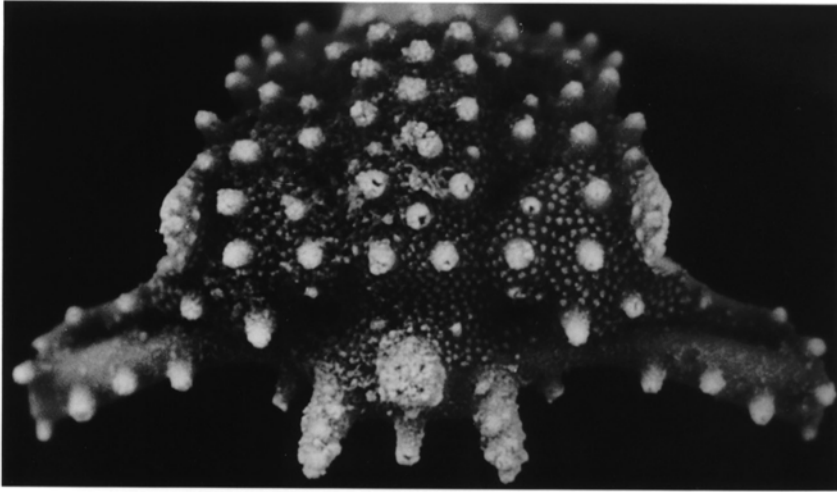
FIG. 72. *1, Diacanthaspis secretus* WHITTINGTON, Ordovician, Virginia. Basal portion of left librigenal spine bearing small spines that have single or multiple openings at the tip, ×60 (Whittington, 1956d, pl. 7, fig. 13). *2, Diacanthaspis ulrichi* WHITTINGTON, Ordovician, Virginia. Dorsal view of cranidium, showing spinose sculpture, opening at tip of spines, and four depressions at tip of median occipital spine, ×45 (Whittington, 1956d, pl. 8, fig. 30).

border, the ridges may curve to run obliquely and curve across the axial region. Such ridges are characteristic of the doublure of trilobites from a wide range of taxa and ages. Examples may be found among Cambrian trilobites (WHITTINGTON, 1988a, 1989), and younger groups including asaphids, nileids, remopleuridids (WHITTINGTON, 1965; CHATTERTON & LUDVIGSEN, 1976); illaenids (WHITTINGTON, 1965; OWEN & BRUTON, 1980); styginids (ŠNAJDR, 1960); and proetids (ŠNAJDR, 1980). As MILLER (1975) pointed out, such terrace ridges are not universally present, being seemingly unknown in Agnostida, calymenids (CAMPBELL, 1967), cheirurids (CHATTERTON & PERRY, 1984), and encrinurids (EVITT & TRIPP, 1977). Although present on the doublure of phacopids (CAMPBELL, 1967), these terrace ridges do not appear to characterize the dalmanitid doublure (HOLLOWAY, 1981; RAMSKÖLD, 1985). Using cross sections and SEM micro-
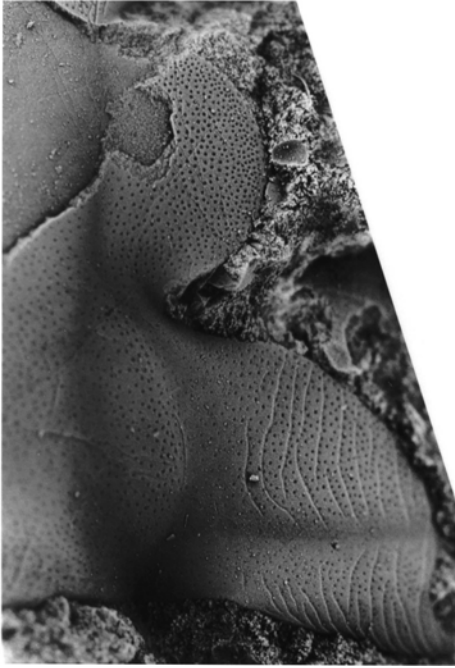
FIG. 73. *Niobe quadraticaudata* (BILLINGS), Ordovician, Newfoundland. Posterolateral portion of cranidium, showing sculpture of terrace ridges on fixigena, pits in palpebral lobe and baccula (the swelling on the adaxial portion of the fixigena, adjacent to the axial furrow), ×30 (Whittington, 1965, pl. 24, fig. 7).

graphs, MILLER (1975) described terrace ridges in several genera, showing the varied profile of the ridges and their association with scattered pits in the outer surface of the cuticle. He claimed that the outer, prismatic layer of the cuticle is absent from the steep, scarp slope of the ridge and that canals, curving through the cuticle, open in a small pit on the scarp. The former claim may not be correct, and neither OSMÓLSKA (1975, p. 204) nor STØRMER (1980, p. 256) considered that canals are present in association with terrace ridges.

Another type of ridge, symmetrical in profile, is the **lira,** known on the dorsal surface of the cuticle of both axial and pleural regions in bathyurids, proetids, and remopleuridids (NIKOLAISEN, 1983), for example. These lirae may form a fingerprint-like pattern on the glabella and axial rings (the so-called Bertillon pattern), but as NIKOLAISEN pointed out their arrangement varies. Similar ridges in the axial region of *Peraspis* (Fig. 75) appear to be continuous with the peripheral terrace ridges, so that the two types of ridges may be transitional. BRUTON (1976) provided many illustrations of these ridges in *Phillipsinella* and of their intimate association with granules and pits. It appears that rows of granules are transitional with the ridges, and MILLER (1975) pointed out that in some styginid and homalonotid genera terrace ridges may form an anastomosing, netlike pattern. A prominent, reticulate pattern of raised, symmetrical ridges has long been recognized in some Olenellina (WHITTINGTON, 1989). In describing a species of *Wanneria,* PALMER (1964) noted that perforations on the inner surface of the exoskeleton outlined the polygons and that the exoskeleton broke along the margins of these polygons, showing that the perforations extended partway through the exoskeleton; no comparable arrangement of perforations has been described in any other trilobite. A prominent, reticulate pattern of raised ridges is known in such other trilobites as *Cryptolithus* (Fig. 76), *Galbagnostus* (Fig. 10), and *Telephina* (WHITTINGTON, 1965). MILLER (1976, fig. 2o) has claimed that there are rows of canals opening into pits along the ridge crests in *Tretaspis.* Much smaller in size (polygons 15 μm or less across) is the polygonal pattern of furrows seen on the external surface of extant arthropod cuticles (MILLER, 1976, p. 346), which appear to be a surface expression of the epidermal cells that secreted the cuticle. A reticulate pattern of raised ridges on the external surface of some Agnostina (MÜLLER & WALOSSEK, 1987, pl. 7–8; WILMOT, 1990a, 1990b) is of similar dimensions and may also result from polygonal cells. The cell polygons in proetids (WILMOT, 1991) are small, 5 μm in diameter. An extraordinary sculpture is the raised, wall-like ridges of the solenopleurid *Badelusia* (SDZUY, 1968), which in one species are extended into spines.
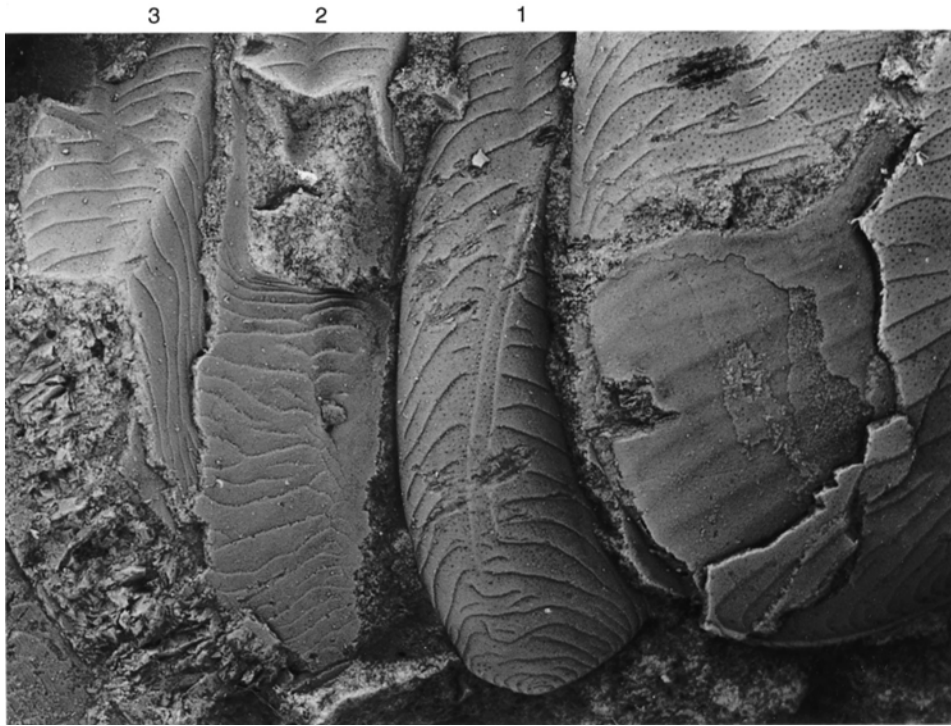
Fig. 74. *Niobe quadraticaudata* (Billings), Ordovician, Newfoundland. Right posterolateral portion of librigena and outer portion of thoracic segments 1 to 3. Terrace ridges visible on external surface of segments 1 and 3 and on mold of doublure of segment 2, ×9 (Whittington, 1965, pl. 24, fig. 6).

A raised sculpture of pustules or ridges may occur in combination with pits (scattered depressions in the external surface of the cuticle), as in *Niobe* (Fig. 73), *Poronileus* (Fortey, 1975b), *Nanillaenus* (Chatterton & Ludvigsen, 1976), and *Asteropyge* (Morzadec, 1983, pl. 18). These pits are tiny and may be depressions rather than the openings of canals through the cuticle. Larger, deeper pits, as in the librigena of *Encrinuroides* (Chatterton & Ludvigsen, 1976, pl. 15, fig. 11–12; Evitt & Tripp, 1977, pl. 10, fig. 1) appear to correspond to low projections on the inner surface of the cuticle. Such pits may be the opposite of domes, being depressions in which the cuticle thins at the base.

The nature and complexity of the sculpture of the exoskeleton and the variations and transitions from one type to another are shown by the references quoted. Silicified material and photographs of details of well-preserved specimens from limestone (Bruton, 1976; Šnajdr, 1980, pl. 61–64; Nikolaisen, 1983; Wilmot, 1991) afford the best examples. While a particular type of sculpture may be widespread within a family or larger taxon, it may be neither exclusive to that taxon or universal within it. Thus while spines and tubercles are characteristic of odontopleurid sculpture, they may be absent in some species. The reticulate pattern of raised lines characteristic of some Olenellina is known in unrelated taxa, whereas both granulation and a Bertillon pattern of raised lines are known on the external surface of other Olenellina.

The microstructure and sculpture of the exoskeleton, together with the form (or architecture), enabled it to accommodate the
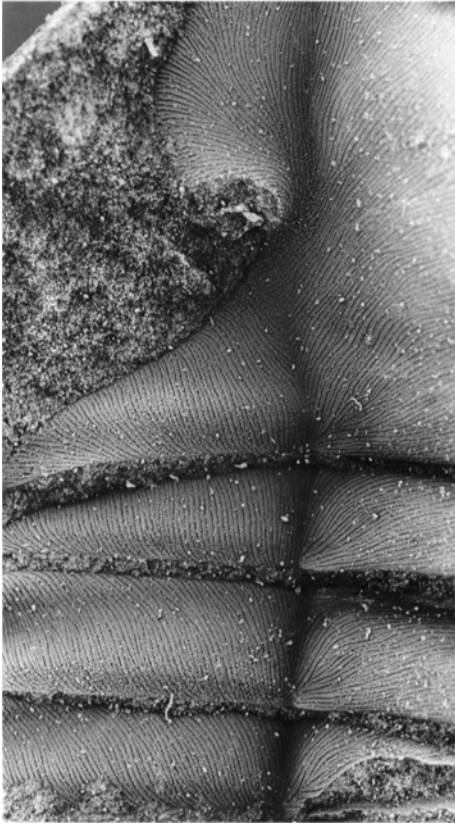
FIG. 75. *Peraspis lineolata* (RAYMOND), Ordovician, Newfoundland. Left portion of cranidium and thoracic segments 1 to 3, to show sculpture of external surface, ×22 (Whittington, 1965, pl. 36, fig. 12).

forces acting on it. These forces may have been external, the result of environmental perturbation or predators, or internal, being the site of attachment of muscles. A pioneer study of biomechanics of trilobite exoskeletons (WILMOT, 1990c) suggested that the cuticle behaved as a ceramic, in a linearly elastic manner. The exoskeleton was analogous to a monocoque shell, thin yet strong, which behaved as a stressed skin. Sculpture has been shown to be related to canals through the exoskeleton, to presumed sensory devices, and perhaps to the need to maintain aeration within the enrolled trilobite. It may have contributed to the strength of the exoskeleton, and a novel suggestion by

CHATTERTON (1980, p. 6) is that granules and tubercles would have reduced the efficacy of sucker disks in obtaining a grip and so protected trilobites from predators relying on such disks.

SUPPOSED COLOR MARKINGS

H. B. WHITTINGTON

Color markings of the exoskeleton have been described as faint, light and dark gray bands crossing the pygidium of a Cambrian trilobite (RAYMOND, 1922), as dark patches outside the eye lobe, on the genal spine, and in the axial and pleural furrows of an Upper Ordovician *Isotelus* (WELLS, 1942), and as symmetrical, dark patches on the axial rings of a Carboniferous proetid (WILLIAMS, 1930). Similarly arranged dark patches on the pygidial axis of Carboniferous species were described by WHITTINGTON (1954a), HESSLER (1965, fig. 1), and PABIAN and FAGERSTROM (1972, pl. 1, fig. 12, 15) as muscle scars. They appear darker when photographed, but whether this is because of traces of original color or because the exoskeleton is of a different thickness over this area is uncertain. TEICHERT (1944, p. 458) described tiny spots scattered over the axial and pleural regions of a pygidium of a Permian proetid, and similar spots were portrayed by HESSLER (1965, fig. 1). Whether such spots are the remains of a color pattern, as TEICHERT claimed, is open to question. A remarkable example of a Silurian phacopid showing darker areas of the exoskeleton was described by CAMPBELL (1976, fig. 1, pl. A). The prominent, larger, symmetrical areas in the axial furrows and region are most probably areas of muscle attachment, as may be some of the smaller spots in the pleural region. CAMPBELL described the specimen as abraded and having associated pyrite and remarked that the tiny spots are not associated with exoskeletal sculpture, but he did not discuss the possibility that some of the small spots in the pleural region may be traces of a color pattern. Supposed color

markings in the exoskeleton of the Devonian *Phacops* and *Greenops* were described by Es-KER (1968) and examined in greater detail by BABCOCK (1982). The latter author considered that the original coloration in these two species, *P. rana* and *G. boothi,* consisted of irregular dark spots scattered randomly over the exoskeleton, larger spots having been concentrated adjacent to the axial furrow, outside the eye lobe, and on the adaxial portion of the pleural region. Examination of thin sections suggests that these spots are related to the Osmólska cavities and are visible externally when the exoskeleton is light in color and the cavities contain fine-grained pyrite. The lines of spots described by ESKER on the pleura of *G. boothi* are considered to be broken tubercles that were molded internally by pyrite. Diagenesis of pyrite that had formed below the exoskeleton is thought to be responsible for dark coloration in the furrows and on peripheral portions of the exoskeleton.

It appears that paired, darker-appearing areas in glabellar, articulating and inter-ring furrows of trilobites may have been areas of muscle attachment, but why such areas appear darker is not understood. Small, dark spots or bands on the exoskeleton may be
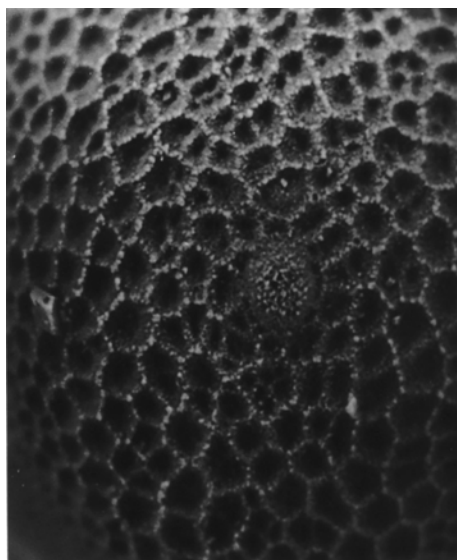

FIG. 76. *Cryptolithus tesselatus* GREEN, Ordovician, Virginia. Median area of glabella, showing tubercle and sculpture of network of raised ridges, ×50 (Whittington, 1959a, pl. 20, fig. 10).

traces of an original color pattern, but a reassessment of supposed examples is needed, particularly with reference to preservation and the role of diagenesis.

THE TRILOBITE BODY

H. B. WHITTINGTON

INTRODUCTION

In exceptional circumstances (see the section on taphonomy below) diagenetic processes have resulted in preservation of the ventral cuticle, particularly that covering the limbs. Spectacular examples of such preservation are the enrolled specimens of *Agnostus pisiformis* less than 1.0 mm in length, described by MÜLLER and WALOSSEK (1987) and coming from localities in the Upper Cambrian of Sweden. Permineralization by phosphatic matter has not only preserved all the limbs (Fig. 77–79) but also the ventral cuticle into which they were inserted, sternites, traces of the alimentary canal, and other organs. The recognition of **sternites,** transversely rectangular plates between the insertions of the limb bases separated one from another by a transverse groove, is unique. Presumably these were sclerotized plates, not mineralized, no evidence of mineralized sternites being known in any trilobite. The ventral cuticle beneath the pleural regions is rarely preserved and when so preserved is wrinkled, suggesting that it was lightly sclerotized, thin, and flexible. Such flexibililty would be necessary in *Agnostus* and any other trilobite that enrolled completely, to allow the limbs, including the antennae, to be packed inside. The ventral cuticle must have been attached to the inner edge of the doublure. The exoskeleton thins towards this edge, but the outline of it is not ragged; rather it is sharp and distinctive in trilobites with no implication of transition. Presumably, the cuticle of the limbs of trilobites was more heavily sclerotized than that beneath the pleural regions and hence is preserved in specimens from different stratigraphical horizons in other countries (see below), by replacement with mineral matter, or by lining or infilling by pyrite. Pyritized specimens have been studied by X rays, and it is claimed that not only traces of the digestive organs and alimentary canal but also of muscles and endoskeletal bars are preserved. The anatomy of the trilobite has been conjectured from these traces and interpretations made of such exoskeletal features as muscle scars, openings, and canals.

LIMBS

Although earlier work on trilobite limbs was summarized by HARRINGTON (in MOORE, 1959, p. 76–82), detailed studies published subsequently have greatly changed our knowledge, and this account refers to the recent work. These newer studies have relied in part on X-ray photography and to a greater extent on mechanical preparation and extraction using acid. Key factors in new interpretations have been the better understanding of taphonomy, the recognition of the probable original convexity of the exoskeleton, and improved techniques.

The appendages of meraspid developmental stages of *Agnostus pisiformis* (Fig. 77–79) from the Upper Cambrian of Sweden (MÜLLER & WALOSSEK, 1987) are the best preserved of any known, despite the minuteness of the specimens. They have not been flattened by compaction or displaced in relation to the exoskeleton, hence the positions of the insertions of the limb series (Fig. 80) may be observed in relation to the morphology of the exoskeleton (Fig. 81). Thus a most detailed reconstruction could be prepared (Fig. 82). The cephalon bears four pairs of appendages, the first being the multijointed antenna having a short, basal shaft and annular podomeres bearing setae and bristles. The antenna is attached at the side of the large, bulging hypostome immediately behind the anterior hypostomal wing. The second appendage is attached on the posterolateral side of the hypostome and has a large coxa with a spinose gnathobase. From the coxa arises a long outer branch, the short
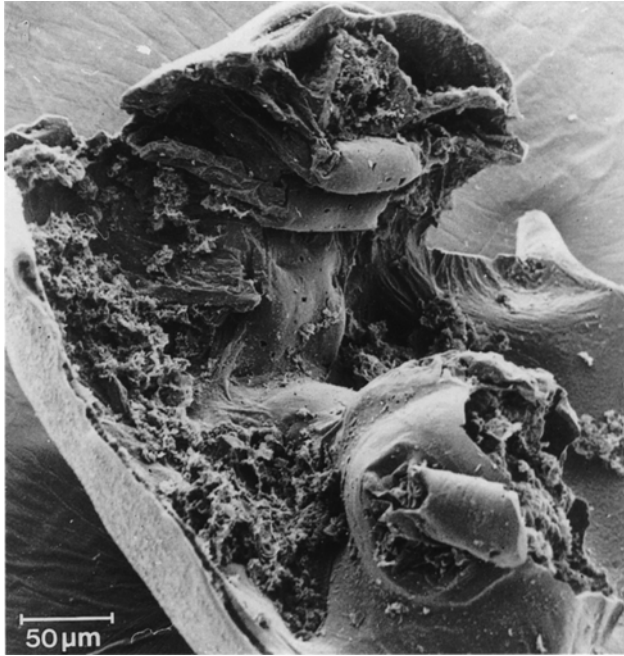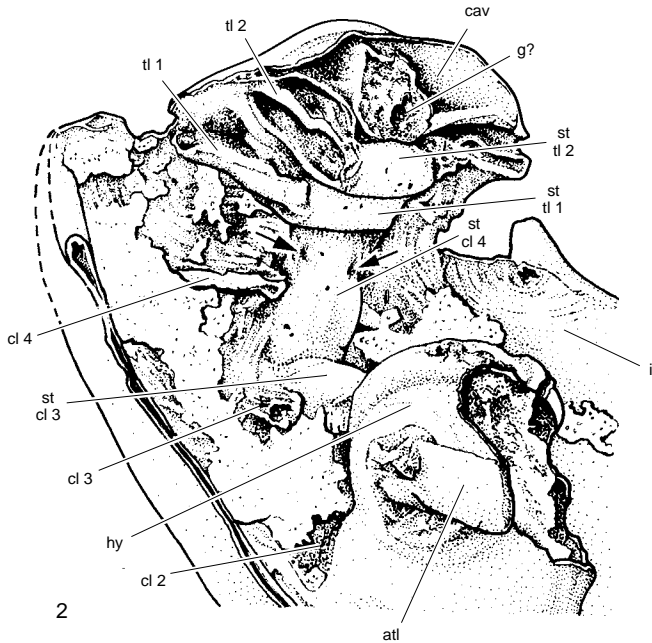
FIG. 77. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Portion of enrolled specimen with cephalic border and most of trunk broken off. *1,2,* Photograph and explanatory drawing of interior, with anterior end of cephalon at bottom right. Hypostome (*hy*) and base of first antenna (*atl*) at lower right; insertions of cephalic limbs (*cl 2–4*) and thoracic limbs (*tl 1,2*) indicated. Sternites of the cephalic region (*st cl 3,4*) and trunk (*st tl 1,2*) are preserved in midregion and portions of the ventral cuticle (*il*) abaxially. Limb musculature may have caused the pair of depressions (see *arrows*) in the posterior cephalic sternite. Abbreviations: *cav,* internal cavity; *g?*, probable gut (Müller & Walossek, 1987, pl. 15, fig. 1).
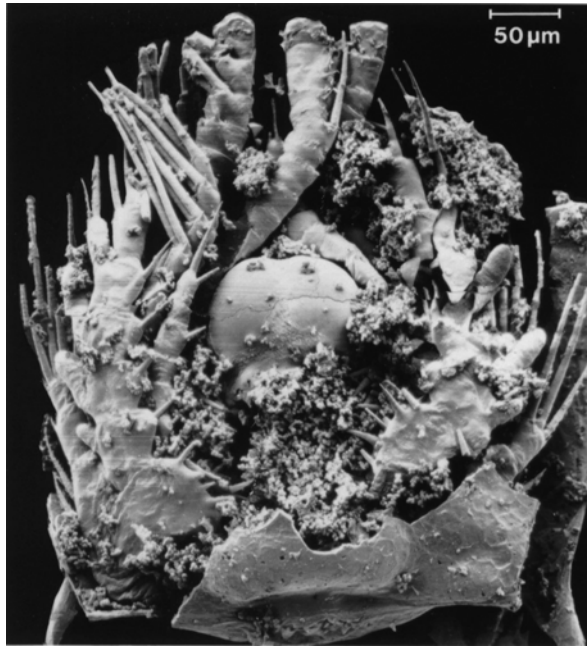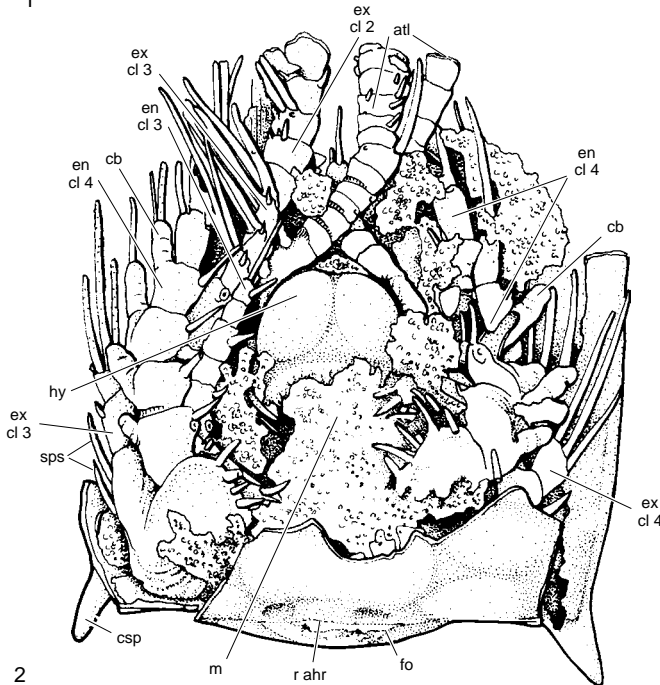
FIG. 78. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. *1,2,* Photograph and explanatory drawing of enrolled specimen with most of transitory pygidium removed to reveal the anteriorly directed cephalic appendages (*atl,* first antenna; *cl 2–4,* succeeding appendages; *ex,* outer branch; *en,* inner branch). Spines (*sps*) and club-shaped appendages (*cb*) of 4th cephalic appendage are preserved. The position of the mouth (*m*) is indicated. Abbreviations: *hy,* hypostome; *csp,* genal spine; *r ahr,* articulating half ring; *fo,* cephalothoracic aperture covered by membrane (Müller & Walossek, 1987, pl. 16, fig. 3).
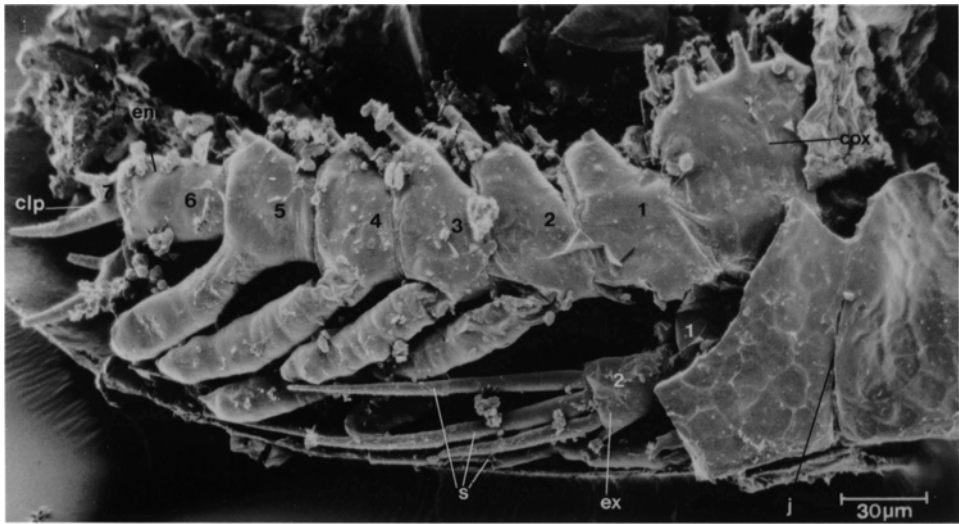
Trilobita

FIG. 79. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. First trunk limb, including coxa (*cox*), seven podomeres (*1–7*) of the inner branch (*en*), and the clawlike terminal podomere (*clp*). Two podomeres (*1, 2*) of the outer branch (*ex*) and setae (*s*) are preserved (Müller & Walossek, 1987, pl. 24, fig. 1).

podomeres of the distal portion bearing a brush of long setae; the inner branch is reduced to a small hump on the distal rim of the coxa. The third and fourth limbs have successively larger coxae with gnathobases, each pair separated by a sternite. On the third limb an inner branch bearing spines is present (shown only on the right limb in Fig. 82), and on the fourth limb the inner branch (shown only on the left limb in Fig. 82) is longer, having spines on the inner side and clublike projections on the outer side. The outer branch of the third limb is longer than the inner, but on the fourth limb the outer branch is much shorter than the inner branch. Five pairs of trunk limbs, similar to those of the fourth (posterior) cephalic limb, follow; these become progressively reduced in size posteriorly (Fig. 79, 82). In the late meraspid stage, the first of these pairs is on the single thoracic segment, and the fifth limb is rudimentary, not divided into podomeres. In the holaspid stage, the second of these five pairs belongs to the second thoracic segment, and there are three pairs on the pygidium, the last pair a short limb that has developed to become like the fourth limb

of the meraspid stage of Figure 82. Sternites separate the thoracic limbs and the first pygidial pair, behind which the axial region narrows rapidly.

A reconstruction of *Olenoides serratus* from the Burgess Shale (WHITTINGTON, 1975, 1980a) shows the multijointed antenna inserted into the ventral cuticle immediately behind the anterior wing of the hypostome and probably linked by muscles to the fossula (Fig. 83). Up to 16 pairs of biramous appendages succeed the antennae, probably three on the cephalon, one on each of seven thoracic segments, and the remainder on the pygidium. Beneath the terminal axial piece of the pygidium one pair of multijointed cerci is attached—a feature unknown in any other trilobite. The biramous limb is borne by a large coxa inserted into the ventral cuticle beneath the axial region, the spinose mesial edges of each pair of coxae close together (Fig. 84). The inner (or leg) branch of the limb is attached to the abaxial edge of the coxa and consists of six podomeres and a group of terminal spines. Clusters of stout spines are present on the ventral side of podomeres 1 to 4. The outer
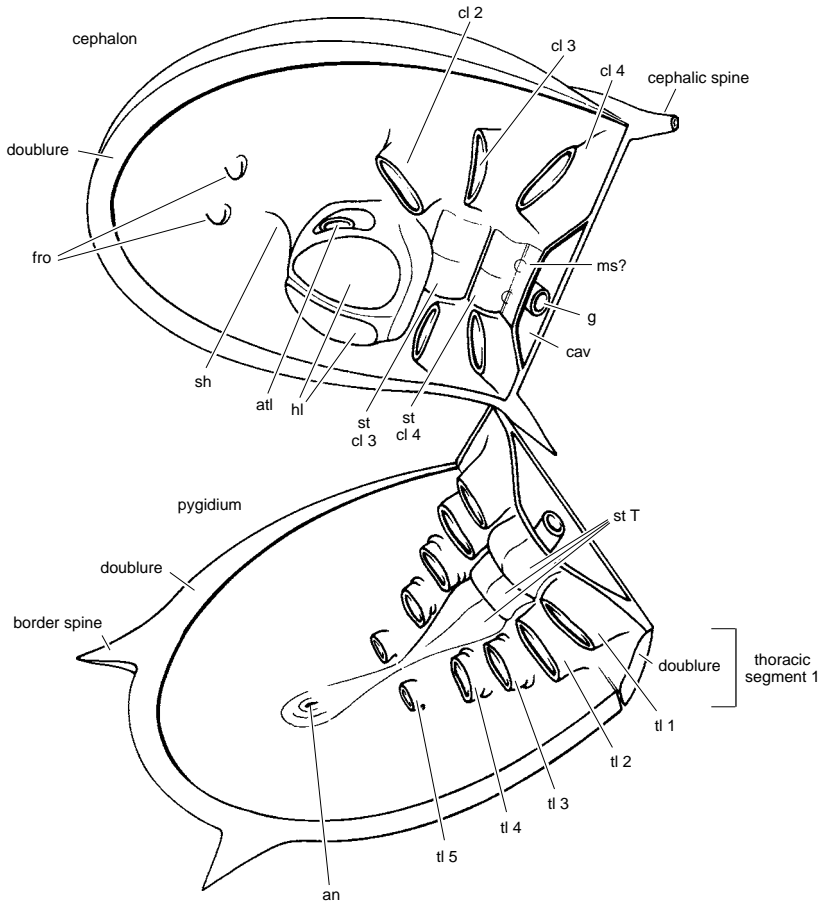
FIG. 80. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Internal view of disconnected cephalon, first thoracic segment, and transitory pygidium of a meraspis. The insertions of the antenna (*atl*), cephalic limbs (*cl 2–4*), the limb of the first thoracic segment (*tl 1*), and four limbs of the transitory pygidium (*tl 2–5*) are shown, as well as the shaft (*sh*) and lobes (*hl*) of the hypostome, the frontal organ (*fro*), and the sternites of cephalic limbs (*st cl 3–4*) and trunk (*st T*); probable muscle scars (*ms?*) indicated. The body cavity (*cav*) contained the gut (*g*), which ended at the anus (*an*). Based on a specimen having a cepahlon of length (sag.) 0.64 mm (Müller & Walossek, 1987, fig. 18).

branch of the limb arises from the inner, posterolateral edge of the coxa and consists of an elongate proximal and an oval distal lobe. The proximal lobe bears long, flattened filaments, closely spaced and forming a sheet that was directed backward and slightly upward and was long enough to overlap partly the filaments of the succeeding two limbs. The way in which the series of limbs is preserved provides evidence that the outer branch was attached to the coxa in a manner that prevented it from being rotated or swung to and fro about the junction with the coxa (Fig. 85). The filaments of the outer branches are preserved in an overlapping series between the exoskeleton and the overlapping series of leg branches, never in an alternating series with the leg branches. The excellent preservation of these specimens of *O. serratus* shows details of the spinosity of coxa and leg branch, bristles on the dorsal side of the leg branch, fine hairs at the tips of the lamellae of the outer branch, and bristles on the posterior cercus. The regularity of
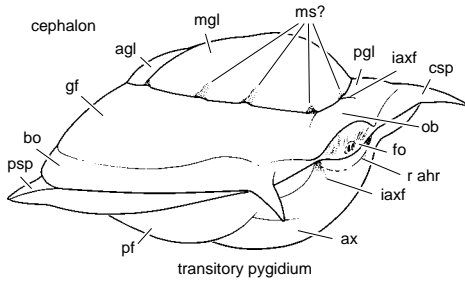
FIG. 81. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Posterolateral view of an enrolled meraspis, showing cephalon and transitory pygidium before the release of any segments of the thorax. Glabella divided into anteroglabella (*agl*), median portion (*mgl*), and posterior portion divided by intra-axial furrow (*iaxf*) into median occipital band (*ob*) and lateral lobes (*pgl*), probable muscle scars (*ms?*) indicated. Genal region of cephalon divided into genal field (*gf*) and border (*bo*) with genal spine (*csp*); axis (*ax*) of pygidium, pleural field (*pf*), and border spine (*psp*) shown. Abbreviations: *r ahr,* reduced articulating half ring; *fo,* membrane covering cephalothoracic aperture. Based on a specimen having a cephalon of length (sag.) 0.32 mm (Müller & Walossek, 1987, fig. 20).

arrangement of the limb series along the body shows that the limbs were held in position by the ventral cuticle during the processes of preservation. This regularity also suggests that the coxa-body junction was such as to have inhibited rotation about a vertical axis but to have allowed some degree of swing about a transverse axis. The junction itself is not preserved, and any trace of the ventral cuticle extremely rare, a possible example being the dark area surrounding the limbs in one specimen (WHITTINGTON, 1975, pl. 11, fig. 1).

The famous specimens from the Upper Ordovician of New York, displaying pyritized appendages, have attracted much attention. Most abundant is *Triarthrus eatoni,* reinvestigated using X-ray stereographs by CISNE (1981). These images were interpreted as showing three (not four as previously believed) pairs of biramous appendages on the cephalon, a coxa that revealed the coxa-body junction, with the two limb branches arising from the outer edge, and a so-called limb-bearing postpygidial

abdomen projecting behind the pygidium. The triangular, spinose endites of the leg branch, known from earlier studies, were omitted from CISNE's reconstruction. A more recent investigation, based on mechanical preparation and photographs taken in reflected light (WHITTINGTON & ALMOND, 1987) has supported CISNE's view on the number of pairs of biramous limbs on the cephalon and has shown the prominent endites on posterior leg branches. It was considered that CISNE's portrayal of the coxa and of the postpygidial abdomen were based on misinterpretations of X-ray stereographs. The new reconstructions of *Triarthrus eatoni* (Fig. 86–87) may be compared and contrasted with that of *Olenoides serratus* as follows.

The cephalon of *Triarthrus eatoni* also has one pair of uniramous antennae and three pairs of biramous limbs and the thorax has one pair of limbs on each segment. The relatively smaller pygidium has 10 or more pairs of limbs that are crowded together, diminishing rapidly in size posteriorly. Posterior cerci are absent. The coxa is also relatively large and spinose on the adaxial edge; but the proximal three or four podomeres of the inner branch are extended ventrally as spinose **endites,** most prominent posteriorly, diminishing progressively anteriorly and disappearing on the cephalon (Fig. 86.3–5). The outer branch of the limb in *T. eatoni* (Fig. 87) consists of an annulated shaft (not a proximal lobe) and small distal lobe and is as long (tr.) as the leg branch; the shaft bears flattened, closely spaced filaments that extend back above those of the succeeding branch. As seen in lateral view, the outer branch in *T. eatoni* is exposed to a far greater extent than that of *O. serratus* (compare Fig. 86.2 with Fig. 83.2), and the long shaft is curved down distally (compare Fig. 87 with Fig. 84). Preservation of *T. eatoni* indicates that, as in *O. serratus,* the outer branch was rigidly attached to the coxa and the filaments formed an overlapping series dorsal to the inner branches. The coxa-body junction and ventral cuticle are not preserved in either species.
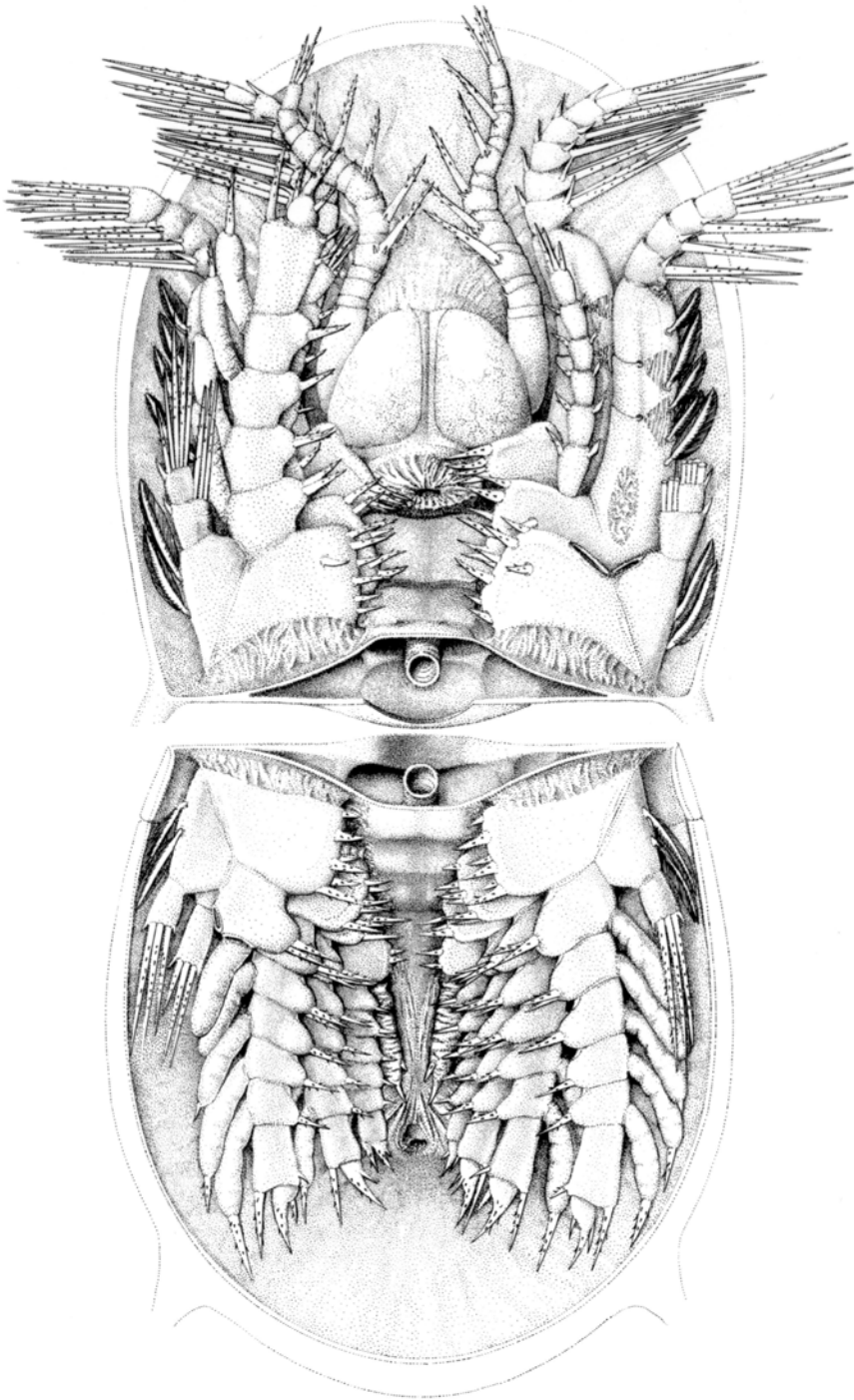
FIG. 82. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Ventral view of reconstruction of meraspis with one thoracic segment, disconnected between cephalon and segment. Based on a specimen having a cephalon of length (sag.) 0.74 mm (Müller & Walossek, 1987, fig. 4).
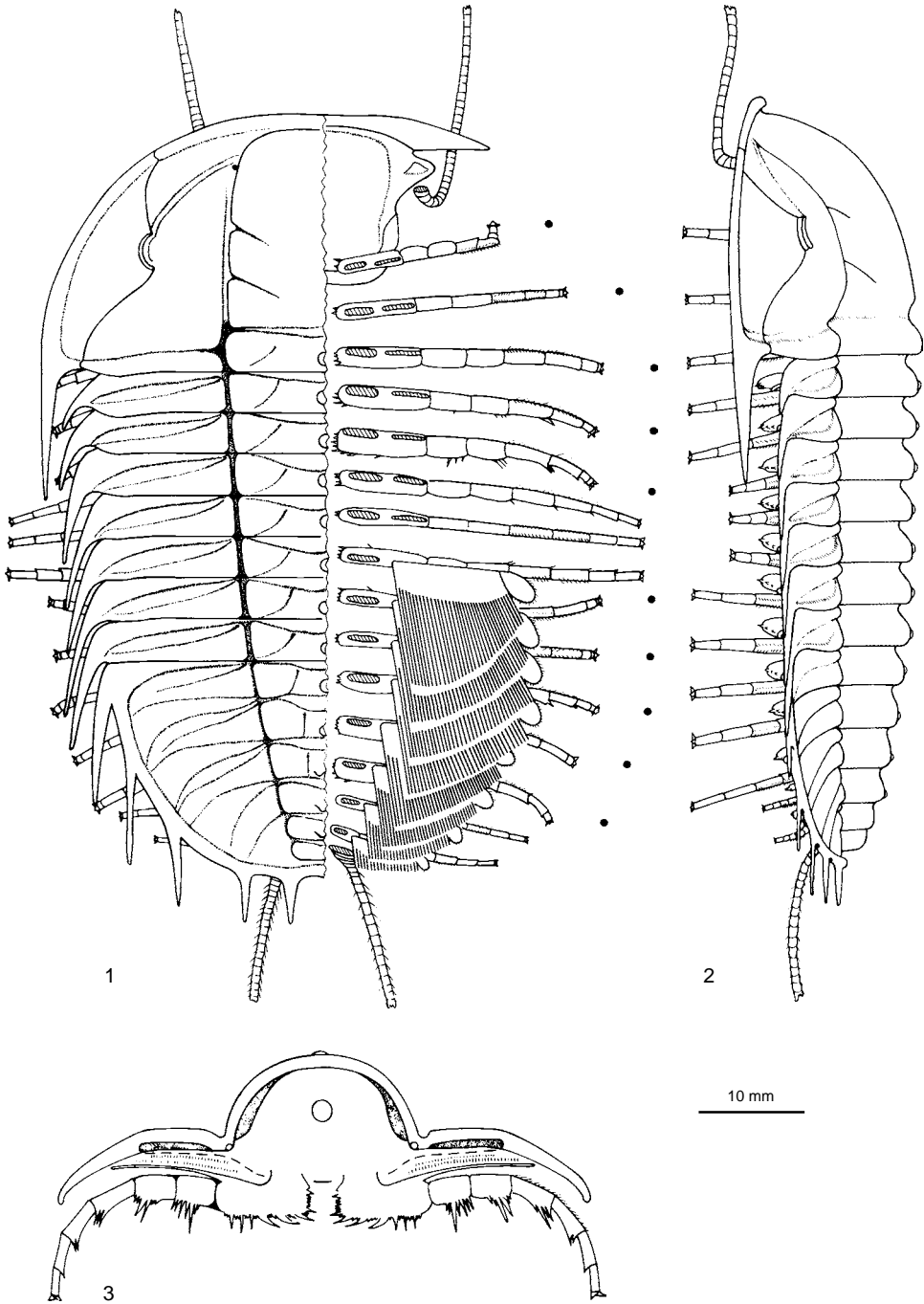
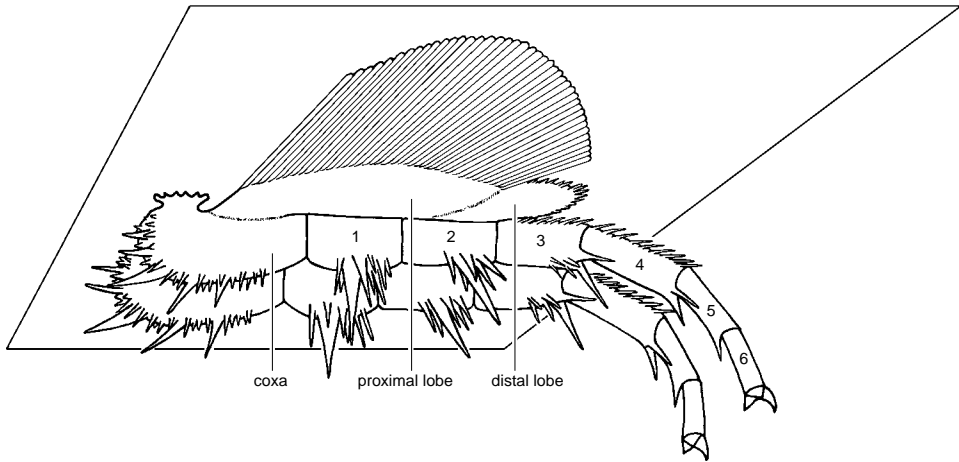FIG. 83. *For explanation, see facing page.*

FIG. 84. *Olenoides serratus* (ROMINGER), Middle Cambrian, Canada. Restoration of two pairs of right appendages, as seen from below and behind; horizontal plane indicated by outline. Inner branch shows coxa and podomeres 1 through 6, podomere 6 with terminal spines. Only the outer branch of the nearer limb is visible in this view, divided into proximal and distal lobes, the long, flat filaments overlapping (Whittington, 1980a, fig. 8).

Of the trilobites with pyritized appendages from the Hunsrück Shale of West Germany, *Phacops* (STÜRMER & BERGSTRÖM, 1973) is most abundant and best known (Fig. 88). There is one pair of multijointed antennae and three pairs of biramous limbs on the cephalon, one pair of such limbs on each thoracic segment, and at least eight pairs on the pygidium. These posterior limbs diminish in size rapidly and are crowded together posteriorly. A spinose gnathobase has been observed at the adaxial end of the large coxa of the posterior cephalic limb. The inner branch of the limb has six podomeres and a short, distal, seventh podomere surrounded by a ring of fine bristles (SEILACHER, 1962). Triangular spinose endites have been observed on distal podomeres of inner branches on posterior thoracic segments. The outer branch appears to have consisted of a relatively short (tr.) basal lobe attached to the coxa, from which long filaments are outwardly directed. The appendages of *Asteropyge* (STÜRMER & BERGSTRÖM, 1973) are less well known, but one specimen has a single pair of antennae and three pairs of biramous limbs on the cephalon. The single pair of antennae and the series of coxae and inner branches of the limbs of *Rhenops* were described by BERGSTRÖM and BRASSEL (1984). It is considered that there were four pairs of biramous limbs on the cephalon. Nine or more pairs were crowded together on the pygidium and show a rapid reduction in size posteriorly; endites were developed on the more proximal podomeres.

FIG. 83. Reconstruction of *Olenoides serratus* (ROMINGER), Middle Cambrian, Canada. *1,* Dorsal view with right half of exoskeleton removed to show appendages and inner view of rostral-hypostomal plate. Antenna and posterior cerci incomplete; *diagonal shading* shows coxa-body junction and bases of outer branches of appendages 1 through 7 where removed. Appendages are shown in a still position of a particular gait (*solid circle* in transverse line with tip of inner branch indicates tip is stepping on sea floor; other branches are swinging forward in a recovery phase). *2,* Left lateral view of animal as shown in part 1. *3,* Posterior view of first thoracic segment, coxa and inner branch of appendage, cross section of ventral cuticle (*dashed line*), and cross section of outer branch of appendage. Between this outer branch and cuticle are cross sections of filaments of next two anterior branches of appendages (Whittington, 1975, fig. 25, 26b,e).

Fig. 85. *Olenoides serratus* (Rominger), Middle Cambrian, Canada. Portion of the counterpart of a specimen (GSC 34694; see Whittington, 1975, 1980a), showing the regular manner in which the series of inner branches of the appendages are arranged and posteriorly the outer branches and posterior cercus (Whittington, 1980a, pl. 20, fig. 4).

Enrolled specimens of *Ceraurus* that contained pyritized appendages were investigated (Størmer, 1939, 1951) using serial sections; models were made from these sections. Størmer concluded that the cephalon has one pair of antennae and four pairs of biramous appendages, with similar pairs of biramous limbs on each thoracic segment. From the large coxa arises an inner branch of six podomeres and a terminal group of spines (Fig. 89). The outer branch arises from the inner, posterior side of the coxa and consists of four podomeres and a terminal lobe bearing long, closely-spaced blade-shaped filaments. In his 1939 account Størmer emphasized the presence of a short, precoxal podomere (Fig. 90) but was less certain about the existence of such a joint in 1951. No evidence for the presence of this joint has

been put forward subsequently, but the most proximal portion of the coxa has not been clearly exposed in any specimen.

The single specimen of *Kootenia* from the Middle Combrian Burgess Shale has been redescribed (Whittington 1975), and most recently two species of redlichioids showing the antenna and biramous limbs from the Lower Cambrian of South China (Shu & others, 1995). Other species showing appendages from the Ordovician Frankfort Shale need reinvestigation. For example, three different interpretations (Bergström, 1972, fig. 2; 1973a, fig. 15; Campbell, 1975, fig. 13) of the appearance of the limbs of *Cryptolithus* have been made subsequently to Raymond's (1920, fig. 20) reconstruction, none based on a critical reexamination of the original material. Beecher's (1895b) and

RAYMOND's work make it clear that endites are developed on the inner branches, most conspicuously on the pygidium.

The limbs of two additional species from the Burgess Shale are trilobite-like, though the exoskeleton is not mineralized. Best known of these is *Naraoia compacta,* which has an oval exoskeleton divided by a simple articulation into two shields (Fig. 91). Beneath the anterior shield are the multijointed antenna and three pairs of biramous limbs; below the posterior shield are up to 16 similar pairs of limbs that diminish in size posteriorly. Each biramous limb is borne on a large, triangular coxa that is spinose on the inner, adaxial side (Fig. 92). The inner branch consists of five podomeres and a short terminal spine. The proximal podomere of the inner branch is enlarged into a triangular, spinose endite. The outer branch arises from the dorsal coxal margin and consists of a slim, tapering shaft with a terminal lobe; the dorsal margin of the shaft bears many long, thin, upward and backwardly directed filaments. The outer branches form an overlapping series that lies beneath the pleural regions of the body. The limbs of the Lower Cambrian species of *Naraoia* from Yunnan, China (W. ZHANG & HOU, 1985) have not been described in detail, but these specimens show the hypostome and a filled alimentary canal.

Only two specimens of the unusually large *Tegopelte gigas* are known from the Burgess Shale (Fig. 93). The appendages include a multijointed antenna and a long series of biramous limbs, diminishing in size posteriorly, the inner branch of which is a jointed walking leg, the outer branch being a shaft bearing long, slim filaments. In this restoration the dorsal exoskeleton is shown divided into cephalon, three thoracic segments, and pygidium. There appears to have been three pairs of biramous limbs on the cephalon, three beneath each thoracic segment, probably four beneath the third segment, and up to 20 pairs on the pygidium. RAMSKÖLD and others (1996) contended that the features interpreted as subdivisions between tergites in *Tegopelte* are preservational artifacts and that the dorsal exoskeleton was undivided. This view is based on an interpretation of the features observed in the dorsal shields of other arthropods (not *Tegopelte*) preserved in the Lower Cambrian Chengjiang fauna of China.

The evidence reviewed above suggests that a single pair of uniramous antennae and many pairs of biramous limbs are characteristic of trilobites. The antenna is attached behind the anterior wing of the hypostome, the first biramous limb beside the posterior portion of the hypostome. The preservation of *Agnostus pisiformis* is such as to show unequivocally that there are three pairs of biramous limbs on the cephalon, but whether three pairs are characteristic of all trilobites is an unsolved question. During the processes of preservation (WHITTINGTON, 1975, p. 102–105; WHITTINGTON & ALMOND, 1987, p. 5–7) the entire series of limbs was held in their original relationship to one another by the ventral cuticle, but this cuticle and the attached appendages may have been moved in relation to the dorsal exoskeleton. Hence, it is difficult to be sure, in any one specimen, how appendages and exoskeleton were related. The weight of evidence available at the time of writing, however, points to three pairs of biramous appendages on the cephalon as having been characteristic of many, if not all, trilobites. The manner of preservation of the outer branch also suggests the relative stiffness of the long, slim filaments attached to it. These filaments are most frequently preserved in overlapping, backwardly directed sheets, always lying immediately below the pleural regions, between exoskeleton and inner branches. There is no evidence that the sheets of filaments were ever directed downward between the inner branches. Alignment of inner and outer branches is characteristic, arguing for a relatively rigid attachment of outer branch to coxa. The original form of the filament of the outer branch—flat sided, bladelike, and suboval or subcircular in section—is less certain. Compressed specimens suggest that
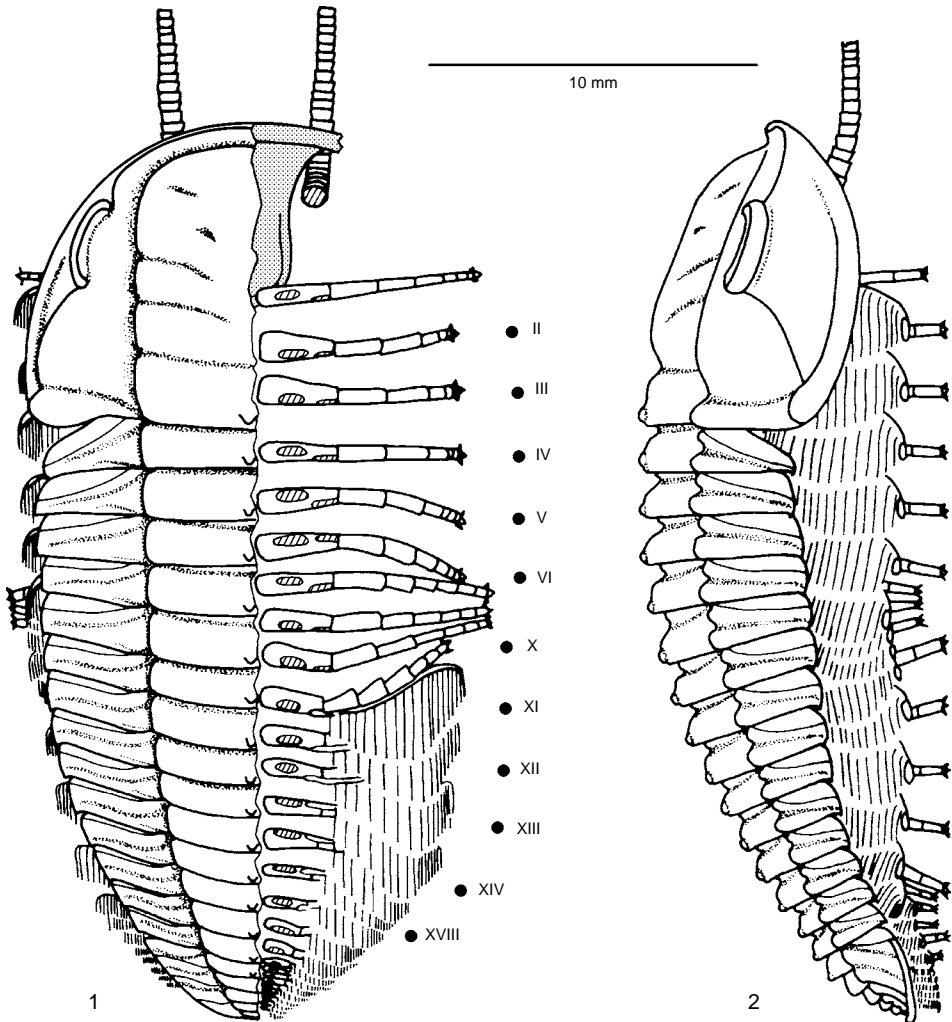
Fig. 86. Restoration of *Triarthrus eatoni* (HALL), Upper Ordovician, New York State, USA. *1,* Dorsal view, in still position of particular gait, with exoskeleton of right side removed to show hypostome and doublure (stippled) and appendages; antennae incomplete. Outer branch of right biramous limbs I through IX removed to show attitude of inner branches. *Solid circles* and *numbers* are opposite tips of inner branches that are on substrate; *diagonal shading* indicates coxa-body junction and base of outer branch where removed. *2,* Right lateral view of part 1; exoskeleton complete; outer branches diagrammatic. *3–5 (see facing page),* Cross sections through exoskeleton, showing respectively biramous limbs III, XI, and XVIII in posterior view with inner branches vertical. *Dashed lines* indicate ventral cuticle and section through alimentary canal; filaments and divisions of outer branch omitted (Whittington & Almond, 1987, fig. 38a, 39a,c,e,f).

they were slatlike (WHITTINGTON, 1980a, p. 189; WHITTINGTON & ALMOND, 1987, p. 38), and cross sections suggested the same form to STØRMER (1939, p. 184, fig. 11, 14), while CISNE (1982) argued from cross sections that the form was elongate-cylindrical.

AXIAL REGION AND ALIMENTARY CANAL

Only in *Agnostus pisiformis* is some trace of the unmineralized ventral cuticle of the axial region preserved (Fig. 77). In these remark-
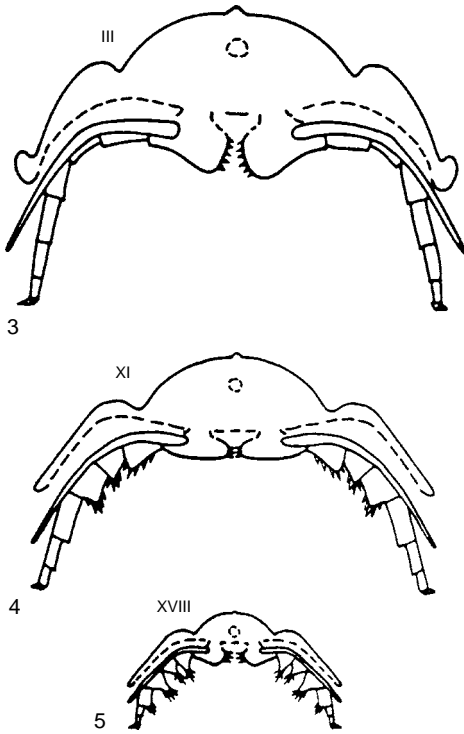
FIG. 86 (continued). *For explanation, see facing page.*

able specimens the mouth opening on the posterior side of the hypostome, the anus, and some trace of the alimentary canal may be seen. In addition, between the coxae of the third and fourth cephalic appendages and between those of the thorax and first pygidial appendage are gently convex sternites, separated from one another by a transverse furrow. Behind the posterior sternite the axial region becomes lower and tapers towards the anus.

A trace of the presumed infilling of the alimentary canal, extending from the anterior lobe of the glabella to the tip of the axis, was first described by BARRANDE (1852, pl. 30, fig. 38–39) in the trinucleid *Deanaspis goldfussi.* An additional specimen was figured by PŘIBYL and VAŇEK (1969, p. 88, pl. 8, fig. 1) and many more by ŠNAJDR (1991). These latter show molds of the hypostome and digestive tract, one specimen showing pellets in the posterior portion of the tract, which

differ in color and petrographic character from the sandy matrix. A single specimen of *Dalmanitina* also shows a mold of the canal in the thorax and pygidium. A similar trace has been described in *Naraoia compacta* (WHITTINGTON, 1977). Pyrite-filled or lined structures in *Phacops* are interpreted as showing the esophagus leading forward from the mouth above the posterior edge of the hypostome to the stomach beneath the anterior portion of the glabella, with ramified structures interpreted as the liver (Fig. 94). The intestine leads back from the stomach to the posterior tip of the pygidial axis (Fig. 88). The alimentary structures of trilobites were reviewed, and a description of these structures in a species of the Upper Cambrian *Pterocephalia* were given by CHATTERTON, JOHANSEN, and SUTHERLAND (1994). STÜRMER and BERGSTRÖM (1973, p. 113) considered that there was no evidence of a **metastome,** a postoral plate; and investigations of *Olenoides serratus* (WHITTINGTON, 1975) and *Triarthrus eatoni* (WHITTINGTON & ALMOND, 1987) have likewise shown no evidence for the existence of such a plate.

PLEURAL REGION, CAECA, AND PANDERIAN OPENINGS

In *Agnostus* (MÜLLER & WALOSSEK, 1987, p. 11) the unmineralized ventral cuticle is preserved, extending from the inner edge of the doublure to the axial region. MÜLLER and WALOSSEK emphasized that this cuticle lies close below the exoskeleton, so that the body was thin in the pleural region, a necessity if the limbs were to be accommodated during enrollment. Arguments used in reconstructing *Triarthrus* (WHITTINGTON & ALMOND, 1987, p. 30, 39) suggest that the bodies of most trilobites may have been shallow in the pleural region (Fig. 86). As the cross sections show (Fig. 86.3–5), this shape would have allowed a hanging stance of the inner, walking leg branches. In this stance (MANTON, 1977, p. 200) the leg was at first directed upward from its origin and then curved downward so that it kept the ventral surface
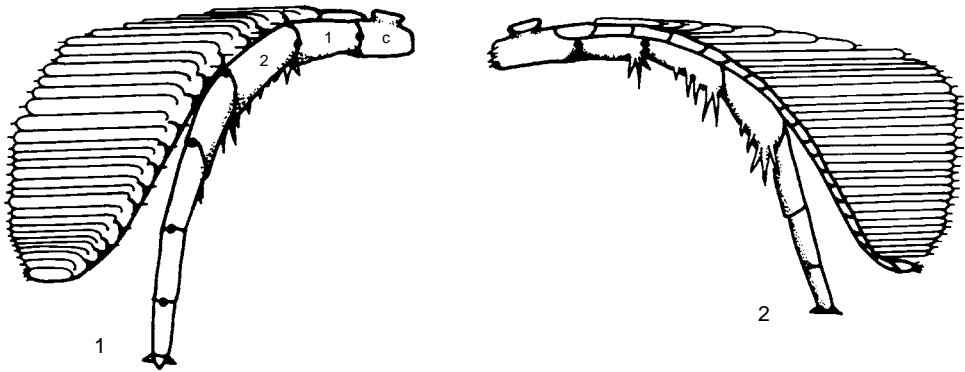
FIG. 87. Restoration of biramous limb from anterior portion of thorax of *Triarthrus eatoni* (HALL), Upper Ordovician, New York State, USA. *1,* Oblique anterolateral view; *2,* oblique view from behind in the midline. *Solid circles* show positions of pivot joint between coxa (*c*) and podomere 1, between podomeres 1 and 2, and of hinge joints between distal podomeres (Whittington & Almond, 1987, fig. 41).

of the body as close to the substrate as possible, promoting stability in cross currents. The shallow body and the flexible ventral cuticle were also necessary to allow the limbs, including the antennae, to be packed inside when the animal was completely enrolled. In trilobites in which the pygidial doublure extended inward almost to the axis (Fig. 61), the body in the pleural region was necessarily shallow. In trilobites in which the border of the cephalon or pygidium was convex, with a convex, rolled doublure below it, there was evidently a deeper, cylindrical, peripheral section of the body. This section did not extend along the tips of the thoracic pleurae.

Ridges on the external surface of the gena (including the coarse, ramifying, radiating rugae in certain Agnostina) and the genal caeca (Fig. 17) have been described above. Rugae are present on the pygidium of Agnostina, and ridges of similar dimension to the genal caeca are present on thoracic segments and pygidium (Fig. 60) of other trilobites. ÖPIK (1961a) considered all these impressions to be of alimentary diverticulae, by analogy with the pattern of such diverticulae in *Burgessia* (C. P. HUGHES, 1975) and *Naraoia* (Fig. 91). CAMPBELL (1975) suggested that the fringe of the trinucleid *Cryptolithus* contained ramifying digestive caeca and also outlined possible ar-

terial and venous systems that were within the fringe and below the gena. JELL (1978a; see also CHATTERTON, JOHANSEN, & SUTHERLAND, 1994) pointed out the difference in width between the coarse rugae of Agnostina and the much finer, branching and anastomosing ridges of the genal caeca in, for example, *Harpides.* He advocated distinguishing between traces of alimentary diverticulae, the coarse ridges and grooves in Agnostina (of uncertain function), and the pattern of finer ridges to which he limited the term genal caeca. He went on to suggest, using analogies with living crustaceans, that the genal caeca were respiratory in function (auxiliary to the outer limb branch), housing a venous system that lay close beneath the exoskeleton. Such a system would have remained exposed to the surrounding water when the animal was fully enrolled.

An opening in the cephalic and pleural doublure of certain asaphids (SIEGFRIED, 1936; HUPÉ, 1955b) is called the panderian opening and is the supposed opening of a segmental panderian organ. This opening may have, immediately behind it, a protuberance that acted to limit enrollment. In other asaphids there is a notch in the inner margin of the doublure, the posterior edge of the notch raised so that it limited enrollment. The notch has been regarded as surrounding a panderian opening, and the term
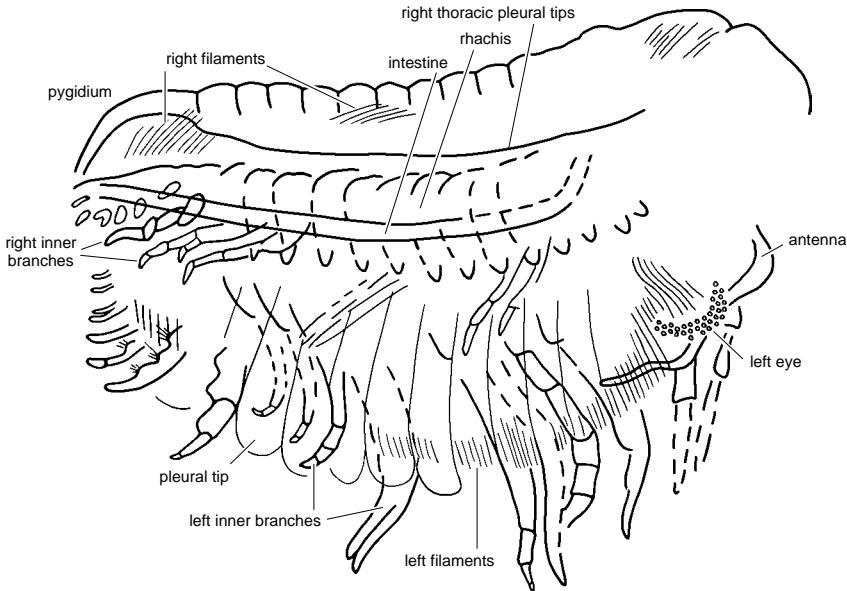
Fig. 88. *Phacops* sp., Lower Devonian, Germany. Drawing from radiograph of a pyritized specimen, buried obliquely so that it is seen from below on the right side. Only the distal portions of the inner limb branches and of the filaments of the outer limb branches are shown (Stürmer & Bergström, 1973, pl. 17b).

panderian notch has hence been applied to similar notches in the doublure of a wide variety of trilobites. Whether the notch in *Proetus,* for example (Fig. 40), surrounded a panderian opening is unknown, and hence whether the so-called panderian organ was present only in some asaphids, or generally in trilobites, may be questioned. HUPÉ (1945, 1955b) suggested that there was no opening, but merely thinner cuticle, associated with a sensory device that detected pleural overlap.

Fenestrae, oval or slitlike unmineralized areas of the exoskeleton of the inner pleural region, situated along the intersegmental boundaries, have been described in asteropyginids and odontopleurids (see earlier sections on thorax and pygidium, p. 43, 59). Best preserved are those in the odontopleurid *Laethoprusia salax* (RAMSKÖLD, 1991a), in which the edges of the opening curve down ventrally, the edge in the pleura continuous with that of the articulating flange and similar in form. RAMSKÖLD speculated that the openings may have been cov-

ered by arthrodial membrane; the function of the opening is obscure.

MUSCULATURE, FLEXURE OF BODY, AND LIMB MOVEMENTS

The form of muscle scars and of invaginations of the exoskeleton (furrows, pits, and apodemes) in and adjacent to the axial region of the exoskeleton (Fig. 8, 10, 20, 26, 51) has been revealed more clearly by silicified specimens (Fig. 26.1, 38–39). These attachment areas, symmetrically arranged in the axial region, rarely median, were for muscles extrinsic to the limbs and other organs of the body and for muscles and ligaments that extended the body and maintained its form. CISNE (1974, 1975, 1981) detected the remains of such muscles in pyritized specimens of *Triarthrus,* but in almost all species in which muscle areas have been observed, traces of soft parts, including appendages, are unknown. Hence, speculations on trilobite musculature have had to
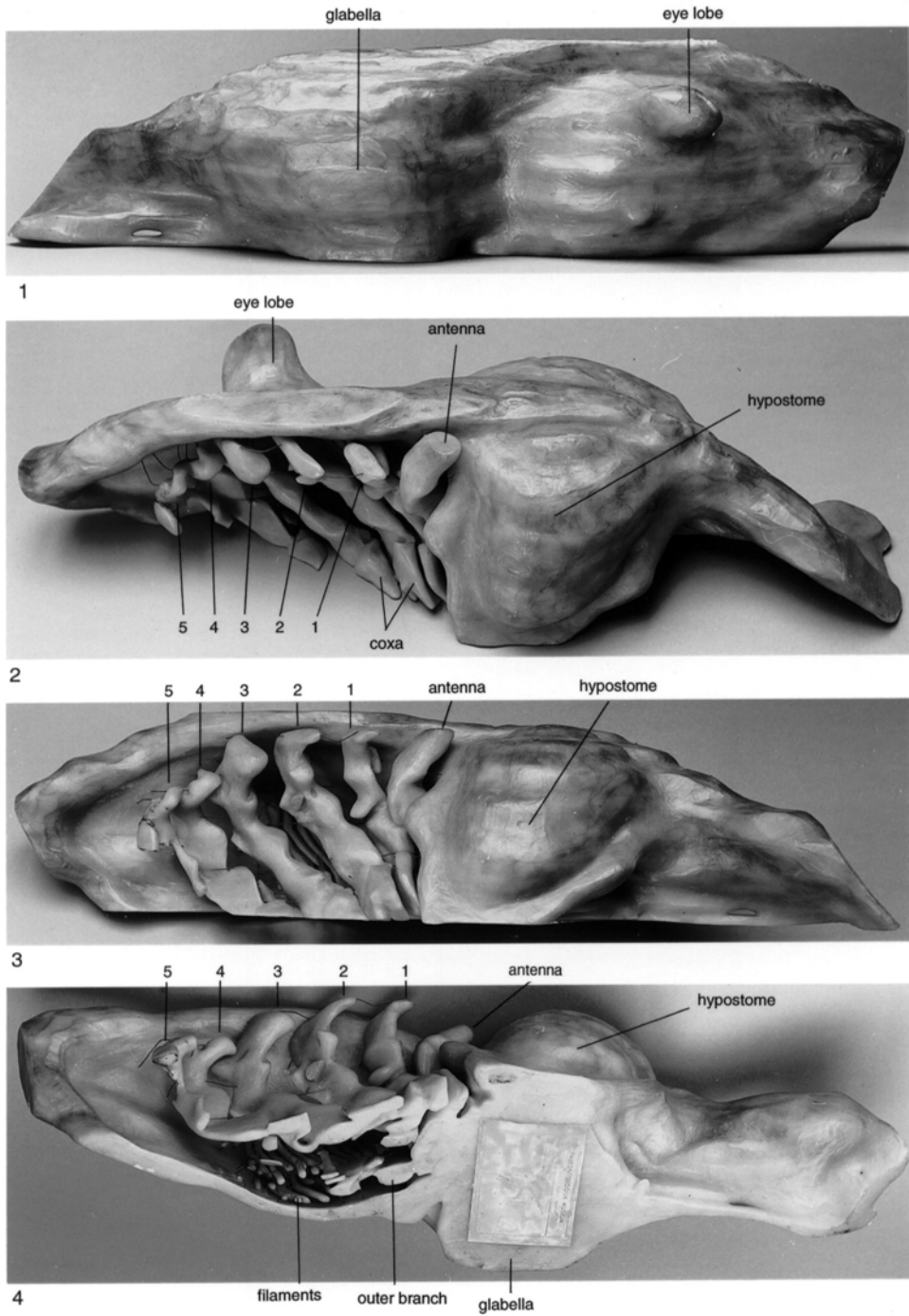
FIG. 89. Wax model (STØRMER, 1951, fig. 2, pl. 2) of part of the cephalon of *Ceraurus pleurexanthemus* GREEN, Middle Ordovician, New York, USA. *1,* Dorsal view; *2,* anterior view; *3,* ventral view; *4,* posteroventral view. *1–5,* inner branches of first 5 limbs (photographs courtesy of Per Aas, Paleontological Museum, Oslo, Norway).
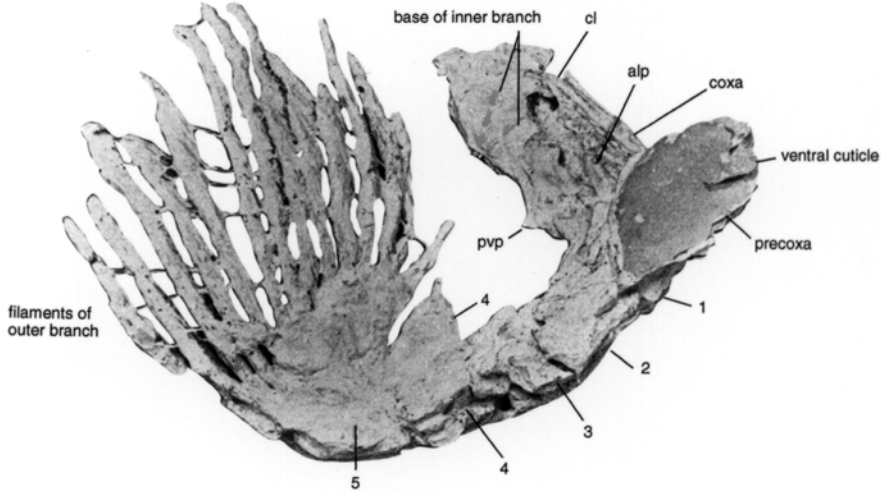
FIG. 90. *Ceraurus pleurexanthemus* GREEN, Middle Ordovician, New York State, USA. Dorsal view of wax model of third thoracic appendage, showing coxa with supposed precoxa and position of junction with ventral cuticle. Only part of the basal podomere of the inner branch is preserved, but podomeres 1 through 5 and filaments of the outer branch are shown. Abbreviations: *alp,* anterolateral process of coxa; *cl,* condyle; *pvp,* postventral process of coxa (Størmer, 1939, pl. 5, fig. 3).

rely on comparisons with extant animals and have been greatly stimulated by the work of HESSLER (1964, 1982) and MANTON (1977). In his X-ray stereographs CISNE (1981) also observed transverse endoskeletal bars, these bars situated on the ventral side of the body adjacent to the intersegmental boundaries. To these bars were attached the ventral longitudinal muscles, dorsoventral muscles (anteriorly descending, vertical, posteriorly descending), horizontal muscles, and ligaments supporting the ventral cuticle (Fig. 95). Such musculature is like that described in living crustaceans by HESSLER and was also proposed by CAMPBELL (1975, 1976, 1977). The recent discovery (WHITTINGTON, 1993a) of a specimen of *Placoparia,* apparently having the endoskeletal bars preserved as external molds, lends support to such reconstructions. Extrinsic limb muscles may also have been attached to these bars, as well as to the infold of the glabellar, occipital, and articulating furrows.

Enrolled specimens of *Placoparia* are well known (e.g., HENRY & CLARKSON, 1975), and a reconstruction shows the arc through which the body was curved and how the relaxed limbs would have been packed tightly within the enclosing capsule (Fig. 96). As HESSLER (1964, 1982) pointed out, the dorsoventral muscles and ligaments were essential to maintain the shape of the body against the pull of the contracted ventral longitudinal muscles. On enrollment the portion of the axial body below the hinge line was reduced in volume, and the larger portion above this line increased in volume. The net effect of this volume change may have reduced hydrostatic pressure within the body, facilitating enrollment and relaxation of the limbs. The fully enrolled position appears to have been essentially temporary, held by the continued contraction of the ventral longitudinal muscles. Extension of the body was effected by contraction of the dorsal longitudinal muscles, aided by contraction of the anteriorly descending dorsoventral muscles, which lay above the hinge line. The volume changes in the body, referred to above, would have been reversed, increasing the hydrostatic pressure as the dorsoventral muscles contracted to maintain the body
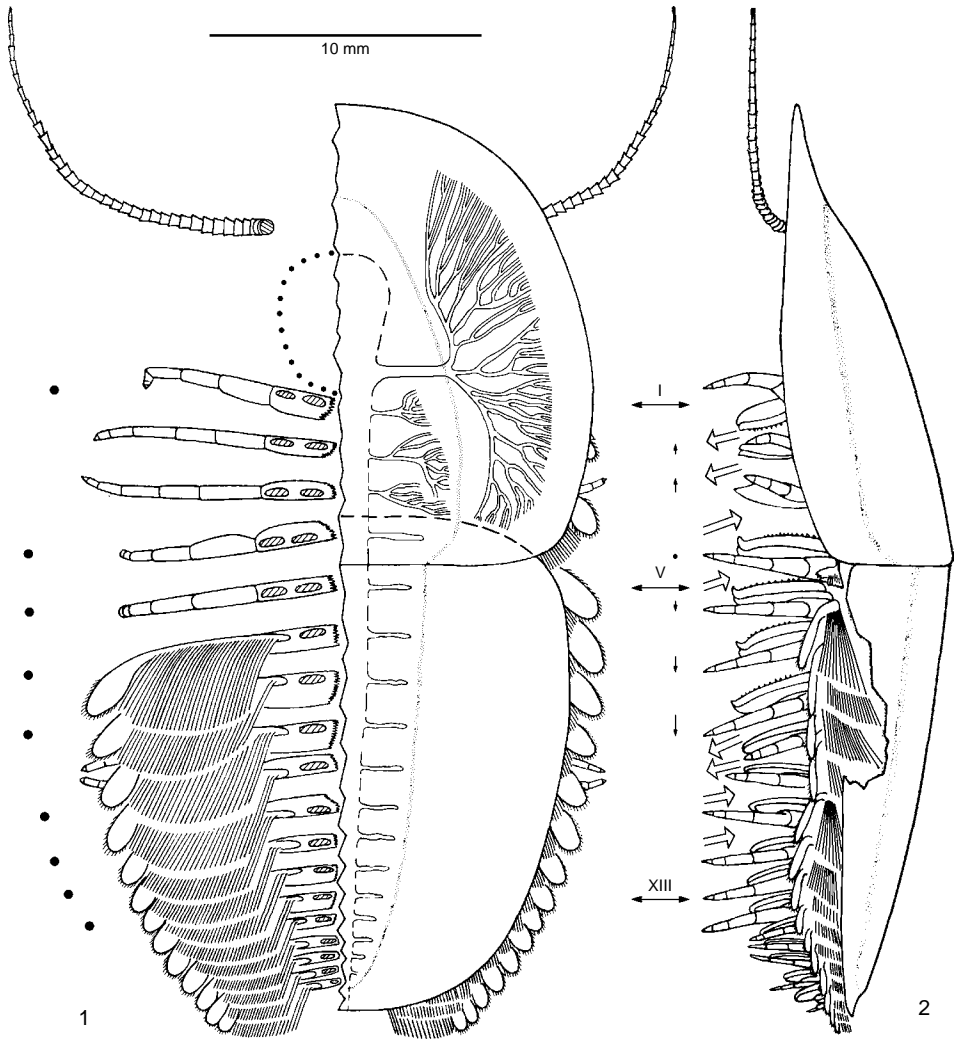
FIG. 91. *Naraoia compacta* WALCOTT, Middle Cambrian, British Columbia, Canada. *1,* Reconstruction in dorsal view, with left half of body cut away to show appendages below; insertion into ventral cuticle is *diagonally shaded.* Outer branches of biramous appendages I through V removed (insertion in coxa *diagonally shaded*). On right side *dashed line* shows outline of alimentary canal, from which diverticula arise. On left side hypostome outlined by *dotted line.* Biramous appendages shown in still position of a particular gait; *solid circle* in transverse line with tip of inner branch that is in contact with sea floor. *2,* Reconstruction in left lateral view, with outer branches of appendages I through III removed, of IV partly cut away, and part of posterior shield cut away to show appendages more completely. Biramous appendages II to VII are in different positions of one metachronal wave, the *arrows* under the tip of each inner branch showing the direction and amount of swing passed through, the *dot* under branch IV indicating the beginning of the remotor stroke. *Arrows with double shafts* indicate directions of water currents caused by movement of limbs; *numbers I, V, XIII* above *horizontal arrows* identify the cross sections shown in Figure 92 (Whittington, 1977, fig. 96).

shape; the increased hydrostatic pressure would have aided the extension. In walking, both dorsal longitudinal and dorsoventral muscles would have been active in keeping the body extended and maintaining its shape and internal pressure. It was considered by STØRMER (1939, fig. 7d) and HUPÉ (1953b, fig. 29) that extension of the body was aided
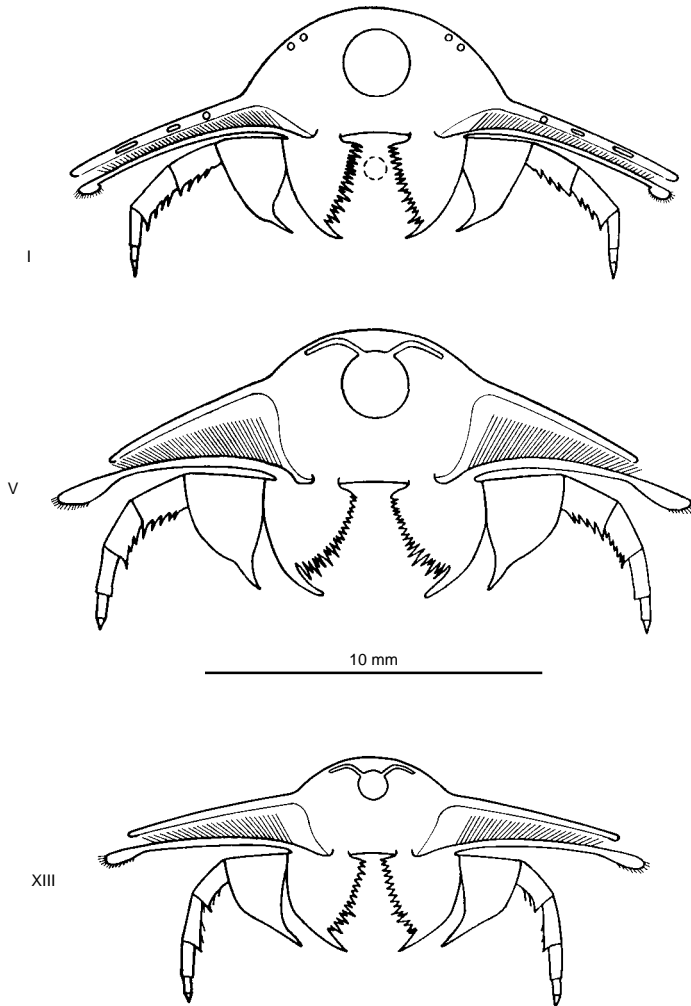
Fig. 92. *Naraoia compacta* Walcott, Middle Cambrian, British Columbia, Canada. Three cross sections (at biramous appendages I, V, and XIII) of the same individual shown in Figure 91. In each section the pair of appendages is seen in posterior view, the alimentary canal and diverticula *outlined;* the *dashed circle* in first cross section indicates the position of the mouth, situated a short distance in front of the section (Whittington, 1977, fig. 97).

by the contraction of auxiliary or external dorsal muscles. These were shown attached to the anterior edge of each articulating half ring and the articulating (or occipital) furrow of the segment in front. Campbell (1975, p. 77; 1976, p. 173–174) argued that such muscles were necessary in *Cryptolithus* and phacopids and were effective because of being situated well above the hinge line. It does not seem necessary in the case of *Placoparia* to invoke the presence of external dorsal

muscles, and the thinness of the exoskeleton of the articulating half ring makes it an unlikely site for muscle attachment.

Muscle areas in the cephalon of lower Paleozoic (mainly Ordovician) species have been investigated by Rudolph (1992), and a new observation is that such areas of the cuticle were traversed by narrow, vertical canals. Axial cephalic musculature is reconstructed in the raphiophorid *Ampyx* and the pterygometopid *Toxochasmops*, and paired
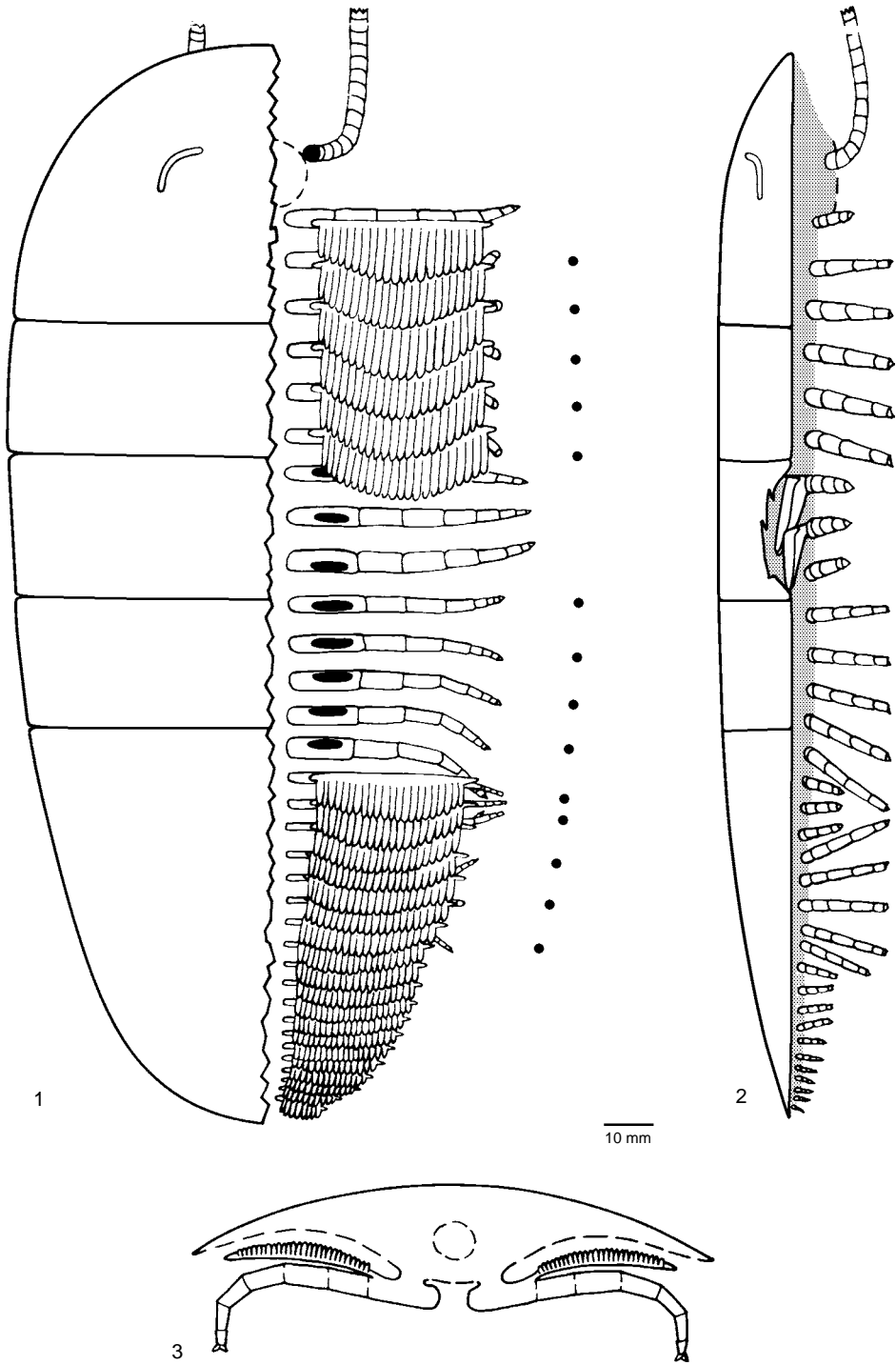
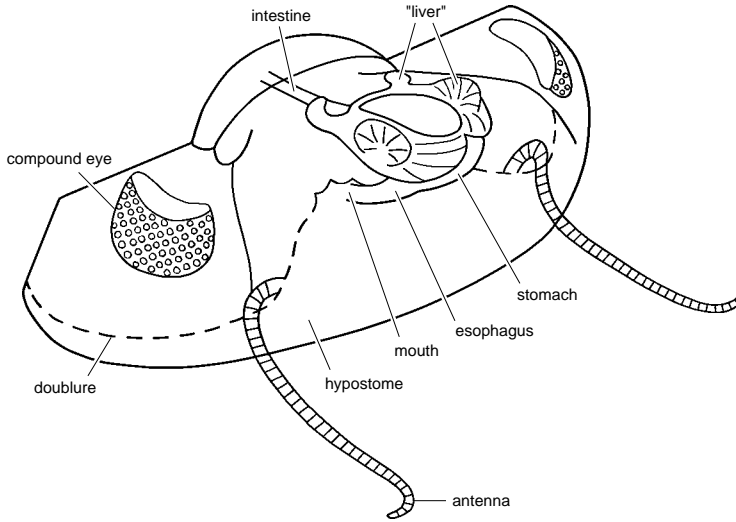FIG. 93. *For explanation, see facing page.*

F‌ɪɢ. 94. Cephalon of *Phacops* sp., right anterolateral view; exoskeleton shown as if transparent; inner edge of doublure and hypostome shown by *dashed line.* Interpretation of alimentary system, internal organs, and antennae from pyritized structures (J. Bergström, new).

and median scars on the anterior glabellar lobe are regarded as having been for attachment of muscles supporting the anterior portion of the alimentary tract. Such scars in Phacopina were described by E‌ʟᴅʀᴇᴅɢᴇ (1971), C‌ᴀᴍᴘʙᴇʟʟ (1976), and S‌ᴛøʀᴍᴇʀ (1980), and E‌ʟᴅʀᴇᴅɢᴇ interpreted them in the same manner as R‌ᴜᴅᴏʟᴘʜ. C‌ᴀᴍᴘʙᴇʟʟ (1976, fig. 2), however, regarded the more anterior of these scars as providing necessary anchorage for the ventral longitudinal muscles. In *Placoparia* the most anterior transverse bar preserved is that of L2 (Fig. 95.1,4), and any more anterior extension of the ventral longitudinal muscles would have unduly restricted space for the anterior por-

tion of the alimentary canal. The same consideration in regard to Phacopina implies that the ventral longitudinal muscles did not extend as far forward as C‌ᴀᴍᴘʙᴇʟʟ suggested. Likewise, in *Triarthrus* these ventral muscles and the bars may not have been present as far anteriorly as C‌ɪsɴᴇ (1975, 1981) suggested. Muscles that controlled movement of the hypostome were shown, for example, by E‌ʟᴅʀᴇᴅɢᴇ (1971, fig. 7). However, the conterminant hypostome was apparently not movable. Muscle scars on or adjacent to the hypostome were probably for muscles attached to the most anterior portion of the alimentary tract or to the dorsal unmineralized cuticle of the hypostome. Cephalic

F‌ɪɢ. 93. Restoration of *Tegopelte gigas* S‌ɪᴍᴏɴᴇᴛᴛᴀ & D‌ᴇʟʟᴇ C‌ᴀᴠᴇ, Middle Cambrian, Canada. *1,* Dorsal view with exoskeleton of right half removed to show appendages beneath, the outline of supposed hypostome indicated by *dashed line.* Appendages are in still position of a particular gait, with outer branches removed from limbs VII to XIV and insertion into coxa shown in *solid black.* Antenna is incomplete, its insertion into ventral cuticle shown in *solid black. Solid circles* on right are opposite tips of limbs that are on sea floor. For simplicity, filaments of outer branches are shown relatively much broader (tr.) than they were; the form of the shaft of the outer branch is generalized and does not show a lobate inner portion. *2,* Right lateral view with portion of exoskeleton removed to show outline of outer branches of limbs VII and VIII; other outer branches not shown. *3,* Posterior view of cross section through tergite 1, showing appendage VI. Ventral integument and alimentary canal shown by *dashed lines;* proximal portions of limbs conjectural (Whittington, 1985, fig. 17).
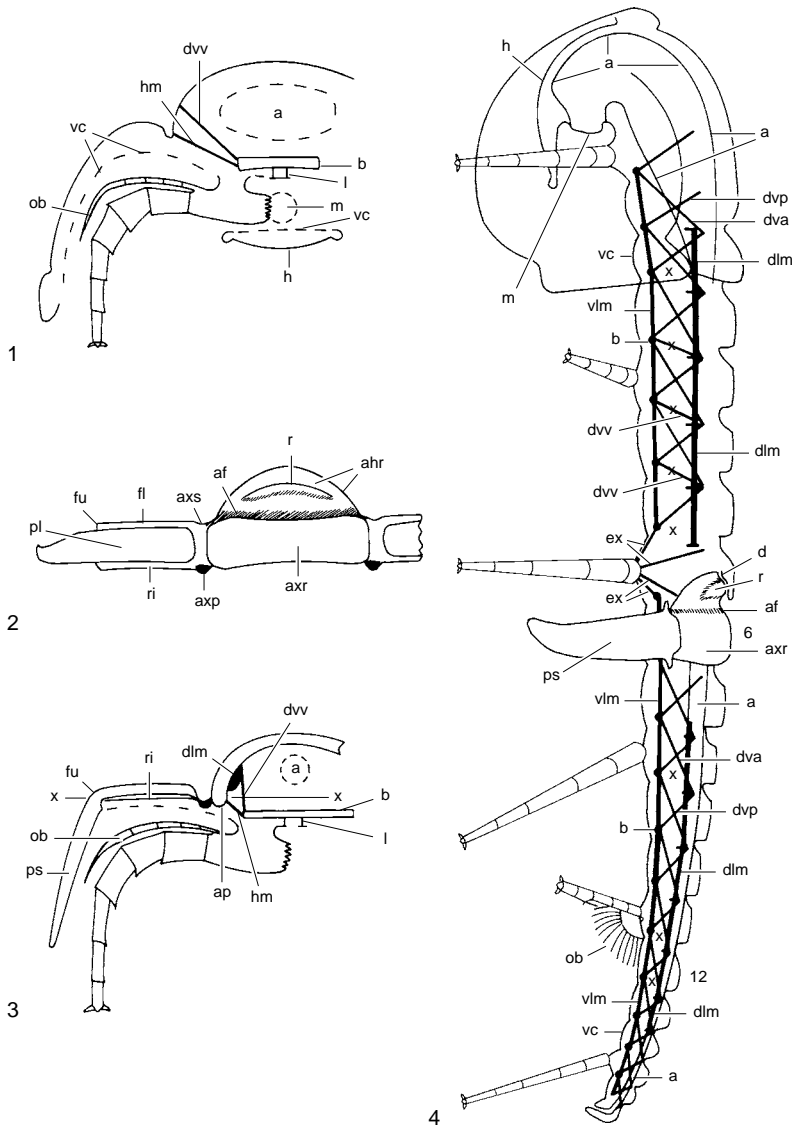
FIG. 95. *Placoparia (P.) cambriensis* HICKS, Ordovician (Llanvirn), U.K. Reconstruction of extended body with the position of the musculature (but not the bulk) shown in heavier lines.——*1,3,* Transverse sections at second glabellar lobe (L2) and sixth thoracic segment, respectively. Left biramous limb shown with inner branch vertical, outer branch (*ob*) in section. *Dashed lines* indicate outline of alimentary canal (*a*), position of mouth (*m*) in front of anterior limb, and unmineralized ventral cuticle (*vc*), which also overlies the hypostome (*h*). The transverse tendinous bar (*b*) is linked to the ventral cuticle by ligaments (*l*). A dorsoventral vertical muscle (*dvv*) and a horizontal muscle (*hm*) extend from the glabellar and axial furrows in part 1, and from the articulating furrow or apodeme (*ap*) in part 3, to the end of the bar. The dorsal longitudinal muscle (*dlm*) is shown in section in part 3; the hinge line between segments is shown by the line *x; ps* is the pleural spine.——*2,* Dorsal view of sixth thoracic segment, showing ridge (*r*) in articulating half ring (*ahr*), the axial ring (*axr*), the axial articulating socket (*axs*) and process (*axp*), the articulating furrow (*af*), the pleura (*pl*) with the anterior articulating flange (*fl*) and posterior ridge (*ri*), beneath which the flange of the following segment fits. The pleura is bent down at the fulcrum (*fu*) to form the pleural spine.——*4,* Profile of exoskeleton in left lateral view, with thoracic segments 6 and 12 (the posteriormost) numbered. Profile broken at segment 6 to show a lateral view of this segment (compare with part 2) and the doublure (*d*) of the axial ring of segment 5. The alimentary canal (*a*) is shown in the cephalon and posteriorly from segment 7. The inner branches (*continued on p. 109.*)
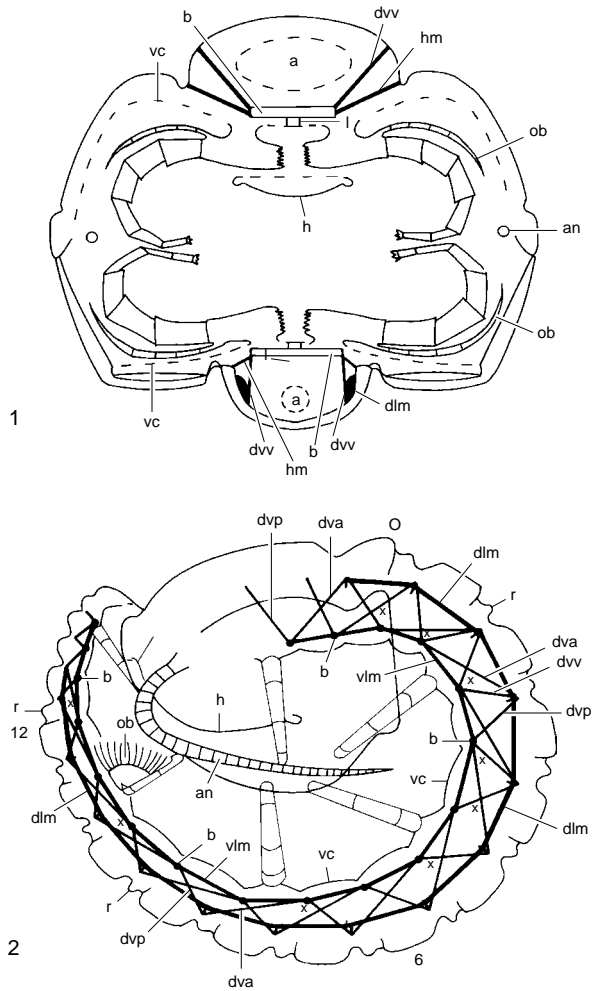
FIG. 96. *Placoparia (P.) cambriensis* HICKS, Ordovician (Llanvirn), U.K. Reconstruction of body in fully enrolled attitude, to indicate the positions of muscles and the manner in which the appendages were accommodated. Position of hinge line indicated by *x. 1,* Cross section through glabellar lobe L2 and thoracic segment 7 (compare with Fig. 95.1,3). *2,* Profile of exoskeleton with antenna (*an*) in retracted position; limbs and musculature as in Figure 95.4. Abbreviations: *a,* outline of alimentary canal; *b,* tendinous bar; *dlm,* dorsal longitudinal muscle; *dva,* anteriorly descending dorsoventral muscle; *dvp,* posteriorly descending dorsoventral muscle; *dvv,* vertical dorsoventral muscle; *h,* hypostome; *hm,* horizontal muscle; *O,* occipital ring; *ob,* outer branch; *r,* ridge in articulating half ring; *vc,* ventral cuticle; *vlm,* ventral longitudinal muscle; thoracic segments 6 and 12 are numbered (Whittington, 1993a, fig. 9).

FIG. 95. *Explanation continued from facing page.*

of limbs I, V, VIII, XI, XIV (with outer branch *ob*), and XVIII are shown in the appropriate positions of the gait shown in Figure 99.2, in which pairs of limbs I to XVIII were participating. The dorsal longitudinal (*dlm*) and ventral longitudinal (*vlm*) muscles and tendinous bars (*b*) are broken between segments 5 and 7 to allow extrinsic limb muscles (*ex*) of limb VIII to be suggested. The positions of anteriorly descending (*dva*), vertical (*dvv*), and posteriorly descending (*dvp*) dorsoventral muscles are indicated, the vertical muscles only in thoracic segments 2 through 4. Position of hinge line shown by *x.* Only the antennae are known in *Placoparia,* the limbs shown being modelled on those of *Ceraurus* (STØRMER, 1939), a cheirurid, and the nearest relative to the pliomerid *Placoparia* in which limbs are known (Whittington, 1993a, fig. 8).
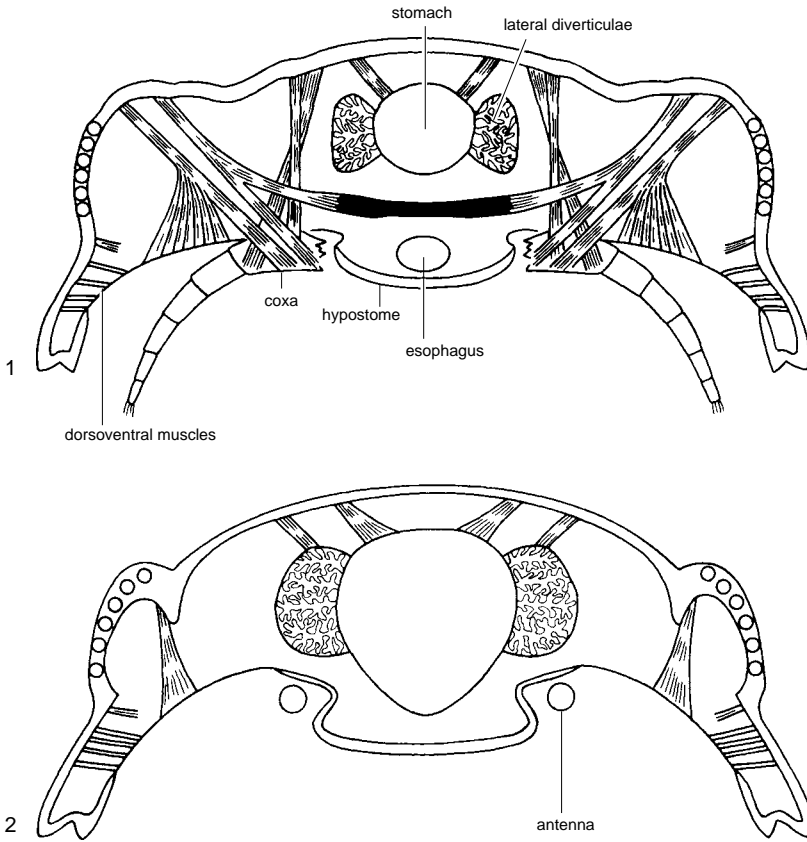
FIG. 97. Cross sections of the cephalon of a generalized phacopid at levels of *1,* posterior and *2,* anterior portions of eyes. Endoskeletal bar *solid black* (Campbell, 1976, fig. 3).

segmentation, the hypostome, and musculature in Phacopinae have been discussed by BRUTON and HAAS (1997).

CAMPBELL (1976) observed muscle attachment areas on the palpebral lobe and elsewhere on the genal area in *Eophacops*, and scars in this area were described by STØRMER (1980, p. 263–266). RUDOLPH (1992) has shown such scars to be present in other Phacopina, as well as in *Ellipsocephalus, Nileus,* and raphiophorids. CAMPBELL suggested that the palpebral scars were for muscles that supported the endoskeletal bar and possibly extrinsic limb muscles (Fig. 97). Both CAMPBELL and STØRMER suggested that muscles supporting the ventral cuticle may have been attached to the scars on the genal region. RUDOLPH (1992, p. 61) has suggested

that rows of scars on the fixed cheek may be for attachment of musculature supporting intestinal diverticulae. Such diverticulae, he remarks, are distinct from the radiating, anastomosing canals of the genal caeca, which extend to the cephalic border and across the preglabellar field. CHATTERTON and CAMPBELL (1993) described not only muscle scars on the frontal glabellar lobe and hypostome of cheirurids and phacopids but also a darker-colored band on the distal area of the inner, horizontal portion of thoracic and pygidial pleurae. They suggested that this band was the attachment site for a longitudinal strip of muscles that may have assisted in maintaining the enrolled position and in resistance to twisting of the exoskeleton.
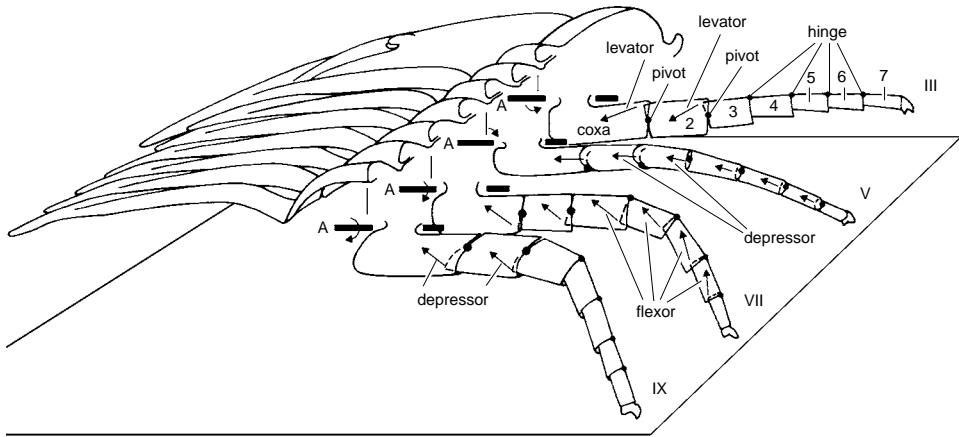
FIG. 98. Oblique diagram, based on *Olenoides serratus* (ROMINGER), Middle Cambrian, Canada, to show probable metachronal movements of right limbs III, V, VII, and IX in walking on the horizontal substrate. Limbs are in positions shown in Figure 99.3. *A* is the axis about which each coxa swung; *solid dots* indicate positions of hinge and pivot joints between podomeres 2 through 7; *arrows* show position and direction of contraction of levator, flexor, and depressor muscles (Whittington, 1980a, fig. 10).

Extrinsic limb musculature is suggested for one pair of thoracic limbs (Fig. 95.4), and such muscles in the cephalon would have been attached to glabellar furrows and endoskeletal bars. This follows the reconstruction of CISNE (1974, 1975, 1981), who suggested an additional lateral muscle attached to the pleural furrow. RUDOLPH (1992, fig. 23, 25) has suggested the possible nature of extrinsic limb musculature in the cephalon of *Ampyx* and *Toxochasmops*, the muscles being attached to the dorsal exoskeleton. Extrinsic coxal musculature was necessary to provide a promotor-remotor swing of the coxa about an approximately transverse, horizontal axis, a swing essential to walking (Fig. 98).

The basic limb movements thought to have been employed in walking are diagrammed in Figure 98 (WHITTINGTON, 1980a, p. 193–195). The leg is lifted off the substrate by levator muscles and extended by hydrostatic pressure and a promotor swing about axis A, as is shown in the figure with limb III about halfway through the swing. Limb V, extended at the beginning of the remotor swing, has its tip pressed firmly into the substrate by the action of depressor muscles on podomeres 2 and 3 (as also shown in limb IX), and the action of flexor muscles on podomeres 4 to 7 bends the limb and transmits a forward-propulsive force to the body. Limb VII is acting in the same way and has reached the midpoint of the remotor swing, the more strongly flexed leg accommodating to the reduced length between coxa and limb tip. Leg IX is extended at the conclusion of the remotor swing, the depressor muscles giving the propulsive force and keeping the tip firmly on the sediment, the flexor muscles relaxed to allow podomeres 4 to 7 to become aligned and extend the limb. The four limbs shown in Figure 98 are part (intervening limbs omitted for clarity) of a metachronal wave of eight pairs of limbs. This gait is considered to be a reasonable one, and successive stages are shown in Figure 99. These stages show how each metachronal wave of movement passed forward along the body.

SUPERFICIAL SENSORY STRUCTURES

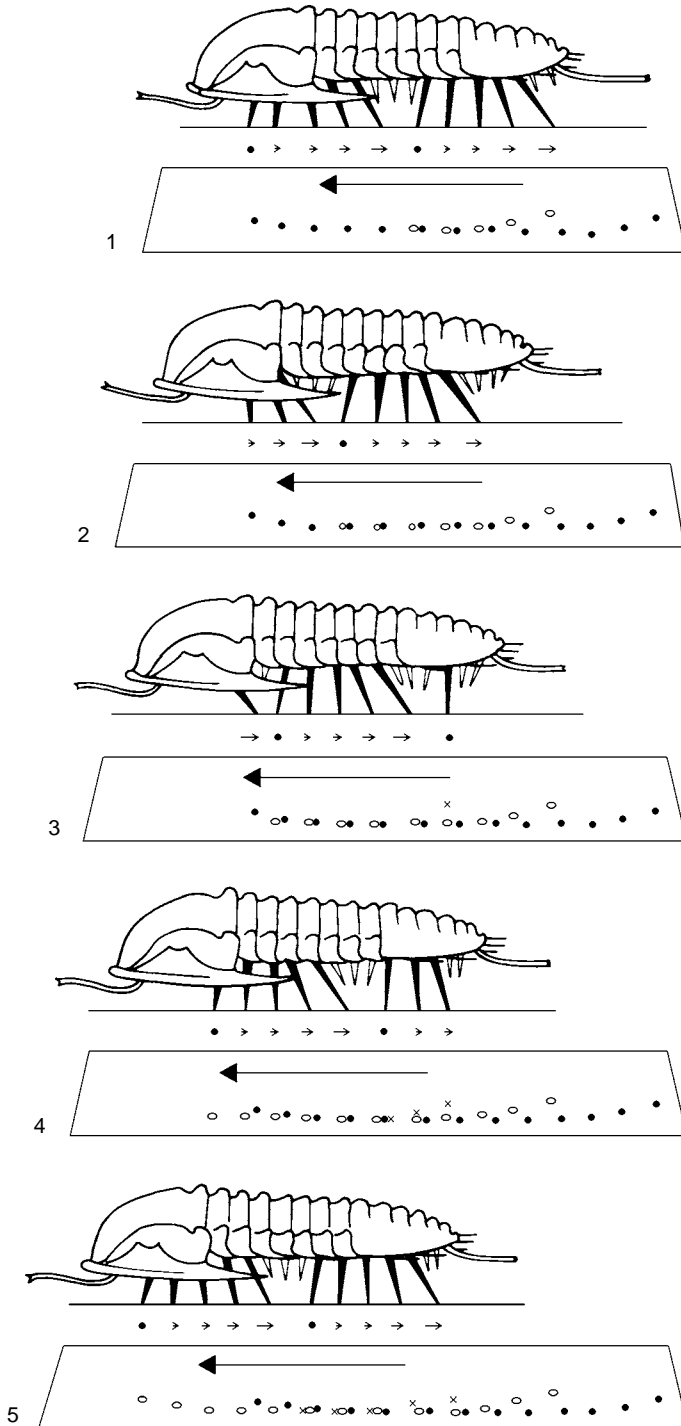Apart from the eye, structures that have been regarded as probably sensory in

FIG. 99. *For explanation, see facing page.*

function include some on the limbs and whatever organs were associated with openings through the exoskeleton. Studies of sensory structures of living marine animals, particular those of crustaceans (LAVERACK & BARRIENTOS, 1985; BARRIENTOS & LAVERACK, 1986), have been used to interpret what is seen in trilobites.

Spines and setae on the limbs of trilobites have been regarded as assisting in swimming, in food gathering, in comminution, and in creating respiratory currents (see discussion of mode of life below). In *Olenoides,* however, rows of fine spines on the upper surface of joints 3 and 4 of the walking leg (Fig. 84) may have functioned to monitor the position of the limb relative to the outer branch or to the exoskeleton, and fine hairs at the tips of the filaments of the outer branch and around the margin of the distal lobe may also have been sensory.

Canals of larger diameter that pass through the exoskeleton (see above section on microstructure and sculpture) are considered to have been the sites of integumental glands or setal ducts. Such canals may emerge at the apex of a tubercle or the tip of a spine, or be surrounded by a rim and situated between tubercles or spines. Openings of this type are numerous around the outer surface of the cephalic and pygidial border and around the tips of pleurae and of major spines. This distribution (Fig. 100) suggests a tactile function for the setae (see also the study of the homalonotid *Trimerus* by HAAS, 1981).

A variety of other presumed sensory organs has been described. One of these is the ventral paired frontal organ anterior to the hypostome in *Agnostus* (Fig. 80). Each node of the pair has a slit at the apex, and the organ may have been a chemoreceptor. In this remarkably preserved material the axial gap in the exoskeleton between the cephalon and first thoracic segment, the **cephalothoracic aperture,** is covered by a membrane in which are a pair of openings (Fig. 81), but it is not known if these ducts to the interior had a sensory function (MÜLLER & WALOSSEK, 1987, p. 9). In *Nileus,* the exoskeleton is thinned over the glabellar tubercle, and FORTEY and CLARKSON (1976) considered it to have been the site of a light-sensitive organ; in illaenids a similar structure is the median posterior depression in the parietal surface of the glabella. Numerous pits in the visceral surface of the exoskeleton of one agnostid have been interpreted as the sites of photoreceptors (WILMOT, 1990a). In the styginid *Raymondaspsis* a low occipital tubercle is impressed by four tiny pits arranged at the corners of a square (WHITTINGTON, 1965, pl. 58, fig. 10). Similar structures in odontopleurids (Fig. 72.2), asaphids, and trinucleids have been referred to by FORTEY and CLARKSON (1976) and compared to a crustacean sense organ by WHITTINGTON (1956d, p. 177). In the latter publication examples are discussed (p. 176–177) of spines elsewhere on the cephalon (Fig. 72) that have a truncated tip pierced by several openings, which are less regularly arranged

FIG. 99. Diagrams of a probable mode of walking of *Olenoides serratus* (ROMINGER), Middle Cambrian, Canada. Parts 1 through 5 show a succession of still-stands in the gait; left limbs I through XV shown, with I through XIII being used in walking and the animal moving in the direction of the *large arrow.* Each selected still-stand shows left legs only (*in solid black* when in contact with sea-bottom, *in outline* when off the bottom and swinging forward). Below tip of each limb on sea bottom is either a *solid circle,* showing that limb tip has just been put down, or an *arrow* of length proportional to amount of backstroke completed. *1,* Legs I through V in first metachronal wave, VI through XIII in second wave. *2,* Legs I through III in first wave, IV through XI in second wave, and XII and XIII in third wave. *3,* Leg I in first wave, legs II through IX in second wave (legs II and III are off the bottom and concealed by the gena), and legs X through XIII continuing the third wave. *4,* Legs I through VII (legs I and II concealed beneath gena) in second wave, VIII through XIII in third wave. *5,* Legs I through V in second wave, VI through XIII in third wave. The panel below each still shows in oblique lateral view the left half of the symmetrical track made in this gait. *Solid circles* are footfalls of first wave, *open circles* are footfalls of second wave, and *crosses* are footfalls of third wave. (Whittington, 1980a, fig. 11).
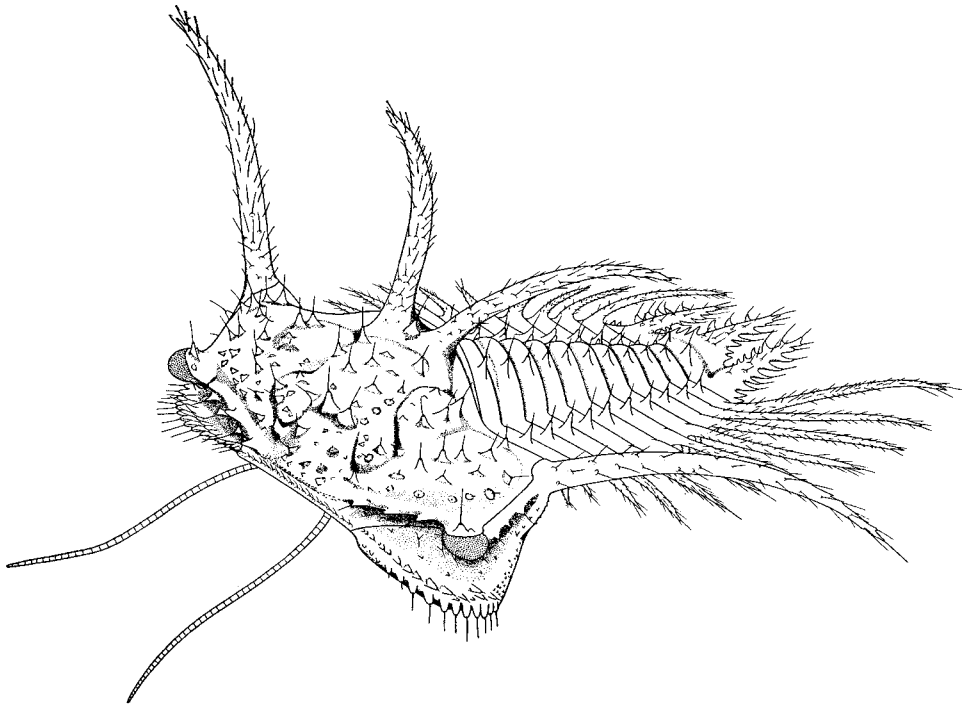
Fig. 100. *Ceratocephala laciniata* Whittington & Evitt, Middle Ordovician, Virginia, USA. Restoration assuming that there were 10 thoracic segments, that the openings in the spines and tubercles were occuped by hairs, and that antennae were present. Other appendages unknown, ✕5.6 (Whittington & Evitt, 1954, fig. 1).

and hence different from the openings in the occipital tubercle or spine.

Apparently unique to *Pricyclopyge* and its close allies is a pair of structures on the axial ring of the third thoracic segment. Fortey and Owens (1987) described these as hollow, inflated structures, circular in plan, and situated within the thickness of the exoskeleton; they argued that the structures may have been luminous organs like those known in some modern crustaceans.

THE EYE: MORPHOLOGY, FUNCTION, AND EVOLUTION

E. N. K. Clarkson

Most trilobites bear one pair of compound eyes on the librigena. The eye ranges from small, consisting of only a few lenses, as in Harpetidae, to extremely large, as in Cyclopygidae. In a few species of *Cyclopyge, Ellipsotaphrus,* and *Symphysops* the eyes are confluent anteriorly (Fig. 101.2). Other than such rare instances, the eyes are separate, and most trilobite eyes are crescentic or kidney-shaped in dorsal view; in transverse section they have a convex profile. Usually the eye is sessile, though it may be set upon a narrow platform, the eye socle. This socle may be provided with sensory pits or **fossettes.** In rare instances, as in Odontopleuridae and some Asaphidae, the eye is extended into a rigid stalk. Above the lens-bearing visual surface lies the palpebral lobe, which may be flat or inflated; this is separated from the visual surface by the facial suture. That part of the facial suture lying between the visual surface and the palpebral lobe is known as the **palpebral suture.**

Since the time of the earlier workers Clarke (1889) and Lindström (1901), it has been generally recognized that two types
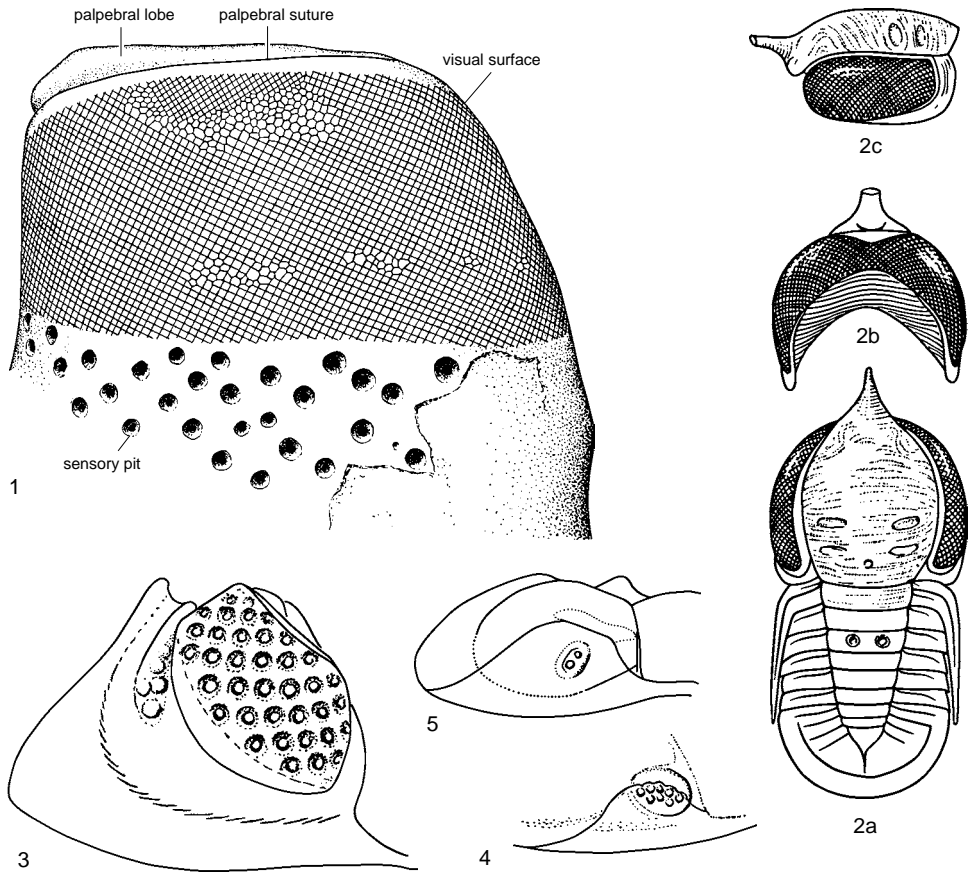
Fig. 101. *1,2,* Holochroal eyes. *1,* Eye of *Asaphus cornutus* Pander, Ordovician, Russia; the patches of large, irregular lenses might result from injury during molting, ×25 (Hupé, 1953b, fig. 31). *2a–c,* Confluent eyes of *Symphysops subarmatus* (Reed), Upper Ordovician, Great Britain, ×1.2; *2a,* dorsal view of exoskeleton; *2b,* ventral view of cephalon; *2c,* left lateral view of cephalon (Hupé, 1955a, fig. 192.2). *3–5.* Schizochroal eyes. *3,* Right eye of *Phacops latifrons* (Bronn), Middle Devonian, Germany, ×25 (Richter, 1932, fig. 2e). *4,* Right eye of *Cryphops cryptophthalmus* (Emmrich), Upper Devonian, Germany, ×7 (Richter & Richter, 1926, pl. 9, fig. 56f). *5,* Left eye of *Nephranops incisus incisus* (Roemer), Upper Devonian, Germany, ×2 (Richter & Richter, 1926, pl. 8, fig. 48d).

of eye are present in trilobites, holochroal and schizochroal (Fig. 101). A third type of eye, abathochroal, was designated by Jell (1975b).

THE HOLOCHROAL EYE

Holochroal (Clarke) or compound (Lindström) eyes have a visual surface of many closely packed, small lenses that are in direct contact with one another (Fig. 101.1–2, 102). The whole ensemble of lenses is covered by a single, thin, pellucid sheet, the cornea, which is calcitic and grades laterally into the outer layer of the cuticle. If the cornea is thin and the individual lens surfaces slightly convex, the lenses can be clearly seen and typically have hexagonal outlines.

The Lower Cambrian Olenellina seem to have had holochroal eyes, though the visual surfaces are at present only commonly found in juveniles. Indeed the record of eyes in adult Cambrian trilobites is poor, at least until the Late Cambrian. This seems to be a direct result of there having been an additional suture, the ocular suture, below the visual surface, so that on death or exuviation, the lens-bearing unit was separated from the rest of the librigena. Even if preserved, such
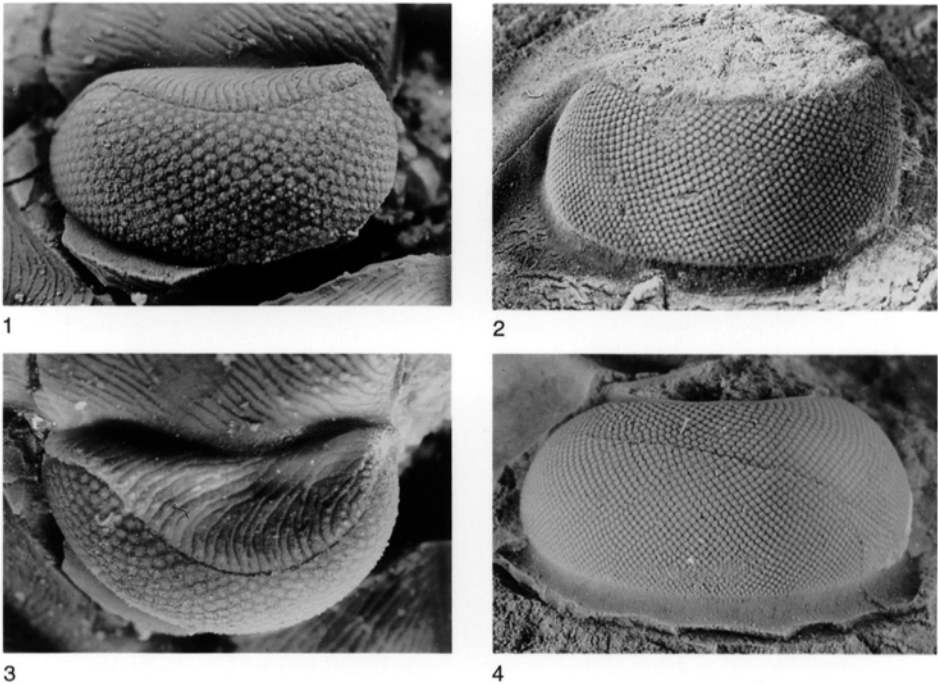
FIG. 102. Holochroal eyes. *1,3, Cornuproetus sculptus* (Barrande), Lower Devonian (Pragian), Hostin, Bohemia; lateral and dorsal views, ×22.5 (Clarkson, 1975, pl. 3, fig. 1–2). *2, Paralejurus brongniarti* Barrande, Dvorce-Prokop Limestone, Devonian, Bohemia; lateral view, ×7 (Clarkson, 1975, pl. 1, fig. 1). *4, Paralejurus campanifer* (Beyrich), Koněprusy Limestone, Devonian, Bohemia; lateral view, ×9.5 (new).

a small object is unlikely to be retrieved. The ocular suture, first noted by Öpik (1967), seems not to have been functional in meraspid Olenellina and juveniles of other Cambrian trilobites, and in the latter the visual surface adheres to the librigena. It is probable that the normal pattern in Ordovician and later trilobites, where the visual surface was part of the librigena, was derived by paedomorphosis from such an ancestral state. Fully developed eyes of abathochroal type have been described in Lower Cambrian eodiscids from China (X. Zhang & Clarkson, 1990). Otherwise, because of the ocular suture and the comparative rarity of well-preserved juveniles, little is known about the eyes of trilobites for the first 50 or so million years of their history.

The earliest eyes that are well known (other than those of the Eodiscina) are those of the Olenidae (Clarkson, 1973b; Clark-son & Taylor, 1995). In the first representatives (*Olenus* and *Leptoplastus*), the ocular suture was functional, and the visual surface is unknown (Fig. 103). Later olenids, however, may retain the eye as part of the librigena, as in *Sphaerophthalmus* and *Ctenopyge* (Fig. 104), where the visual surface is globular and the lenses thin and biconvex, and in *Peltura* and *Parabolina,* where the eye is flatter and sessile and lenses are arranged differently.

Much more is known about the eyes of post-Cambrian trilobites, for in these, with a few exceptions (notably most Calymenidae), the ocular suture was not developed, and hence the visual surface was retained. In most Ordovician groups the diversity in the form and size of the eye is singular; although most of these trilobites have eyes of moderate size with a few hundred lenses, in some the eyes became gigantic as in some Cyclo-
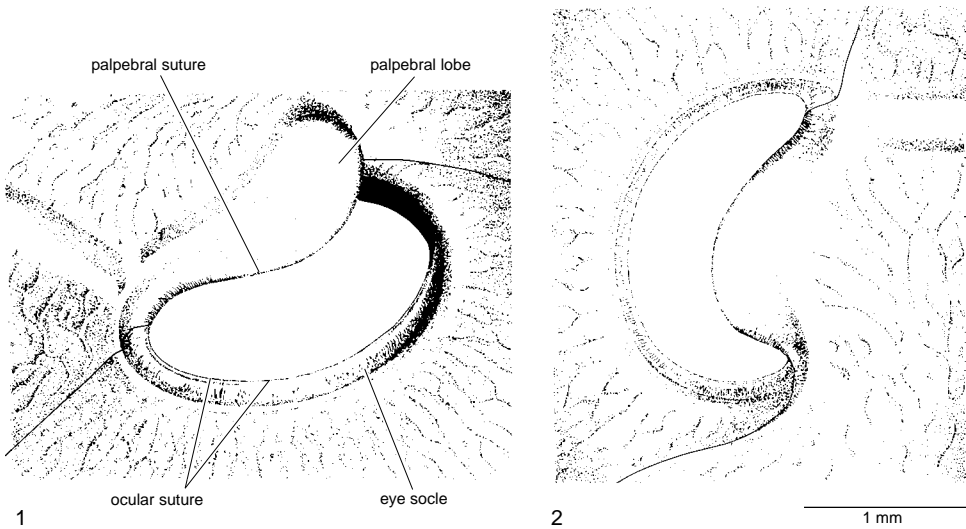
FIG. 103. Olenid eyes. *Olenus wahlenbergi* WESTERGAARD, Upper Cambrian, Skane, Sweden. Reconstruction of eye region in adult, showing the functional ocular suture, by means of which the visual surface was separated from the librigena; *1,* oblique-lateral and *2,* dorsal views (Clarkson, 1973b).

pygidae (Fig. 105) and even fused anteriorly (Fig. 101.2). The striplike eye of *Remopleurides* has over 15,000 tiny lenses. Many Ordovician forms are blind. Holochroal eyes are normally quite large and distinct in post-Ordovician trilobites; they are usually reniform with well-developed lenses, and this kind of rather conservative organization persisted in trilobites through the Carboniferous and to the end of the Permian.

Geometry of the Visual Surface and Lens-Packing Systems

During the ontogeny of trilobites, the eye first appears in the protaspid stages at the anterolateral margin and in successive molts migrated inwards and backwards, taking the facial suture with it. The first lenses are emplaced in a generative zone lying directly below the palpebral suture, initially forming a single horizontal row. This generative zone (and the palpebral suture) has the form of a horizontal, anteriorly expanding logarithmic spiral. Subsequent lenses are always emplaced below existing ones at the bottom of the visual surface, so that as the eye grows, the generative zone moves away from the palpebral suture, all the while contributing lenses in regular sequence to the base. Characteristic patterns of lens packing emerge, which are normally constant for the species and sometimes even within a family or superfamily. On the whole these are based upon a system of hexagonal close packing, and departures from a simple pattern have little to do with the optics of the eye; they are simply solutions to the problem of accommodating (initially) disc-shaped objects on a curving surface. Two categories can be distinguished. In the first the lenses are all of the same size, and inevitable irregularities in packing develop in certain regions of the visual surface. In the second type the lenses are graduated in size and are regularly arranged. The primary control seems to be the spacing of the lens centers and whether it remains constant or changes arithmetically or logarithmically as the eye grows. Several such patterns have been analyzed by CLARKSON (1975).

Visual Fields

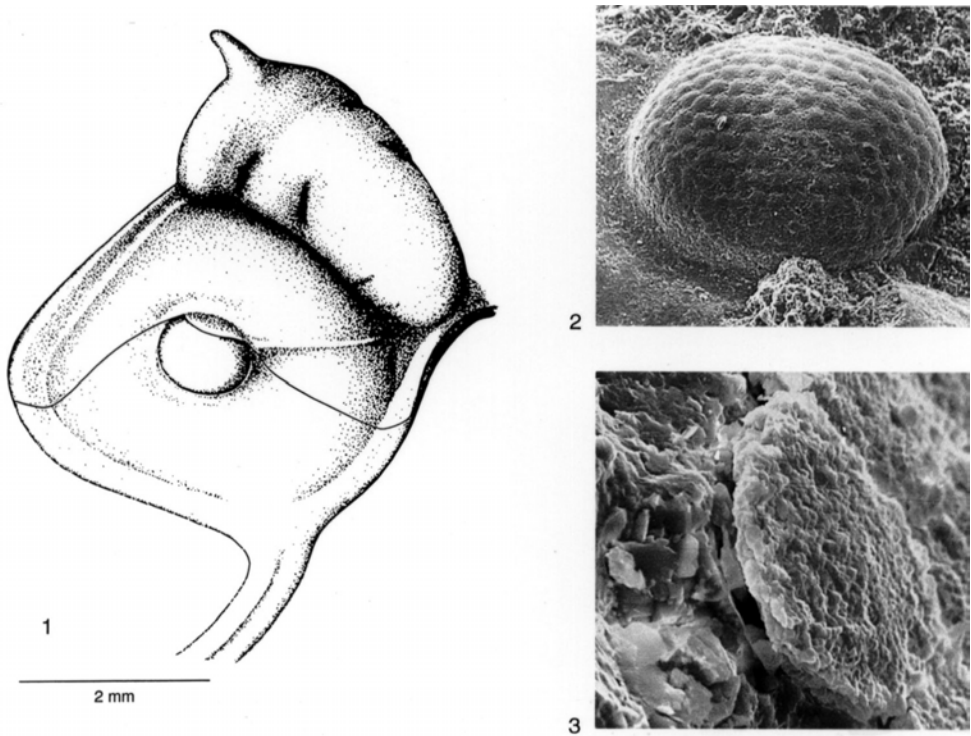The angular range subtended by the outermost lenses is known as the minimum

FIG. 104. Olenid eyes. *1, Ctenopyge (Mesoctenopyge) similis* HENNINGSMOEN, Upper Cambrian, Norway, ×12 (Clarkson, 1973b, fig. 6e). *2, Sphaerophthalmus alatus* (BOECK), Upper Cambrian, Sweden, ×105 (Clarkson, 1973b, pl. 95, fig. 1). *3, S. humilis* (PHILLIPS), Upper Cambrian, Sweden; single lens partly detached from matrix, ×950 (Clarkson, 1973b, pl. 95, fig. 3).

visual field. Its angular dimension depends upon the size of the eye and its surface curvature. Since in holochroal eyes the periph-
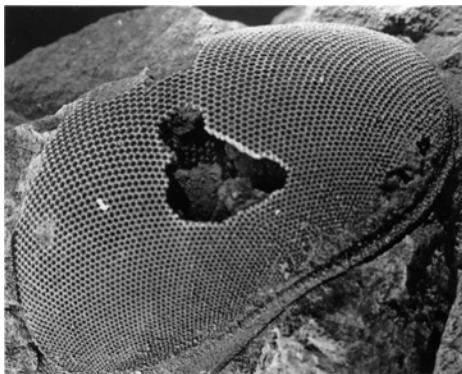

FIG. 105. *Pricyclopyge binodosa* (SALTER), Šárka beds, Ordovician, Bohemia. Internal mold of left eye in lateral view, ×6.5 (Clarkson, 1975, pl. 2, fig. 1).

eral lens-axes are usually normal to the visual surface, the field of view can be worked out simply by measuring their angular bearing, at specific points along the edge of the eye. The technique was described by CLARKSON (1966a). Two basic types of angular visual field are encountered in trilobites with reniform eyes and are exemplified by the eyes of two species of the Devonian styginid *Paralejurus* (Fig. 106). *P. brongniarti* has a striplike field of view, extending from front to rear, with a latitudinal range of no more than 30° above the horizontal. In *P. campanifer,* on the other hand, the visual field extends from below the horizontal to 90° above, so that the animal could see directly upward, and the fields of the two eyes overlap at front and rear. The differences in these forms may relate directly to mode of life; they may, on the other hand, be more a
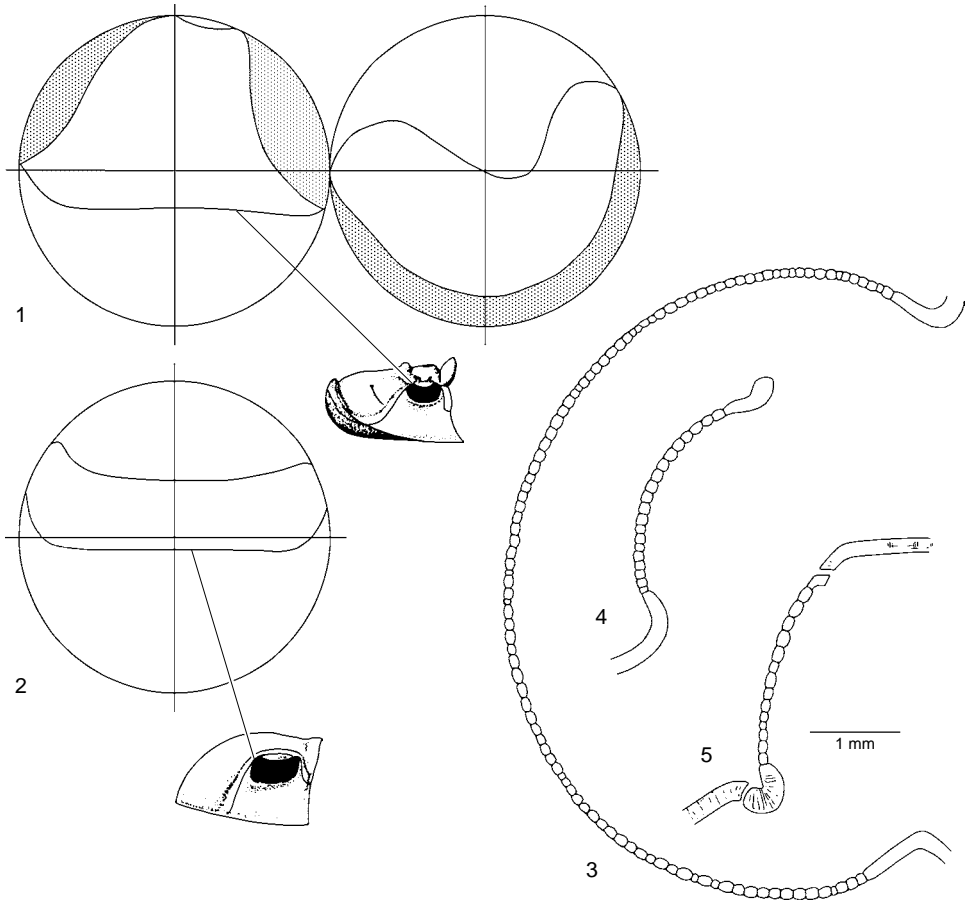
FIG. 106. *1,3,4, Paralejurus campanifer* (BEYRICH), Devonian, Bohemia; *1,* visual field of left eye plotted in equatorial (*left*) and polar (*right*) projection on a Lambert equal area stereographic net. *Coarsely stippled pattern* represents overlapping areas of the visual field; *3,4,* horizontal and vertical sections through left eye. *2,5, Paralejurus brongniarti* (BARRANDE), Devonian, Bohemia; *2,* visual field of left eye in equatorial projection; *5,* vertical section through left eye (Clarkson, 1975, fig. 4).

function of the highly vaulted form of *P. brongniarti* as opposed to the flattened *P. campanifer.* Peculiar visual fields, such as the wide, laterally directed outlook of many cyclopygids, have implications for their swimming mode of life.

Lens Composition, Structure, and Optics

The lenses of the holochroal eye (and of all other trilobite eyes) were constructed of primary calcite (TOWE, 1973), which was probably set in an organic base. Each lens (or, in some instances, small groups or domains of lenses) behaved as a single crystal with its c axis normal to the visual surface. In this way birefringence was minimized. Where lenses have been unaffected by diagenesis, they show a radial pattern (LINDSTRÖM, 1901; CLARKSON, 1979a) that is visible in thin sections of lenses ground parallel with their principal planes and confirmed by acid etching of whole specimens of lenses. Each lens consists of thin, originally contiguous, calcitic lamellae that are radially arranged around the c axis (Fig. 107). The lamellae themselves are formed of slender calcite fibers (trabeculae), which in convex lenses turn outwards in a fanlike manner so
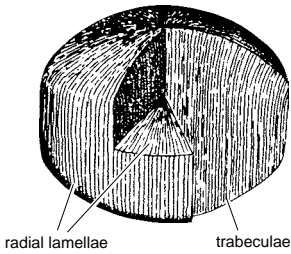
FIG. 107. Reconstruction of a single lens of a holochroal-eyed trilobite, based on *Paladin eichwaldi shunnerensis* (KING), Namurian, England (Clarkson, 1979a, fig. 1d).

that their distal terminations are nearly normal to the cambered outer surface of the lens. This apparently complex system may result from its manner of growth; possibly lenses could increase in size only by addition of trabeculae at the edges.

The lenses of thin-shelled trilobites are normally thin and biconvex, as is seen in the olenids (Fig. 104.3). Thicker lenses are more common in such post-Cambrian trilobites as styginids and proetids. They may be biconvex or planoconvex, the latter type being especially common in thick-shelled trilobites with very long columnar or prismatic lenses such as are found in *Asaphus.* In some species of this genus, the lenses form elongated calcitic pillars, like basaltic columns, as first was recognized by LINDSTRÖM (1901). These lenses have semicircular lower terminations (CLARKSON, 1973a, 1979a), and ray tracing analysis shows that they would bring light to a focus at about the same relative distance below the lens as would the thin biconvex lenses of the olenids or any of the intermediate types. The thickness of the lens is thus mainly a function of the thickness of the exoskeleton rather than being of other significance; what is important optically is the relative convexity of the surfaces.

Nothing is known of the internal structure of holochroal eyes. It is highly probable that an ommatidium-like unit lay below each lens, and both facet diameter and interommatidial angle lie within the same range as modern nocturnal compound eyes (FORDYCE

& CRONIN, 1993). The function of the holochroal eye is thus considered to be similar to that of modern arthropods, adapted to moderate to dim light intensities.

THE SCHIZOCHROAL EYE

Schizochroal eyes appeared quite suddenly in the Early Ordovician and were confined to the suborder Phacopina (Lower Ordovician to Upper Devonian). Whereas the eyes of some other taxa have particular features in common with the schizochroal eyes of Phacopina, these latter have unique, distinctive characters which are unknown elsewhere in the animal kingdom. Schizochroal eyes are normally large, and the visual surface approximates to a lunate segment of a cone (Fig. 108). The lenses are thick, biconvex, and much larger and normally fewer than those of holochroal eyes. They are separated from each other by material known as **interlensar sclera,** which is identical in structure with the exoskeletal cuticle. The lenses are normally arranged in a regular system of hexagonal close packing.

When schizochroal eyes are cut in transverse section, their difference from holochroal eyes becomes most apparent (Fig. 109). Each biconvex lens is set at the outer end of a cylindrical cavity, the sublensar alveola. The outer lens surface is covered by a thin, pellucid corneal covering; this continues at the lens margin to cut through the sclera as a cylindrical ring, the **intrascleral membrane,** free of contact with the lens. In rare instances (CLARKSON, 1967a, 1969a) this membrane has been observed projecting below the visual surface as a tapering cylinder, closed off below. The sublensar alveoli, in plan, are set radially, but in vertical section, at least in *Ananaspis,* they are all parallel and horizontally disposed.

Visual Surface Geometry, Growth, and Lens Packing

In most schizochroal eyes the lenses are arranged in the economical system of hexagonal close packing, and this is usually regular. In an eye such as that of *Acaste,* the

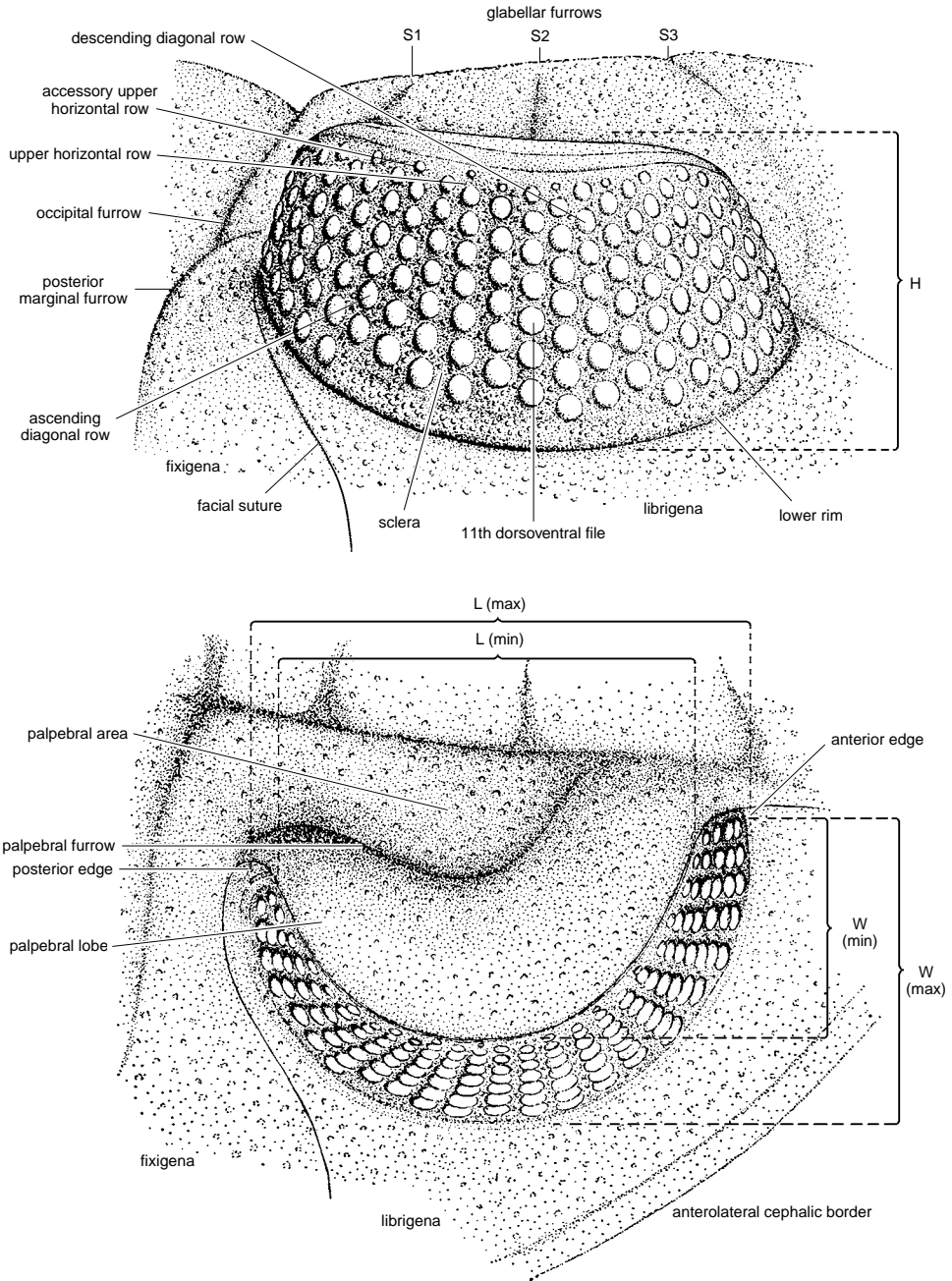FIG. 108. *Acaste downingiae* (SALTER); external morphology of schizochroal eye and immediate environs (*H,* height; *L,* length; *W,* width), ×17.5 (Clarkson, 1966a, fig. 1a,b).

dorsoventral files and ascending and descending diagonal rows can easily be distinguished (Fig. 108). The lenses vary in size within any eye, however, and this variation is a function of the growth geometry of the visual surface.
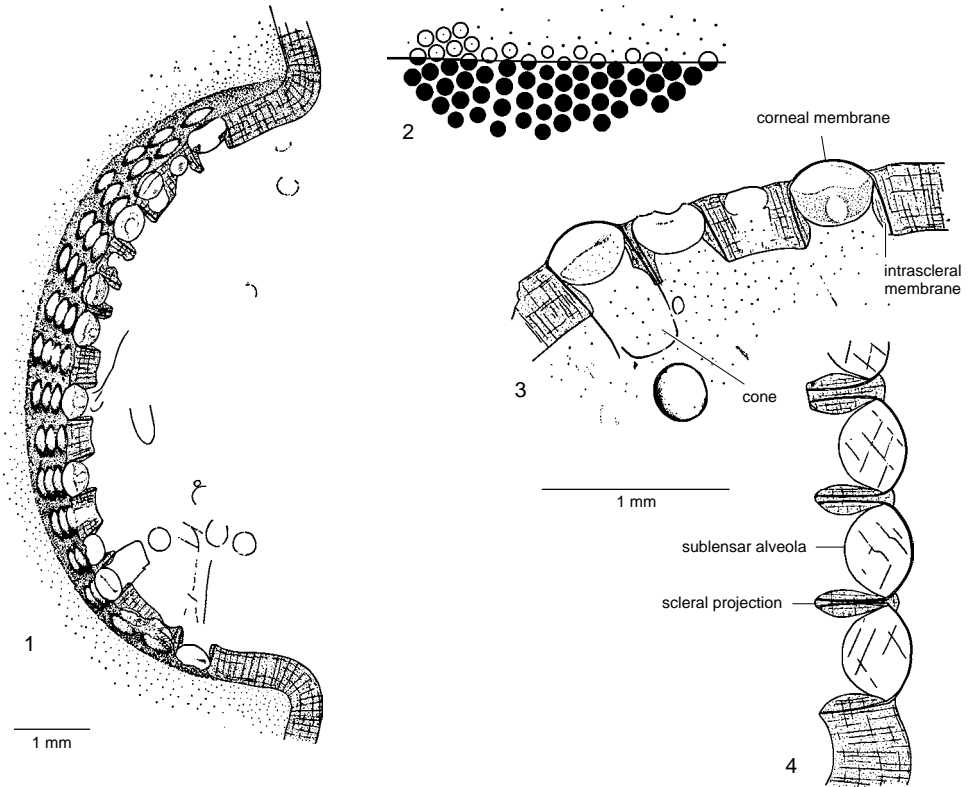
FIG. 109. *Ananaspis fecunda* BARRANDE, Silurian, Bohemia. *1,* Horizontal section through left eye along the line shown in part 2; *3,* enlargement of part of the same horizontal section to show a cone or capsule below the 14th dorsoventral file; *4,* vertical section through eye where lenses have been recrystallized (Clarkson, 1967a, fig. 1a,b,c,i).

As with holochroal eyes, the earliest formed lenses are emplaced in a generative zone that lies directly below the palpebral suture. This zone forms an anteriorly expanding logarithmic spiral that keeps the same form throughout successive molts, though it increases in size. The earliest lenses may form a single upper horizontal row, as in *Ananaspis;* but more often, especially if the eye has many lenses (*Odontochile*), there may be one or more accessory, upper, horizontal rows above the first, full, horizontal row. These were emplaced during the very first stages of growth, when the eye was very small but rapidly growing forward. New horizontal rows are always emplaced below existing ones, the lenses of each new row being offset from the ones above, so that the characteristic packing system emerges. As the eye grew the generative zone moved away from the palpebral suture, contributing lenses in regular sequence until the eye was fully grown. There is no direct relationship between the basic shape of the visual surface and the packing of the intersecting rows of lenses. The generation of the visual surface and lens emplacement were governed by different developmental programs, but since the visual surface expanded as it grew downwards, extra space became available for new lenses, a matter that had implications for the packing of lenses.

In nearly all schizochroal eyes the size of the lenses varies across the visual surface, and it is clear that the size to which the lenses grew depended upon the relative spacing of the lens-centers when newly introduced in the generative zone. If the lens-centers were closely spaced, lenses never grew large; if, on the other hand, the centers were wide apart,
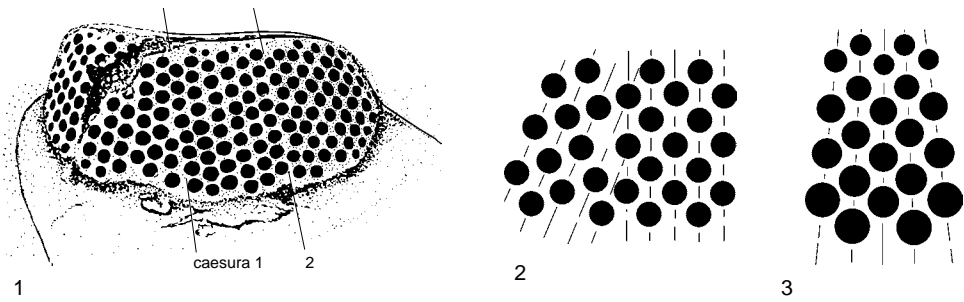
FIG. 110. *1,* Right eye of adult specimen of *Ormathops atavus* (BARRANDE), Ordovician, Bohemia, showing irregular packing and caesurae, ×10 (Clarkson, 1971, fig. 2h). *2,3,* Schematic drawing of lens packing in *2, Ormathops* and *3, Phacops* sensu lato (Clarkson, 1975, fig. 5b,c).

the lenses grew much larger. When the lens-centers were programmed to develop in sequence without any change in spacing, the lenses were all of the same size and lay in parallel dorsoventral files. In one of the earliest phacopid genera, the Ordovician *Ormathops* (Zeliszkellinae) (Fig. 110.1), this is exactly what happened (CLARKSON, 1971). Since it is geometrically impossible to pack uniformly sized lenses upon a curving, downwardly expanding surface in regular sequence, the ideal arrangement of hexagonal close packing breaks down. Sometimes areas of loose and irregular lens-packing are visible on an otherwise regular surface. In other specimens of the same species, blocks of parallel, regular dorsoventral files lie against the truncated edges of other such blocks, the line of junction being termed a **caesura**. New lenses arose when a critical spacing arose (presumably at each molt stage) between the generative zone and the lenses above it. The downward expansion of the visual surface created extra space and this was filled by one or more lenses, which were generated through the automatic operation of the program. Each new intercalated lens then acted as a focal point for the generation of further lenses, either in parallel blocks truncated by caesurae or by irregular areas, depending on the precise conformation of the eye.

In all other Phacopina the problem of achieving regularity was solved simply by the introduction of a constant arithmetical increase in spacing as the eye grew (Fig. 110.3).

The result was that the lenses increased in size downwards (and usually also to the front and rear). Irregularities in such eyes are thus seldom found.

Structure and Optics of the Lenses

The internal structure of phacopid lenses is usually diagenetically altered, but in rare instances there has been no major change; and some or all of the original internal organization can be elucidated. LINDSTRÖM (1901) illustrated sections through the eye of *"Phacops macrophthalmus,"* each lens of which seems to consist of a doublet structure with two adjacent components (Fig. 111). Although LINDSTRÖM believed that these doublets were diagenetic artifacts, their presence as original structures has been amply confirmed by recent work. Schizochroal lenses, like those of holochroal eyes, were constructed of lamellae arranged radially around the *c* axis. In sections normal to the principal plane it is apparent that the lower part of each lens was occupied by an intralensar bowl; this interlocked with a mushroom-shaped upper unit. As in holochroal eyes, the *c* axis was normal to the visual surface. There are at least three patterns of lens construction within Phacopina, and these seem to have operated on slightly different optical principles. Some early Phacopina such as *Dalmanitina* have rather parabolic lenses, and the intralensar bowl in each was flattened with a central indentation (Fig. 112.2). The contemporaneous *Crozonaspis,* on the other hand, had more biconvex lenses
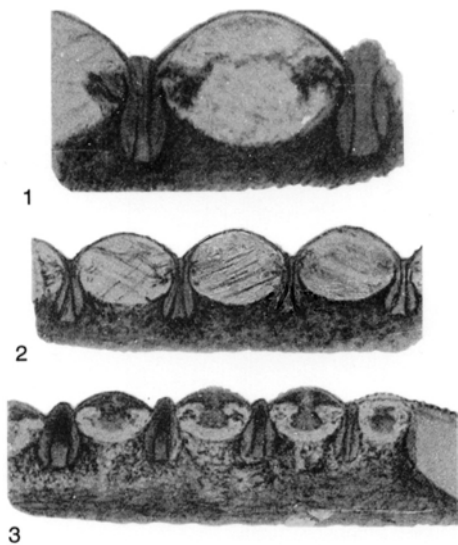
Fig. 111. Internal structure of schizochroal lenses of "*Phacops macrophthalmus* Burmeister," Devonian, Germany; *1,2,* longitudinal sections showing lenses separated by interlensar sclera, and *3,* with intralensar bowls present (Lindström, 1901, pl. 4, fig. 3–5).

in which the bowl was thicker and had a wavy upper surface (Fig. 112.4). It has been shown (Clarkson & Levi-Setti, 1975) that the upper units of these correspond respectively to ideal, thick, but aplanatic lenses designed by Descartes and Huygens in the 17th century (Fig. 112.1,3). Experimental models have been made with intralensar bowls of differing refractive indices; these show that a slight difference in refractive index between the upper unit and the bowl, operating together with the correcting surface, focuses light very sharply a short distance below the lens.

The lenses of the Devonian *Phacops* (Fig. 113–114, 115.3–4) are ultrastructurally very complex (Clarkson, 1979a; Miller & Clarkson, 1980). The bowl consists of dense calcite and thins to be absent proximally. The upper unit is built of calcite sheets, radially arranged around the *c* axis of the lens. Each of these sheets in turn consists of a palisade of calcite fibers parallel with the *c* axis proximally but fanning outwards near the outer surface of the lens. This may have

minimized the effects of birefringence. As Campbell (1976, 1977) noted, a central core of dense calcite may also have had a correcting function. After ecdysis the lens is reformed. In the earliest postecdysial stages, the cuticle was still flexible and the lens had the form of a small cone suspended from the center of the cornea. Subsequently, the lens spread to the periphery, thickening and becoming saucer shaped, and ultimately acquiring the characteristic wavy proximal surface of a Huygensian lens. The bowl and core differentiated last of all. Horváth (in Horváth & Clarkson, 1993) calculated the successive forms of an idealized lens of *Phacops,* optimized for correction of spherical aberration at all stages of postecdysial development. The actual growth series conforms very closely to the theoretical computation; vision was bio-optimized from the earliest post-ecdysial stages. The differentiated intralensar bowl probably functioned not only as a correcting element but also reduced reflectivity and thus optimized the transmission of light to the photoreceptors below.

Origins, Functions, and Use

The earliest schizochroal eyes were probably derived paedomorphically from a holochroal ancestor (Clarkson & Zhang, 1991, p. 283). In the few examples in which early growth stages of holochroal eyes are known, the lenses are relatively very large and separated from each other by interstitial material. The retention of this juvenile condition by paedomorphosis into the adult phase would be the first and most important stage in the origins of the schizochroal condition. Although the earliest known eyes of Phacopina are typically schizochroal, *Ormathops* (Fig. 110.1–2) has an eye with a different lens-packing system from that of later Phacopina, contingent upon its lenses all being of the same size. It may well have retained the identical lens size from a holochroal ancestor, but this early system was abandoned and regularity was achieved at the expense of identical lens size. This

must be important in some way to the functioning of the eye as a whole.

It is not yet known how the schizochroal eye operated, but certain lines of evidence are suggestive. The visual field normally formed a relatively narrow horizontal strip, with the upper limit of vision rarely rising above 40° latitude (Figure 115.1,3). The lens axes were not distributed uniformly within the visual field. They were usually clustered towards the base of the visual field (*Phacops*), and in some genera (*Acaste*) the plan curvature of the visual surface is so much greater than the profile curvature that the lens axes of the dorsoventral files tended to form visual strips traversing the narrow visual field from top to bottom (Fig. 115.2,4). Such eyes as these seem initially to be well adapted for movement perception, since a passing object would register as a flicker across the visual field. This could have been achieved, however, with much simpler lenses than the elegant lens doublets actually possessed by Phacopina, and clearly schizochroal eyes had higher levels of function than perception of movement alone. The interpretation thereof, however, depends upon the nature of the sublensar structures, and evidence is still very limited.

STÜRMER interpreted the subparallel dark lines seen inside the eye facets in X-ray photographs of pyritized *Phacops* (Fig. 88) as ommatidia (STÜRMER, 1970; STÜRMER & BERGSTRÖM, 1973, p. 112–113). Doubts as to the validity of this interpretation have been expressed by CLARKSON (1973a, p. 441–442; 1979a, p. 16) and CAMPBELL (1976, p. 175), and Professor J. BERGSTRÖM (personal communication, March 1995) does not accept it. He pointed out that these supposed optical fibers form part of a series with the filaments of the outer limb branches (Fig. 88) and may continue outside the eye. Further, they are in a single, subparallel row, not in a radially arranged bunch in relation to the eye facets. Accordingly, Figure 94 has been modified from the original version (STÜRMER & BERGSTRÖM, 1973, fig. 5a, p. 115) to omit the ommatidia, and the label
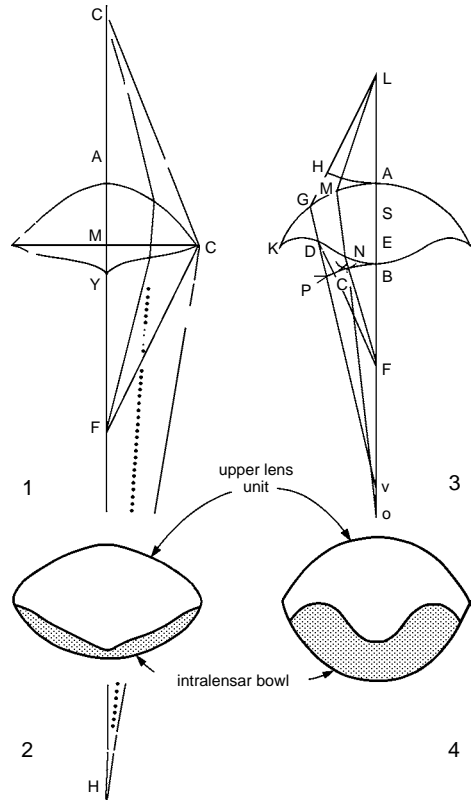

FIG. 112. *1,* An aplanatic lens in air constructed by Descartes in 1637; *2,* reconstructed lens of *Dalmanitina socialis* (BARRANDE), Ordovician, Bohemia; *3,* an aplanatic lens in air constructed by Huygens in 1690; *4,* reconstructed lens of *Crozonaspis struvei* HENRY, Ordovician, Brittany, France (Clarkson & Levi-Setti, 1975, fig. 4).

ommatidia has been removed from Figure 88.

The view is now generally held that, rather than an ommatidium, there lay below each schizochroal lens a relatively short ocellar capsule floored by a flat layer of narrow cells forming a retina. This was first proposed on the basis of poorly known, short, cylindrical tubes below the lenses (termed *cone* in Fig. 109.3) and on possible modern analogues (CLARKSON, 1967a, 1979a; CAMPBELL, 1976) (Fig. 116). More recent physicomathematical analysis of the lens optics (HAACK, 1987; FORDYCE & CRONIN, 1989, 1993) lends considerable support to the retinal-capsule
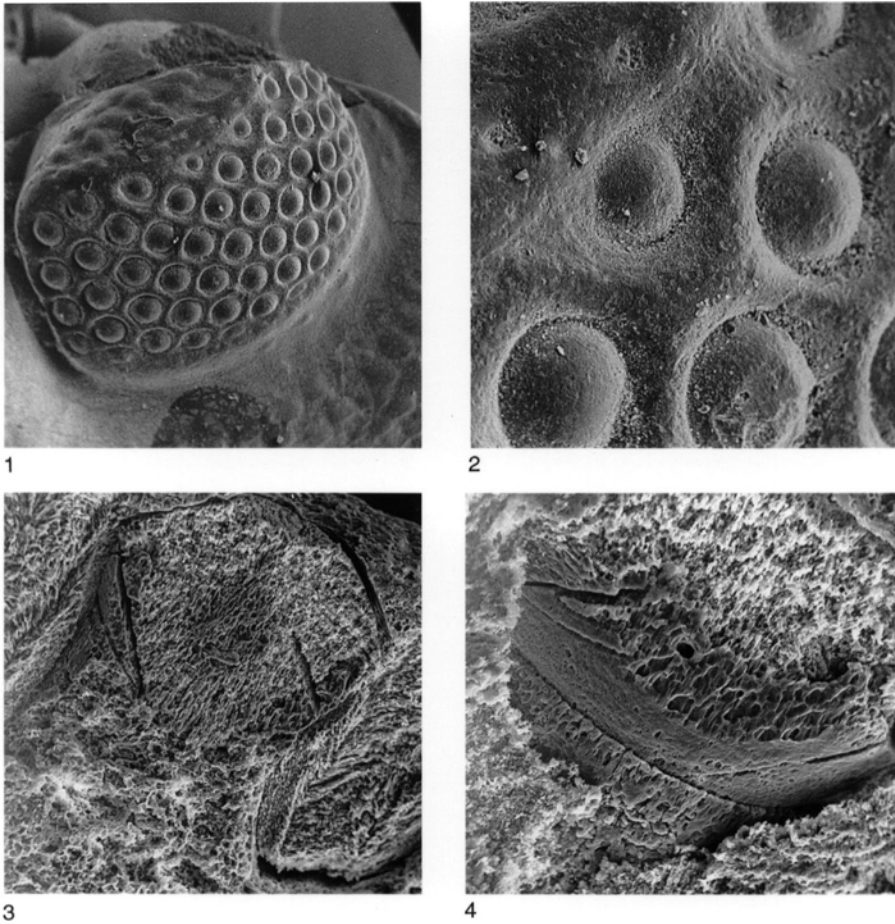
FIG. 113. Schizochroal eyes of *Phacops rana. 1,2,* Left eye of *P. rana rana* (GREEN), Middle Devonian, Ohio; *1,* anterolateral view, ×20 (new); *2,* enlarged anterolateral view, showing part of visual surface, ×105 (new). *3,4, P. rana milleri* STEWART; *3,* lens cut vertically and etched with weak acid, showing core, intralensar bowl, trabeculae, and laminae, also intralensar sclera; the etching has opened up cleavage planes in the calcite (compare with Figure 114), ×100; *4,* obliquely cut and etched lens showing junction of massive-textured intralensar bowl and more open-textured upper unit (compare with Figure 114), ×160 (Miller & Clarkson, 1980, fig. 28, 34).

model. From this work it emerges that eyes of Phacopina are best regarded as an assemblage of simple retinal eyes rather than as an ommatidial eye. In theory, starting from an array of simple visual units, visual acuity could be improved in two ways. One is by generating many identical ommatidia and packing them closely together to make a standard compound or holochroal eye. The other would be by increasing the number of light detectors beneath individual lenses—in other words, to have a retinal layer below each one. This seems to have taken place in the Phacopina, and the resolving power of each lens in a schizochroal eye of advanced type, in which the lenses are very large and relatively few, has been estimated as ten times that of modern compound eyes, comparable to that of a frog. A further consequence of retinular organization, which also takes account of the extreme convexity of each lens, is that adjacent lenses within the
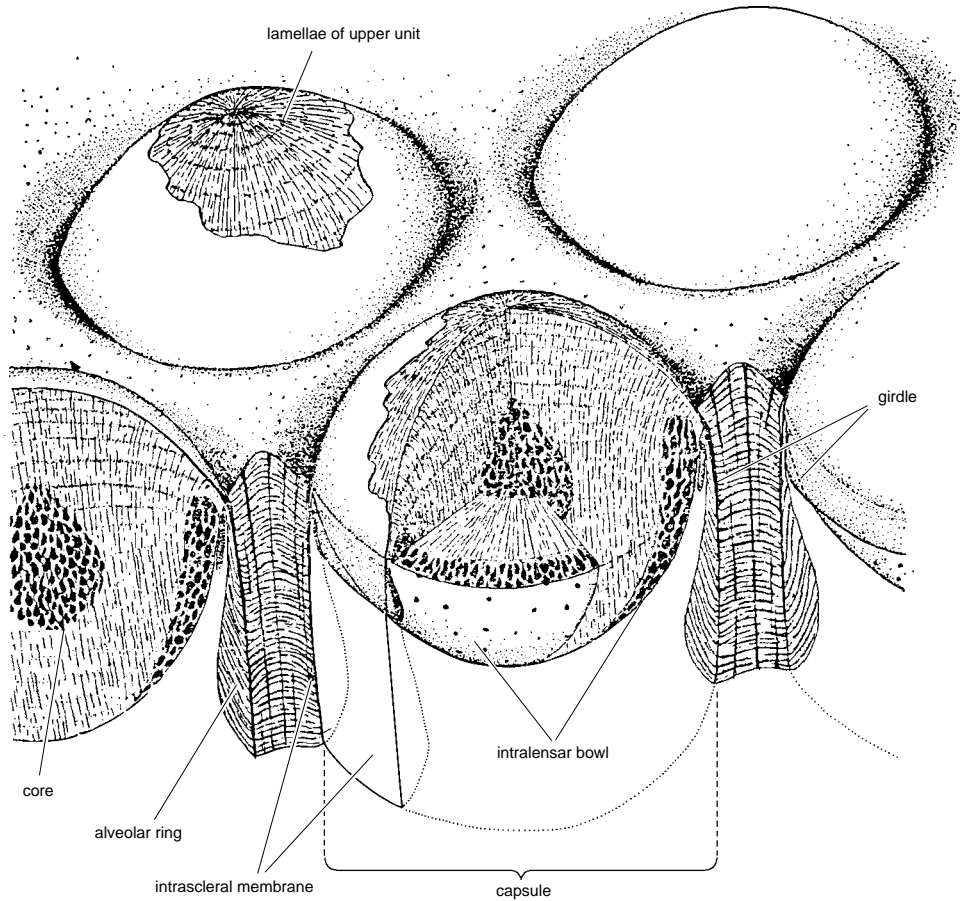
Fig. 114. *Phacops rana milleri* Stewart; reconstruction of part of lens array with lenses dissected to show internal structure (Miller & Clarkson, 1980, fig. 3).

one eye could have been used for stereoscopic vision (Stockton & Cowen, 1976). A pair of adjacent lenses covering a particular region of the visual field could both have picked up the same moving object on opposite sides of their respective retinas. As it moved towards or away from the trilobite, its distance could have been inferred by comparison of images in adjacent retinas at any one time, whereas its movement could be detected by comparison at successive times. The schizochroal eye might thus have functioned primarily to give a warning of the presence and movement of nearby objects and in particular a three-dimensional appreciation of actual distance. Such a system

could have operated if the neural relay system had been as advanced as the lenses. Several groups of living arthropods have eyes with comparatively few and separated lenses (and those of male strepsipterid insects appear remarkably similar in many ways to the schizochroal eyes of trilobites). Other arthropods, including the larval sawfly *Perga* and the water bug *Notonecta,* have separated lenses with an internal, aplanatic doublet apparatus. Even so, none of the modern counterparts are so similar to the schizochroal eyes of trilobites that they give unequivocal evidence about how these eyes actually worked (Horváth, Clarkson, & Pix, 1997).
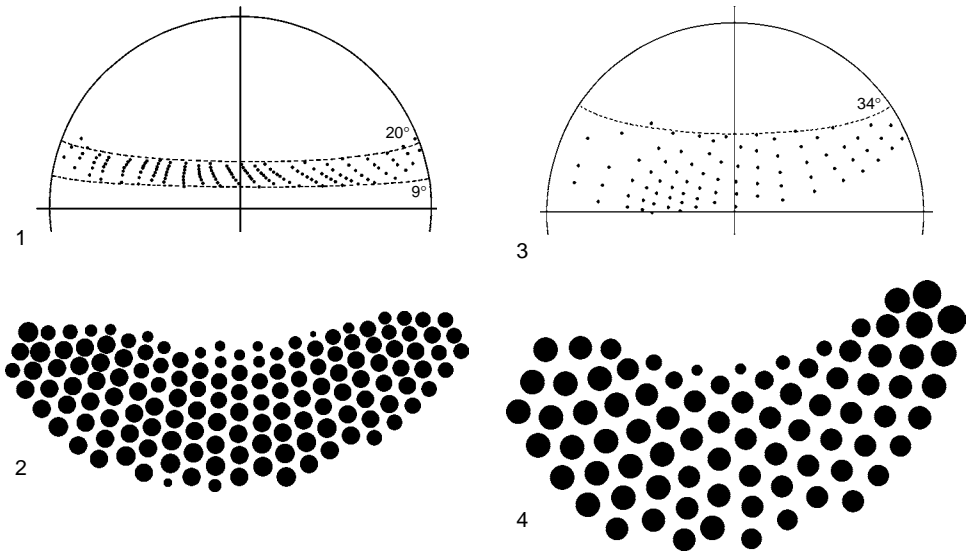
F<small>IG</small>. 115. Visual fields of schizochroal eyes shown by plotting the angular bearing of individual lens-axes on a Lambert equal-area net (*left* is anterior). *1,2, Acaste downingiae* S<small>ALTER</small>, Silurian, England; *1,* visual field of adult left eye; *2,* projected visual surface of same eye (Clarkson, 1966a, fig. 1e). *3, 4, Phacops rana crassituberculata* S<small>TUMM</small>, Devonian, Ohio; *3,* visual field of adult left eye; *4,* projected visual surface of same eye (Clarkson, 1966b, fig. 2b,c).

Clearly the eyes of Phacopina were organs of high biological quality. Although blindness is not uncommon in trilobites (in species closely related to those having either schizochroal or holochroal eyes), it may be environmentally related and does not imply that the eyes were of poor enough quality to have been easily dispensed with. There is a general correlation between the possession of large, well-developed eyes and the ability to enroll, and major changes both in eye structure and enrollment ability seem to have taken place in many early Ordovician groups at about the same time. It seems reasonable that the trilobite eyes functioned primarily as distant, early-warning sensors for the detection of approaching predators, and the combination of advanced visual and protective systems may have been a major factor in prolonging the existence of trilobites until the end of the Permian.

THE ABATHOCHROAL EYE

A third type of eye, designated abathochroal, has been described by J<small>ELL</small> (1975b) in the Cambrian Eodiscina. First described in such Middle Cambrian genera as *Pagetia* and *Opsidiscus,* this kind of eye has recently been recorded (X. Z<small>HANG</small> & C<small>LARKSON</small>, 1990) in the Lower Cambrian *Neocobboldia* from China, making eyes of this kind among the oldest known.

The abathochroal eye superficially resembles a small schizochroal eye, having a relatively small number (50 to 70) of biconvex lenses separated from each other on the visual surface, with a semiregular arrangement of hexagonal, closely packed rows and files. It does not, however, have any indication of a deep interlensar sclera between the lenses, and evidence for an interscleral membrane is limited. It is possible instead that each lens had a separate corneal membrane, which may have been fixed to the interlensar areas round the lens margin. If these differences can be confirmed, the abathochroal eye may safely be considered a distinct type. Although the eye of *Neocobboldia* is of this kind, that of the closely related *Shizhudiscus* is of a more normal holochroal type.

Bearing in mind the ontogeny of holochroal eyes, which initially had separated

lenses, it is probable that the abathochroal eye was derived by paedomorphosis from an ancester of holochroal type, as is considered likely for the origin of the much more elaborate schizochroal eye. Internal molds of *Neocobboldia* from China frequently show a small dimple in the center of each lens (Fig. 117). This indicates that the lenses were of the corrected, aplanatic kind described by Descartes, able to bring light to a sharp focus though they were of moderate thickness. Despite the elegance of these early eyes, many Eodiscina lost their visual organs altogether, and this loss may have been environmentally related.

EYE REDUCTION AND BLINDNESS

Compound eyes are primary structures in trilobites, appearing in the earliest genera and persisting in most trilobites until the final extinction of the group in the Late Permian. Secondary blindness, however, is not uncommon, especially in such long-lived major taxa as the Agnostida and Trinucleoidea, in which it is characteristic of the group. It also occurs in some representatives of taxa in which the eyes are normally developed.

There are many modern, deep-sea animals in which the eyes are either hypertrophied or reduced and lost, and blindness is also the norm in endobenthic forms. In many of the blind trilobites, the loss of the eye is likewise probably related to living in dark or infaunal habitats, and it is probably no coincidence that in some blind groups sense organs of a different kind were highly developed and seem to have been the dominant environmental monitor. The trinucleoids present a particularly interesting case. The earliest (Tremadocian) and probably ancestral genus is *Orometopus,* in which the eye and facial suture are present but the pitted fringe, so characteristic of later trinucleids, is undeveloped. In the later trinucleids, however, the fringe becomes large and prominent, with the fringe pits regularly arranged, while the suture becomes marginal, and the eye is lost. If, as has been often suggested, the fringe
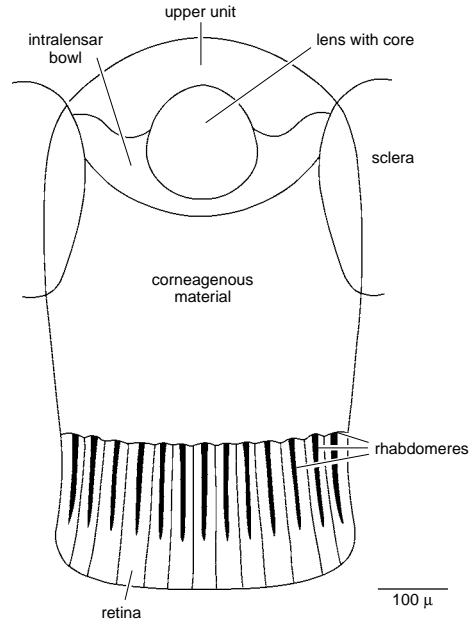

FIG. 116. Diagrammatic reconstruction of an optical unit of a phacopid trilobite, showing inferred retina with rhabdomeres, corneagenous material, sclera, and lens with core, upper unit, and intralensar bowl (Campbell, 1976, fig. 8).

acted as a compound ear—a vibro- or possible chemosensory organ—it is quite possible that this became the primary sensory organ when vision was lost. A parallel situation may have existed in the Harpina, in which the pitted fringe is large but the eye is reduced to a few lenses only. The evidence for this suggestion is no more than circumstantial and is clearly not applicable to the Agnostina or other groups where there is little or no evidence of other kinds of sense organs.

A few instances are known in which secondary eyes have developed in otherwise blind groups. Thus the lateral eye spot described by STØRMER (1930) on the gena of the trinucleid *Tretaspis* was probably an organ of secondary origin. A further example was given by COURTESSOLE (1973) in the Middle Cambrian Conocoryphidae of the Montagne Noire in southern France. All conocoryphids in this region are blind except for the one species *Conocoryphe oculata,*
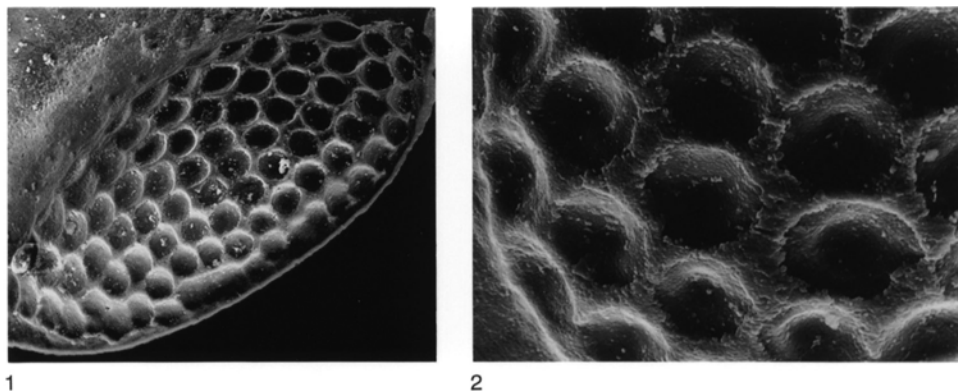
Fig. 117. Abathochroal eye of *Neocobboldia chinlinica* Lee, Lower Cambrian, southwestern China. *1,* Internal mold in phosphate, ×220; *2,* detail of internal mold, showing a dimple in the center of each lens, indicating an original lens of the aplanatic type described by Descartes, ×550 (X. Zhang & Clarkson, 1990, pl. 4, fig. 1a, 6a).

which is otherwise very similar to related species in the same area. This species has a curving lobe of normal eyelike form on the gena, though the suture remains marginal. It is poorly preserved, but there is little doubt that it is an eye. Presumably, in this case, genes for eye development were masked and not lost, and a secondary eye of a kind could develop with the removal of the masking genes.

The clearest examples of progressive reduction of eyes are to be found in Middle and Upper Devonian Proetida and Phacopina in western Europe. Richter and Richter (1926) recorded examples of both these groups from the Devonian of Germany, showing lateral migration of the facial suture accompanying eye degeneration and finally blindness. A clear morphological series in Phacopina is well known (Fig. 118), and Erben (1961) showed various paths to eye

loss in Proetida. These works were based upon morphology alone, however, since at the time of writing the stratigraphy was poorly known. It has been shown, however, that in Tropidocoryphinae from southern France, eye reduction is truly progressive and can be followed through time (Feist & Clarkson, 1989). In the Middle and Upper Devonian carbonate succession in the Montagne Noire, an unbroken series of conodonts allows a precise stratigraphical zonation. Tropidocoryphinae occur throughout the sequence. Whereas these had been a stable group for some 40 million years prior to the middle Givetian, they underwent a rapid evolution in their last few million years, exhibiting some striking transformations of the cephalon and the regression and virtual disappearance of the eye within a relatively short interval of time (Fig. 119). They also diminished markedly in size and lost
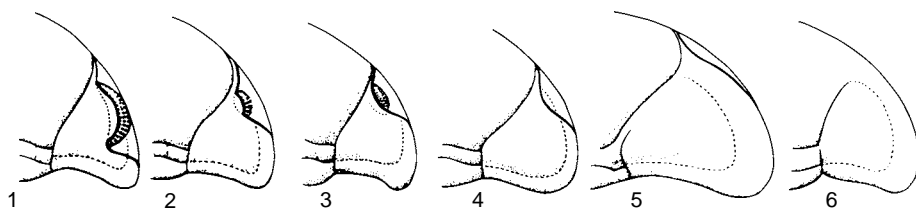
Fig. 118. Lateral migration of the facial suture accompanying migration, reduction, and disappearance of the eyes in Upper Devonian Phacopidae from Germany. *1, Phacops circumspectans* Paeckelmann; *2, Phacops wedekindi* Richter & Richter; *3, Cryphops? ensae* (Richter & Richter); *4, Trimerocephalus mastophthalmus* (Reinhard Richter); *5, Dianops limbatus* (Reinhard Richter); *6, Ductina ductifrons* (Richter & Richter) (Moore, 1959, fig. 47).

FIG. 119. Evolution of the last Tropidocoryphinae in the Devonian of France, showing two separate lineages with eye reduction. Dominant environments indicated; *vertical bars* show stratigraphical range; *stippled lines* suggest relationships (Feist & Clarkson, 1989, fig. 2).

their original relief so that the glabella became virtually flush with the surface of the cephalon, probably adaptations to an en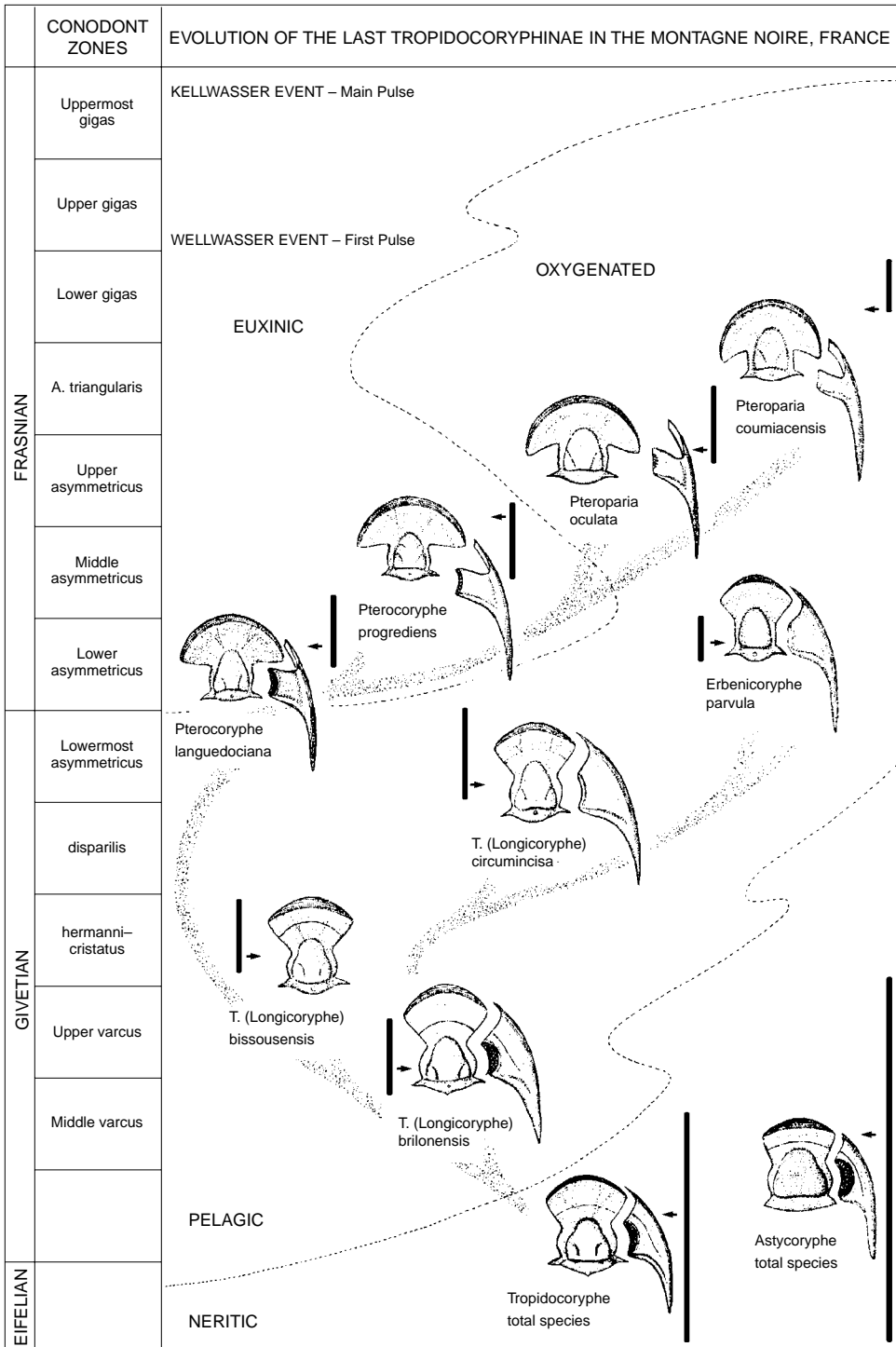do-benthic life. Two separate lineages show eye reduction and blindness. In the first, the *Tropidocoryphe (Longicoryphe)-Erbenicoryphe* lineage, the cephalon retained the same pattern as the ancestral rootstock, but the eye was progressively reduced to a slightly convex surface, indistinctly defined and lacking lenses. The second lineage, *T. (Longicoryphe)-Pterocoryphe-Pteroparia,* shows a remarkable, backward migration of the anterior branch of the suture, which progressively swung posteriorly in successive species over about 3 million years. Here again the eye degenerated progressively so that the last forms were blind. Sutural migration and eye reduction are not genetically linked, however, and the unusual form of the cephalon and suture probably resulted from an adaptation to the euxinic environment in which *Pterocoryphe* originated. The reduction of the eye and the association with the adoption of an endo-benthic habit is thus parallel in the two lineages but superimposed upon a different original cephalic configuration.

Eye reduction and blindness in these Upper Devonian Tropidocoryphinae can be related to local environmental controls. Diminution and loss of the eye, however, seem to have been widespread generally in proetids and phacopids during the Late Devonian. Among the rich proetid faunas of the late Upper Devonian of southern China (Yuan, 1988), many endemic genera and species have the eye reduced or absent (e.g., *Bapingaspsis, Skemmatocare*); and it has proved possible to trace their phylogeny. Feist's (1995) study of eye reduction in Upper Devonian phacopids showed it to be the result of progressive paedomorphosis, so that the early larval configuration of the visual organs is retained in the adult of the descendant. Feist suggested that Upper Devonian eye reduction on a global scale is probably linked to periods of eustatic deepening, and the trilobites became adapted to life on, or burrowing within, a muddy sea floor beyond the limit of light penetration.

CEPHALIC SEGMENTATION

H. B. Whittington

The number of segments that were originally fused to form the trilobite cephalon has been a subject for discussion because of its possible significance in high level classification of Arthropoda. It is assumed that each segment of the thorax and pygidium is the exoskeleton of a single somite. The occipital ring of the glabella, the posterior border, border furrow, and adjacent area of the gena are similar to the axial ring, posterior pleural band, and pleural furrow of a thoracic segment and hence are assumed to represent much of the posterior cephalic segment. Lateral glabellar furrows, separated by a distance (exs.) similar to the length (exs.) of the occipital ring, suggest the presence of more anterior cephalic segments. Such glabellar segmentation is most evident in early developmental stages, and clues to the number of cephalic segments have been sought from such stages, and the holaspides, of stratigraphically early trilobites. Prominent among the latter have been Olenellina, the views of Walcott (1910), Størmer (1942), Raw (1953), Palmer (1957), and Bergström (1973a, 1973d) having been derived largely from American and European species. Hupé (1951, 1953a) introduced new ideas into the discussion from his studies of Early Cambrian Olenellina, such as *Daguinaspis,* from Morocco. The early developmental stages of *Olenellus* (Palmer, 1957) have an occipital ring and three distinct axial segments between it and the frontal glabellar lobe, and these divisions are also shown by *Daguinaspis* and species of other genera. Differences of opinion arise over the number of segments represented by the frontal lobe. This lobe, into which the ocular lobe runs (Fig. 16), is undivided in the early developmental stages of *Olenellus,* and Palmer concluded that it represented a single segment. The ocular lobe is divided into two ridges in *Holmia,* the posterior passing into the most posterior portion of the frontal lobe, the anterior into a more anterior portion of that lobe (Fig. 120). Bergström (1973a) there-
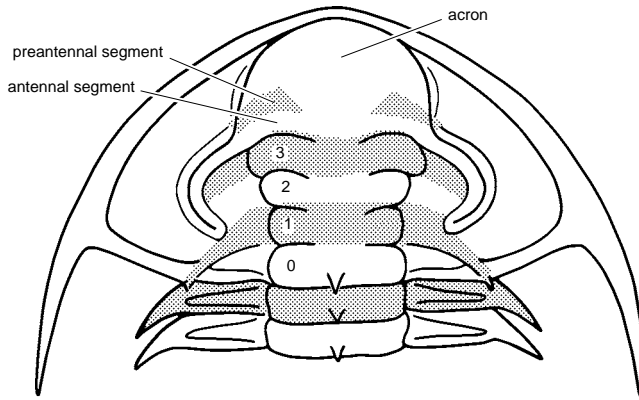
FIG. 120. *Holmia kjerulfi* (LINNARSSON), Lower Cambrian, Norway. Diagram to show the inferred segmentation; alternate segments *shaded;* the acron is a presegmental complex to which the extraocular cheeks probably belong (Bergström, 1973a, fig. 5).

fore concluded that the frontal lobe included two segments and an assumed segmental complex, which he referred to as the acron. HUPÉ concluded that the frontal lobe in cephala of *Daguinaspsis ambroggii* (about 5 mm in length) was subdivided by two pairs of lateral glabellar furrows and hence may have included three segments (Fig. 121), the antennal and preantennal segments, and segment x. STØRMER's (1942) studies of development and segmentation led him to recognize, from ridges and furrows in the adaxial genal region and the ocular lobe, that the pleural region of the preoccipital segment

curved back into the intergenal spine (Fig. 122). This deduction was amply confirmed by the earliest developmental stages described by PALMER (1957). It is also clear that the ocular lobe (or the inner band of it) is the pleural region of the fourth segment in front of the occipital, and by STØRMER and BERGSTRÖM this was regarded as the antennal segment. The fossula lies in the axial furrow immediately in front of where it meets the ocular lobe, and the antenna is presumed to have been attached to the slope of the fossula. A corollary of STØRMER's recognition of this segmentation was that the pleural
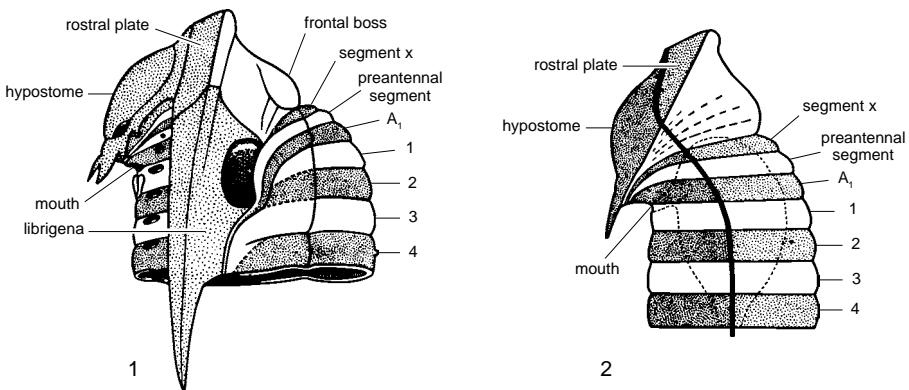
FIG. 121. Theoretical scheme of the cephalic segmentation of a trilobite; ventral surface is shown convex but was in reality concave. *1,* Cephalon in left lateral view. *2,* Schematic section of the cephalon, showing the segments, alternately *shaded; dotted line* shows the alimentary canal; *solid line* separates the tergal region on the right from the sternal region on the left. Abbreviations: A_1, antennal segment; *1–4,* postantennal segments (Hupé, 1951, fig. 5).

FIG. 122. *Holmia kjerulfi* (LINNARSSON), Lower Cambrian, Norway. Diagram showing the supposed relationship between primary and secondary segmentation in the cephalon and two thoracic segments; primary segments *shaded* alternately on left side (Størmer, 1942, fig. 14).

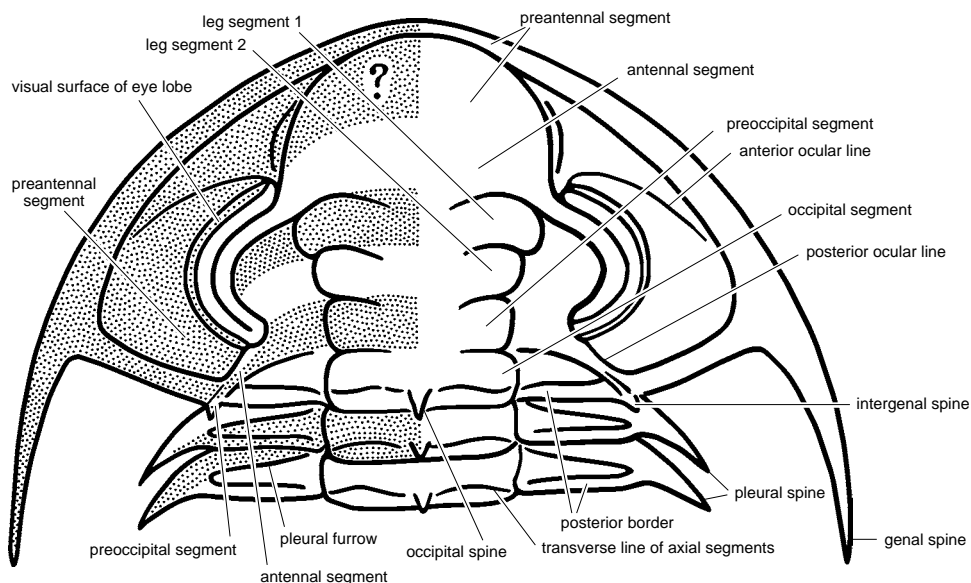portion of the occipital segment included the anterior band and pleural spine of the first thoracic segment. Hence the joint between cephalon and first segment (and between the remainder of the thoracic joints) was secondary, cutting across original segmentation (Fig. 122). This view was embraced and extended by PALMER (1957) but rejected by BERGSTRÖM (1973a, 1973d).

It is generally accepted that the trilobite cephalon included at least five segments, the eye ridge having been part of the fourth segment in front of the occipital segment. The fossula appears to have been the apodeme of this fifth segment, to which the anterior wing of the hypostome was linked and the antenna attached. As summarized above in the section on trilobite limbs, known cephalic appendages included three (or perhaps four) pairs of biramous limbs. Presumably the three pairs were linked to the occipital (O) apodeme and those of the next two anterior segments (1, 2), segment 3 not bearing such limbs. In Olenellina only the antenna is known (DUNBAR, 1925), and appendages of protaspides are unknown. In their recent re-

construction of the protaspis of *Encrinuroides,* SPEYER and CHATTERTON (1989, fig. 15a) showed the antenna apparently attached to the apodeme of segment 3, but it was more likely to have been attached farther forward, immediately behind the anterior wing of the hypostome. How many more segments may have been fused to form the cephalon is a matter of debate. STØRMER (1942) suggested that a sixth, preantennal segment may be represented by the most anterior portion of the frontal glabellar lobe, the anterior and lateral cephalic borders, and the visual surface of the eye lobe and extraocular genal area (Fig. 122). HUPÉ (1951) added a seventh segment x in the axial region (Fig. 121) and considered that the preglabellar area, the visual surface of the eye lobe and extraocular area, and the rostral plate and hypostome were formed from the fusion of several more anterior segments. BERGSTRÖM (1973a) considered, however, that the axis terminated at the preglabellar furrow and that the area in front of it was pleural (Fig. 120). He also suggested that because a presegmental acron is present in all extant

arthropods, the acron was probably present in trilobites and included the eye. He suggested that a sixth, preantennal, segment was present that extended into the outer band of the ocular lobe. Pillola's (1991, p. 77–84) consideration of Hupé's views in relation to Lower Cambrian trilobites led him to conclude that the glabella had six distinct segments at the maximum (the anterior being the preantennal segment of Hupé) (Fig. 121). In addition is an anterior portion, which may be part of the glabella or may form the parafrontal band. He considered that the segmental nature of segment x (of Hupé) is uncertain (since it includes a less prominent portion of the eye ridge), and he referred to the view of Jell (1978a) that the parafrontal band may be part of the network of genal caeca.

MODE OF LIFE, HABITS, AND OCCURRENCE

H. B. WHITTINGTON

Speculation on this subject began in the middle of the last century and has broadened as appendages were discovered, the significance of facies relationships was appreciated, and the study of trace fossils intensified. The abundance and variety of trilobite remains in relatively shallow-water sediments, in contrast to the limited kinds in deeper waters farther off shore suggest that most trilobite species were part of the shelf benthos. Exoskeletal morphology and comparisons with living animals were used to interpret mode of life in earlier work by DOLLO (1910), RAYMOND (1920), and Rudolf RICHTER (see summary by SCHEVILL, 1936); and this approach continues to be valuable as, for example, in THOMAS and LANE's (1984) use of morphology in discussing the ecology of Silurian trilobites, HAMMANN's (1985) work on calymenoids, and ELDREDGE's (1970, 1971) comparisons with living animals in discussing mode of life. Comparisons with extant crustaceans are inevitable but must be used with caution because trilobites were not crustaceans. BROOKS's (1957) summary of the literature shows that from an early date authors were considering how and in what types of rock trilobites occur and the modes of life implied.

SPECIES IN WHICH LIMBS ARE KNOWN

Widely differing views have been expressed on the mode of life of Agnostina, as deduced from exoskeletal morphology and mode of occurrence. Authors have considered these trilobites to have been not only benthic but also planktonic (ROBISON, 1972a; JAGO, 1973), parasitic (BERGSTRÖM, 1973a), or living attached to algal strands (PŘIBYL & VANĚK, 1976, p. 13; PEK, 1977; HAVLÍČEK, VANĚK, & FATKA, 1993). The discovery of the ventral cuticle of *Agnostus pisiformis* (Fig. 82) has enabled the mode of life of this species to be discussed in greater

detail. MÜLLER and WALOSSEK (1987) pointed out that when the animal was completely enrolled, all the appendages would have to have been packed inside (Fig. 123.1), despite the relatively large hypostome. When the trilobite was partially enrolled (Fig. 123.2), the antennae could have projected through the gape; the antennae were relatively short and were considered not to have been sensory in function, but rather to have entangled food particles and swept them back under the hypostome (as illustrated by arrows 1, 2, 3 in Fig. 124). The inward pointing spines of the inner branches of the trunk limbs may then have trapped these particles and moved them into the midline to be carried toward the mouth by the coxae (Fig. 124, arrow 4). A sucking mouth may have aided ingestion. Branches of the limbs specialized for respiration are thought to have been absent. MÜLLER and WALOSSEK suggested that the ventral integument and the club-shaped projections on the outer side of the inner branch of the trunk limb (Fig. 82) were well adapted for respiration. Perhaps the plumose setae on the outer branches of these limbs were used to create respiratory currents that bathed these structures. The second and third cephalic limbs of *A. pisiformis* had respectively either no inner branch or a much reduced one but had a long, flexible, outer branch that was spinose distally. When the exoskeleton was partly enrolled, these limbs could have been curved and swept back in a propelling stroke, curved more strongly and folded in a recovery stroke, enabling the animal to swim. This gaping, partly enrolled attitude (Fig. 123.2) appears to have been the most likely one for feeding and swimming. MÜLLER and WALOSSEK considered that when the body was outstretched (Fig. 123.3) the relative lengths of the limbs made it unlikely that the animal could have walked on the sea bottom. Furthermore, the alimentary canal appears to have been severely constricted in this
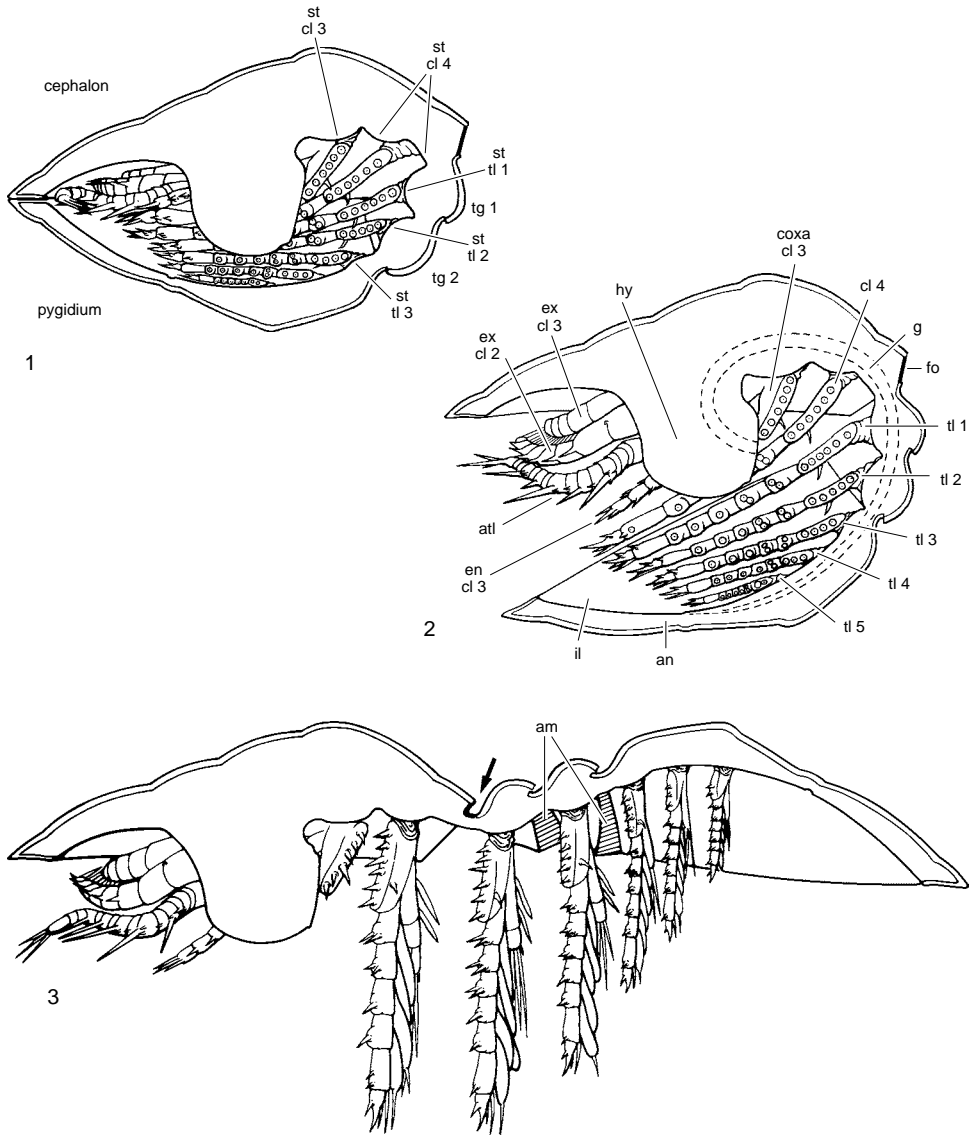
FIG. 123. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Possible positions in life, the right side viewed from a sagittal section; *1,* enrolled; *2,* partially open; *3,* body outstretched, with cephalic limb 4 and trunk limbs vertical (considered a most improbable position). *Arrow* in part 3 points to deformed membrane covering cephalo-thoracic aperture. Abbreviations: *am,* arthrodial membrane; *an,* anus; *atl,* antenna; *cl 2–4,* cephalic appendages; *en,* inner branch; *ex,* outer branch of appendage; *fo,* membrane covering cephalothoracic aperture, in which there was a foramen; *g,* gut; *hy,* hypostome; *il,* ventral integument; *st,* sternite; *tg 1–2,* thoracic segments 1 and 2; *tl 1–5,* appendages of thorax and pygidium (Müller & Walossek, 1987, fig. 25).

position and the membrane covering the cephalothoracic aperture folded. Thus, to these authors the outstretched position seemed to have been an unlikely one for either feeding or locomotion (cf. ROBISON,

1964, p. 515). MÜLLER and WALOSSEK concluded, because of its occurrence in dark, bituminous shale and the associated fauna, that *A. pisiformis* was probably a benthic animal, feeding on the abundant detritus in
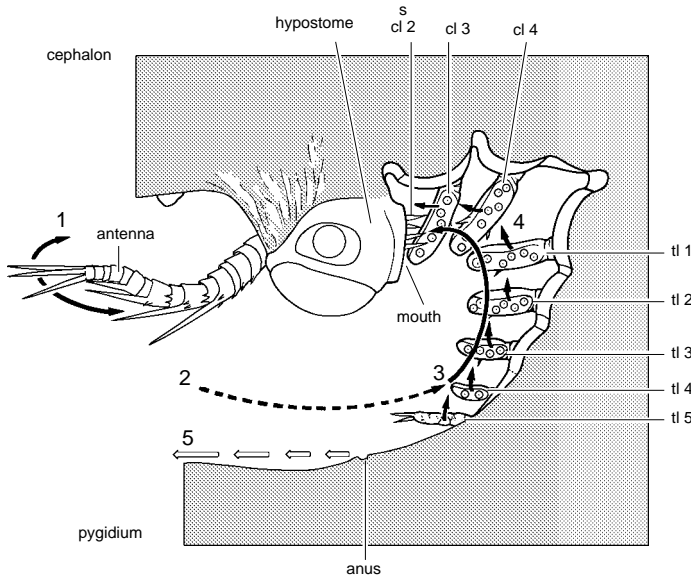
FIG. 124. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Sagittal section of partially enrolled body (*stippled,* with sternites at inner edge), inside which are shown the right antenna, hypostome, position of mouth and coxae and setae (*s*) of right cephalic (*cl 2–4*) and trunk (*tl 1–5*) limbs. See text for discussion of probable mode of food intake (*arrows 1–4*); the anus and exit of feces (*arrow 5*) are shown (Müller & Walossek, 1987, fig. 24).

a flocculent zone, its limbs being not adapted for filter feeding.

The limbs of the Middle Cambrian *Olenoides* (WHITTINGTON, 1980a) are known in considerable detail (Fig. 83–85), making it possible to suggest the types of joints between the podomeres of the leg branch and the nature of the limb movements in walking (Fig. 98–99). Flexure of the leg branches, which were armed with bunches of ventral spines, may have enabled the animal to seize prey or decayed material and to have pushed it into the median groove, lined by the spinose coxae. Metachronal movements of the coxae (WHITTINGTON, 1980a, fig. 9) presumably enabled food to be squeezed and shredded as it was passed forward to the mouth, which was positioned at the back of the hypostome. The search for food on the sea bottom may have been conducted not only by walking but also by the animal launching itself off the substrate and drifting in a favorable current (Fig. 125). It is questionable, however, whether *Olenoides,* once launched off the bottom by a backward swing of a few successive pairs of limbs, had any means of

swimming. The filament-bearing, outer branch of the appendage appears to have been rigidly attached to the coxa so that if the coxa swung about a transverse axis, the outer branch would have been moved up and down with it. Whether the branch itself could have been flexed is not known. Thus feeble currents may have been created as the outer branch moved toward and away from the ventral integument. Such currents would, at best, have provided only poor swimming powers.

The activities possible for *Triarthrus eatoni* (WHITTINGTON & ALMOND, 1987) appear to have been similar. In this species the inner branches are notable for the development of spinose endites on the proximal podomeres. These endites were triangular in outline and deep on the short podomeres of the posterior branches, becoming less deep on successively more anterior branches (Fig. 86.3–5). The endites may have aided in trapping food and holding it as it was conveyed into the midline. Such endites on the posterior leg branches are characteristic of trilobites otherwise very different in morphology from
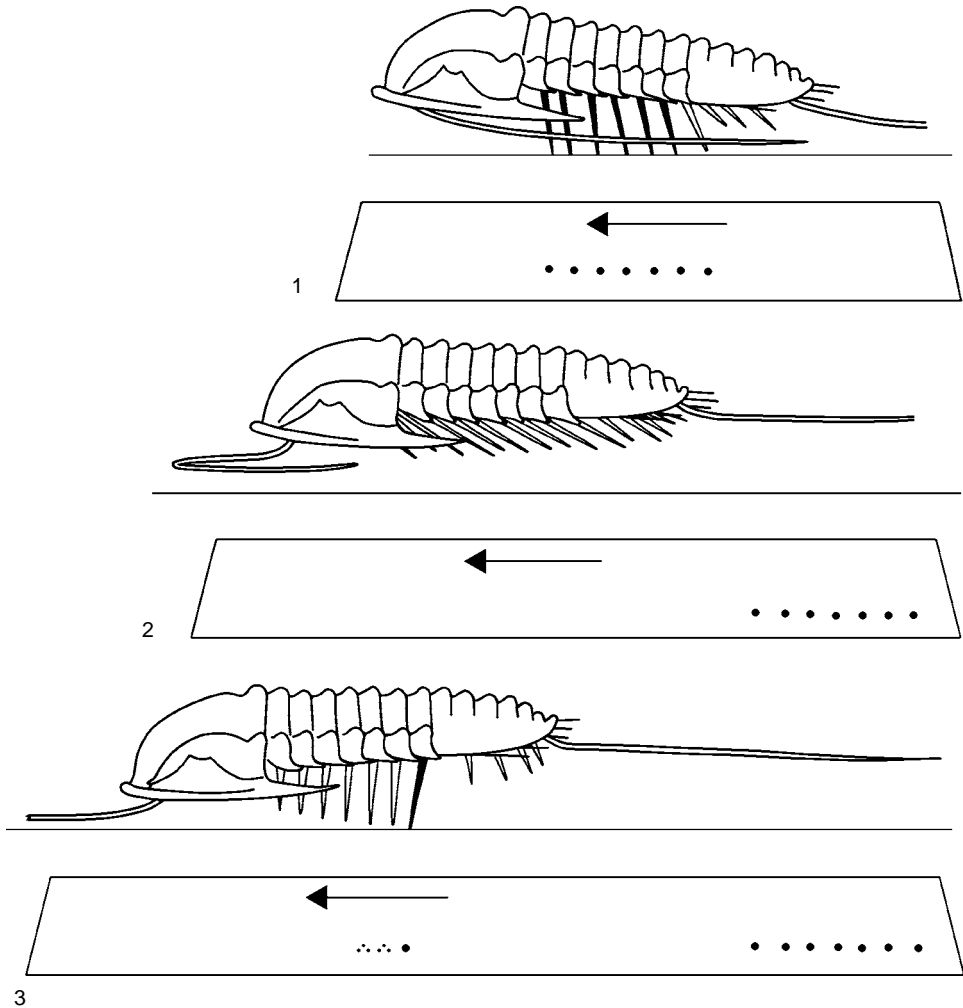
FIG. 125. Left lateral stills showing how a trilobite such as *Olenoides serratus* (ROMINGER) may have launched itself off the sea bottom (*horizontal line*) to drift or swim a short distance before descending to the bottom (compare with Figure 99). Limbs that are in contact with sea bottom are *solid black;* others are shown in *outline.* Below each drawing is a panel showing an oblique view of part of the sea floor with the imprints made by the left legs only; *arrow* shows direction of movement. *1,* Leg pairs IV to X swung back quickly to launch animal; *2,* animal drifts or swims above sea bottom with pairs of legs swung back to offer less resistance; *3,* leg pairs IV to X in promotor swing; pair X completes swing and touches bottom, to be followed in succession by pairs IX to IV, giving a second set of impressions; antenna incomplete, but cercus complete (Whittington, 1980a, fig. 13).

Triarthrus, for example *Cryptolithus* (RAYMOND, 1920, fig. 20), *Rhenops* (BERGSTRÖM & BRASSEL, 1984, p. 70, fig. 1–3), and *Phacops* (STÜRMER & BERGSTRÖM, 1973, p. 118–119).

Triarthrus eatoni could enroll completely (ROSS, 1979), the pygidium fitting closely inside the cephalic border, as could *Placoparia* (Fig. 96) and many other trilobites, the close fit achieved in different ways. In enrollment of such species, as with *Agnostus,* all the limbs would have to have been accommodated within the capsule formed by the exoskeleton, packed beside the hypostome, with the antennae folded back. Space was thus at a premium, and the body beneath the inner

pleural region must have been of severely limited depth so that most of the body was concentrated within the axial region. Such considerations and the probable need for a hanging stance or upward curvature of the limbs to give stability were weighed in drawing the cross sections of *T. eatoni* (Fig. 86.3–5) and *Placoparia* (Fig. 95–96). A cross section such as that by SCHMALFUSS (1981, fig. 7), with a deep body in the pleural region, seems highly improbable for trilobites that enrolled completely.

MÜLLER and WALOSSEK (1987, p. 47–49) compared the biramous appendages of *Agnostus pisiformis* with those of other trilobites, commenting that the general construction was the same—the large coxa and gnathobase, the main branch being the inner one composed of six podomeres plus a terminal spinose one. The special form of the antenna of *A. pisiformis* and the differentiation of the anterior two biramous appendages from the remainder of the series are considered to be related to their function in food gathering and swimming. The specialization was related to the mode of life, one of swimming and drifting above the bottom but not walking on it. Other trilobites in which limbs are known have long, slim, tactile antennae followed by a series of biramous appendages of similar form, which show only gradational change in length of branches, spines, or endites. A series of inner branches of similar length and distance apart (exsag.) are essential to a gait that supported the animal along the length of the body. Thus, the similarity in form of the biramous series of limbs reflects the mode of life, walking on or digging and plowing into the sea bottom.

FORMS IN WHICH ONLY THE EXOSKELETON IS KNOWN

However well the exoskeleton is known, inferences on mode of life and habits are restricted by uncertainty about the nature of the limbs. In the spinose odontopleurids WHITTINGTON (1956d) suggested that the form of the cephalon and relative length of border spines (Fig. 22, 42) resulted in the animal's resting on the substrate on the margins of the cephalon with the thorax and pygidium stretched out a short distance above the bottom. CLARKSON (1966a, 1966b) showed that the visual field of the eye in phacopids is striplike, restricted vertically, but covering a wide field laterally. Orientation of this field horizontally gave an attitude of the body, when resting on the sea floor, similar to that in odontopleurids. CLARKSON (1966c, 1969b) suggested that the thorax and pygidium could be stretched out above the sea bottom or inclined slightly downward to rest on the border spines (in odontopleurids) or on the margins of pleurae and pygidium (in Phacopina). CLARKSON (1966a, 1966c) drew attention to the anterior arch of the cephalic border, curving up to the sagittal line, in phacopid cephala when oriented in this fashion. Such an arch is characteristic of many trilobites, e.g., the Lower Cambrian *Crassifimbra* (PALMER, 1958), proetoids, Phacopina, cheiruroids, calymenids, and the olenid *Triarthrus eatoni* (WHITTINGTON & ALMOND, 1987, fig. 40). CLARKSON emphasized the importance of this arch as an entry for respiratory or food-bearing currents when the animal was on the sea bottom. The appendages of *T. eatoni* were well suited to such a direction of entry. The anterior arch, however, is also coaptative, a necessary form to accomodate the posterior portion of the thorax and pygidium in complete enrollment; it may not have been related to respiration or food gathering.

The evidence from exoskeletal morphology may be tested against the geological evidence of the enclosing rock and associated fossils. A recent study of this type was by N. C. HUGHES (1993) on large collections of *Dikelocephalus;* it exemplifies the problems in reaching firm conclusions on the mode of life of this probably epibenthic trilobite. The difficulties in interpreting morphology have given rise to disparate views on the habits of Illaenidae (SIEGFRIED, 1939; WHITTINGTON, 1964; BERGSTRÖM, 1973a; WHITTINGTON, 1997). In some species of illaenids, the
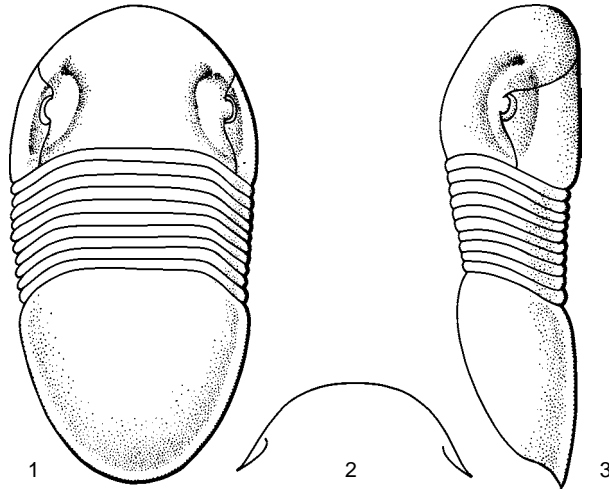
Fig. 126. *Meitanillaenus niagarensis* (Whitfield), Middle Silurian, Wisconsin. *1,* Dorsal view, *2,* transverse section through anterior portion of pygidium, and *3,* right lateral view, ✕2 (Whittington, 1964, fig. 1c–e).

convex cephalon is deeper than the thorax and pygidium, but not in all (Fig. 126). Illaenidae lack transverse furrows—that is, they lack glabellar, articulating, inter-ring, and pleural furrows, and the axial furrow is not deeply impressed. The thorax may be fulcrate or nonfulcrate, with a wide (tr.) axis giving an even smoother, rounded form to the exoskeleton, as in *Bumastus* (Fig. 1). Bergström (1973a) suggested that illaenids lived with the cephalic margin resting on the sea bottom, the lower margin of the eye lobe hence parallel to the bottom surface, the thorax and pygidium curved down at a steep angle in a burrow; this posture was attained by burrowing backward. Such burrows, however, have not been observed, and the specimen illustrated by Bergström (1973a, pl. 5, fig. 5–6) is not buried in this attitude (Whittington, in press). The morphology of the illaenid thorax (Fig. 47 and discussion) gives it exceptional flexibility, and it may be that these trilobites were vagrant benthos, specially adapted to crawling over the uneven surfaces of the reef habitat in which they occur abundantly. Stitt (1976) argued that the Upper Cambrian *Stenopilus* (Plethopeltidae) may have lived with the thorax and pygidium in a vertical burrow

(Fig. 127) and have used the anteriorly facing terrace ridges that traversed the pygidium to assist in burrowing. Stitt also thought that the morphology of the thorax was such that the animal could have walked on the bottom (Fig 127.1). For such walking to have been possible, the inner branches of the limbs would have to have been of similar length, not successively shorter as portrayed. Species of *Stenopilus* occur in association with reef mounds and may have inhabited mud patches between the mounds; no trace of burrows has been found with them. Westrop (1983) coined the term illaenimorph for illaenids and other such trilobites as *Stenopilus,* which had a smooth convex exoskeleton, and linked this form with life in a burrow. Fortey (1986) argued for a like habit for the Ordovician *Symphysurus,* as did Brezinski (1986b) for the Carboniferous proetid *Proetides.* Fortey and Owens (1990a; see section on evolution, p. 249) discussed the occurrence of illaenimorphs during the Paleozoic. The term illaenimorph is being used in a broad, general manner, and it is doubtful that it should imply that all such species dwelled in burrows. So-called illaenimorphs are frequently referred to as *effaced,* a term that presumably

implies a species that lacks the furrows that were present in its ancestors. Unless such an ancestral relationship has been demonstrated, a particular species is best described as smooth rather than effaced.

Arguments for the long-standing view that some large-eyed Ordovician trilobites were pelagic have been marshalled by Fortey (1974a, 1985). He considered that an elongate body with a narrow (tr.) pleural region, convex axis, and deep apodemes was to be correlated with strong musculature and good swimming powers and that the large eye gave an all-around view. A vaulted cephalon is not thought to have been consistent with a benthic life, and the eye is unusual in having increased relatively in size during ontogeny. Analogy is with extant pelagic crustaceans that have large eyes. Geological distribution, particularly of *Opipeuter* (Fortey, 1974a) and *Carolinites* (Fig. 128.2–3)—in presumed warm waters and in all facies—is consistent with an epipelagic habit. The occurrence of cyclopygids such as *Pricyclopyge* (Fig. 128.1) is confined to what are considered to have been deeper-water, off-shelf facies and is taken to suggest that they were mesopelagic, swimming at the lower limit of the photic zone. The peculiar paired organ on the third thoracic segment of some species may have been light sensitive, a special adaptation for this habit. Fortey also distinguished two groups of pelagic trilobites: those like *Carolinites* (Fig. 128.2–3), having a broad, globular cephalon, long genal spines, and the poorly streamlined body of a sluggish swimmer, and others like the streamlined *Novakella* (Fig. 128.4), which may have been a faster swimmer and possibly predatory.

The large eye and wide geographical distribution have also been used as arguments for a pelagic habit of the Upper Cambrian *Irvingella* (Fig. 128.5), which has a wide (tr.) pleural region and is spinose. Largely on the grounds of their worldwide distribution, I considered that burlingiids such as *Schmalenseeia* were planktonic in habit (Whittington, 1981). These grounds alone are not adequate for such an assumption;
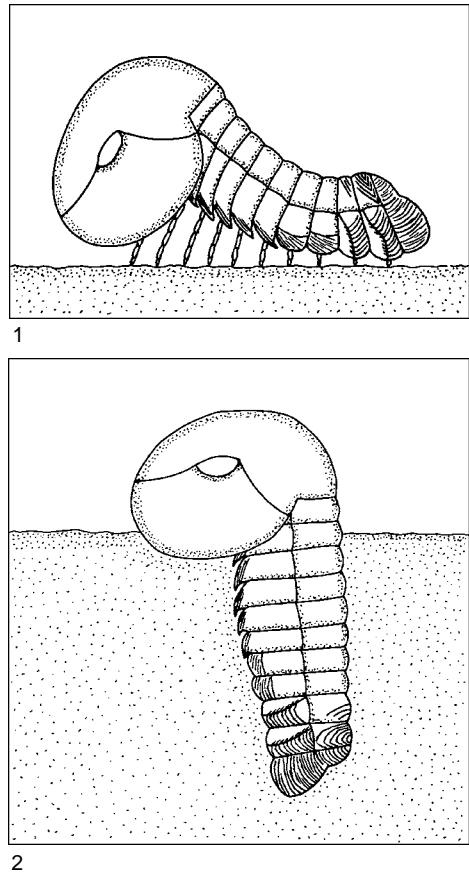

Fig. 127. *Stenopilus pronus* Raymond, Upper Cambrian, North America; reconstructions in lateral view; *1,* standing on the substrate and *2,* partially buried in a living position (Stitt, 1976, fig. 5–6).

burlingiids characteristically occur in outer shelf or slope facies, and their morphology affords no compelling evidence for assuming a planktonic mode of life (Whittington, 1994).

Spinosity and wide distribution have long been used as arguments favoring a planktonic habit in odontopleurids. However, the convex cephalon, the border of which may bear spines including a long genal spine, appears to be well adapted, as explained above, to resting on the sea floor. Clarkson (1969b) argued that two attitudes in life were possible for some odontopleurids, one
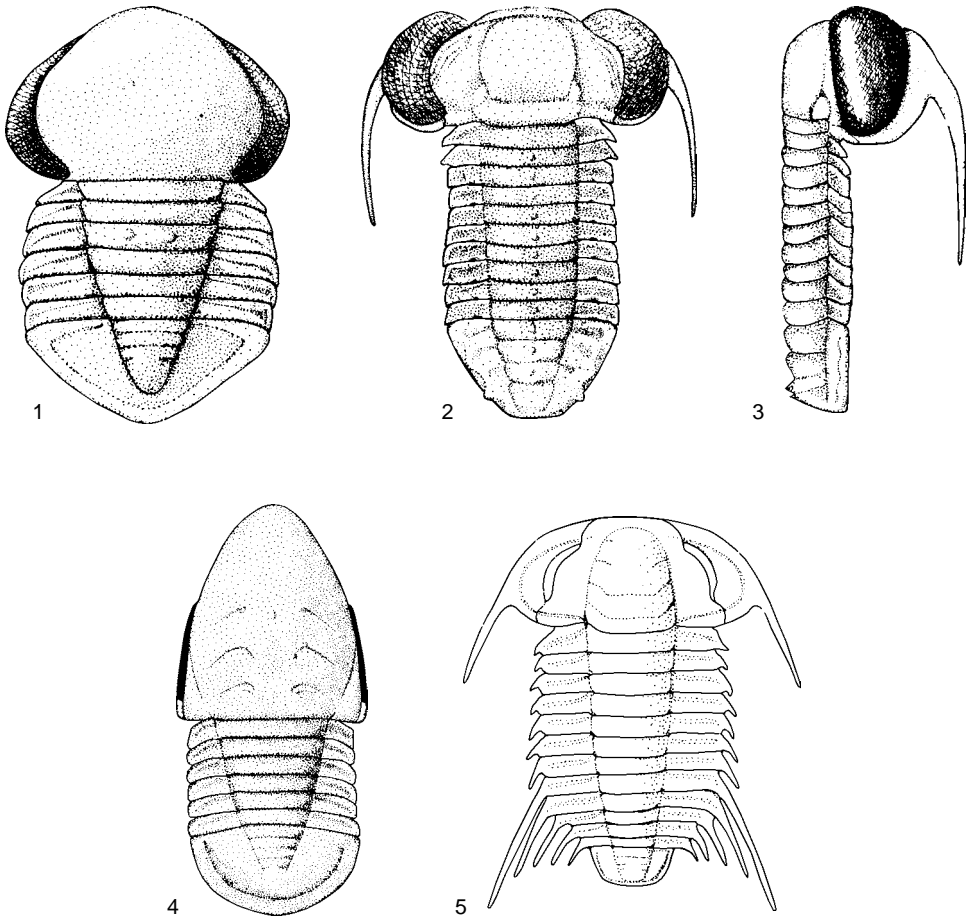
Fig. 128. Pelagic trilobites. *1,* Dorsal view of *Pricyclopyge binodosa* (SALTER), Lower Ordovician, ×1.5 to ×2. *2,3,* Dorsal and right lateral views of *Carolinites genacinaca* ROSS, Lower Ordovician, ×1.5 to ×2. *4,* Dorsal view of *Novakella bergeroni* (KLOUČEK), Ordovician, ×1. *5,* Dorsal view of *Irvingella* sp., Upper Cambrian, ×2. Reproduced by permission of the Royal Society of Edinburgh and R. A. Fortey (Fortey, 1985, fig. 1a,c,h, 5b, 9a).

with the thorax and pygidium stretched out horizontally above the bottom and a second with the cephalon tilted slightly back, the thorax and pygidium inclined downward and backward. The relative length and direction of the cephalic border and genal spines and of the pleural spines allowed these two attitudes, but in some odontopleurids the second was not possible. Arguments on habit based only on exoskeletal morphology are notoriously open to question, but a case can be made for regarding some holaspid odontopleurids as having been benthic, drifting and swimming over the sea bottom, rather than planktonic. The wide distribution may be accounted for by the early growth stages having been planktonic. On the other hand, a detailed investigation of the morphology and occurrence of the Ordovician *Selenopeltis* (HAMMANN & RABANO, 1987; cf. FORTEY & OWENS, 1987, p. 106), a characteristic odontopleurid from cooler waters, has suggested active swimming and little contact with the sea bottom, that is, an epi- or mesopelagic habit.

Exoskeletal spines may have been in part protective, projecting around and upward when the animal was resting on the sea floor

and making it more difficult to attack when enrolled; they may have also inhibited sinking or aided in balance when drifting or swimming. Such spines are known in a wide range of trilobites, including *Nepea* (Fig. 23), odontopleurids such as *Apianurus* (WHITTINGTON, 1956d, fig. 19), the lichid *Ceratarges* (THOMAS & HOLLOWAY, 1988, fig. 313–317), and the styginid *Ancyropyge* (ORMISTON, 1967, pl. 2). A graduated array of genal spines (Fig. 22) and thoracic pleural and pygidial border spines may have propped the animal in position on the sea bottom, especially perhaps on a muddy bottom. The long, curving genal spines of some olenids (CLARKSON, 1973b, p. 761) and of some raphiophorids (e.g., of *Ampyx*, WHITTINGTON, 1959a, fig. 6) have been interpreted as an adaptation for this purpose (FORTEY & OWENS, 1978, p. 238), though their length and delicacy and the presence of a frontal glabellar spine in *Ampyx* and other raphiophorids suggests perhaps an additional flotational and balancing function. The long, curved macropleural spine in *Biceratops* (Fig. 44), for example, may have served a similar function. INGHAM (1968) referred to the stabilizing function of the thoracic macropleural spine of *Cybeloides* when the animal was digging into the sediment for concealment.

The frontal process was developed in very different groups—for example, in *Seleneceme* (WHITTARD, 1960), in asaphids, and in dalmanitids (where it may be bifid or trifid or an extraordinarily long spine)—and was spatulate in the calymenid *Spathacalymene* (TILLMAN, 1960) and species of the lichid *Platylichas* (THOMAS & HOLLOWAY, 1988, fig. 179). The pygidial mucro was developed in the asaphid *Megistaspis* (WANDÅS, 1984), which also has the frontal process (BOHLIN, 1960), and in some encrinurids (Fig. 57). In activity that required strong flexure of the body, the frontal process or posterior axial spine or mucro may have helped to keep the body in position on the substrate or may have aided in burrowing for concealment. Righting of the body after overturning may

also have been aided by these spines, as well as by a median axial thoracic spine (cf. FORTEY, 1974b, p. 27–28). Such an activity would have required the ability to flex the body dorsally.

The mode of life of *Cryptolithus* (Fig. 129) and other trilobites with a bilaminar pitted fringe has long been a subject of discussion (RICHTER, 1921; STØRMER, 1930; PŘIBYL & VANĚK, 1986). CAMPBELL (1975) reexamined *Cryptolithus* using silicified specimens of the exoskeleton to reconstruct the musculature and combined this with what is known of the appendages and a study of trace fossils. A sound case was made for attributing these traces to the activity of *Cryptolithus*, although the role of the outer branches of the appendages in burrowing has been questioned (WHITTINGTON, 1980a, p. 189–190). CAMPBELL concluded that *Cryptolithus* was a benthic mud-feeder, able to dig down into the substrate, and with limited powers of walking and swimming. He argued that *Cryptolithus* had the ability to rapidly outroll the thorax and pygidium and that such an ability might have been used in swimming and in righting the animal if it were rolled over. The animal would have rested partially buried in the substrate on the outer portion of the fringe and genal spines, the innermost rows of pits exposed above the sediment. CAMPBELL argued that the fringe probably had a sensory function and that it contained a branching system of digestive glands. This study is exceptional in marshalling the range of evidence available in coherent support of arguments.

The general form of trinucleids such as *Cryptolithus* (Fig. 129)—the strongly vaulted cephalon, the bilaminar fringe, and long genal spine—is repeated in dionidids and is characteristic of *Harpes* and its allies, in which the fringe is prolonged posterolaterally. In harpidids (Fig. 17) and entomaspidids the form is similar, but the bilaminar fringe is less steeply inclined. LUDVIGSEN (1982) regarded *Bowmania* (Fig. 21) as an entomaspidid; the horizontal fringe of spines projecting from the cephalic border
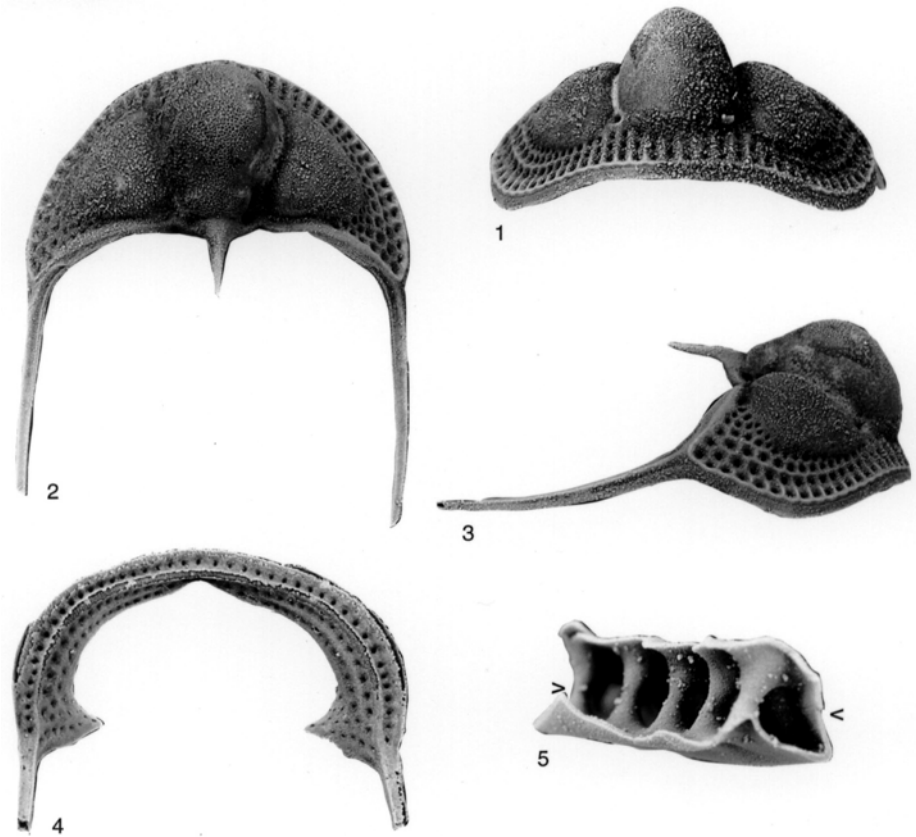
FIG. 129. *Cryptolithus tesselatus* GREEN, Middle Ordovician, Virginia, USA. *1–3,* Anterior, dorsal, and right lateral views of cephalon, ×4.5; *4,* ventral view of isolated lower lamella of fringe; genal spines incomplete, ×4.5; *5,* fragment of external portion of fringe, viewed from broken edge at girder, showing form of opposed pits; *arrows* point to position of suture, ×12.5 (Whittington, 1959a, pl. 20, fig. 1–3, 8).

and genal spine of *Bowmania* may have supported the cephalon on the sea bottom in the same manner as did the fringe of trinucleids and other groups mentioned above. These groups of trilobites were probably not all closely related; still much more distantly related were bathyurids (WHITTINGTON, 1953; LUDVIGSEN, 1978a, 1978b; FORTEY, 1979), in which the highly vaulted cephalon and concave cephalic borders, prolonged posteriorly, repeated the general form of trinucleids and harpetids. Bathyurids had large eye lobes and were typical of shallow-platform waters in North America. FORTEY (1979, p. 82) argued that bathyurids such as *Petigurus,* which had a relatively thick exoskeleton, sought partial

burial in the sediment as a protection against nautiloid predators. *Punka* (FORTEY, 1979, p. 98) had a fan-shaped pygidium, and FORTEY argued that this bathyurid did not live in a burrow in the manner suggested for some illaenids but that the broad, concave border assisted the animal in gliding over the soft sediment. The convex axial region of bathyurids and other trilobites has been interpreted as providing a large area for muscle insertion, and hence as suggesting relatively powerful appendages. The vaulted cephalon and broad border seen in these very different Ordovician trilobites reappears, for example, in the Devonian *Mystrocephala* (WHITTINGTON, 1960a) and in *Cordania* (CAMPBELL,

1977), although in the latter the cephalic border is convex. The fringe, spines, or border around the vaulted cephalon of these different trilobites propped the cephalon on the sea bottom so that the thorax and pygidium were either stretched out well above it or inclined down toward it.

Articulation of the exoskeleton allowed flexure of the body in the sagittal plane, not only partial or complete enrollment but also concave-dorsal flexure (see discussion of thorax, p. 43). Many specimens of entire exoskeletons are preserved without disarticulation and show such back-arching or a sinuous combination of back-arching and partial enrollment. The *Rusophycus* type of excavation (see below) is also associated with back-arching. In odontopleurids the preannulus was most developed in anterior segments, suggesting that the strongest dorsal concavity was in this region. Geyer (1990b, p. 58–62) pointed out that the backward curvature (in dorsal view) of the anterior margin of the first four axial rings of the ellipsocephalid *Kingaspsis* made possible a dorsally concave flexure in the anterior portion of the body. The absence of such curvature in more posterior rings required dorsally convex curvature, giving an S-form in longitudinal profile. This suggested that it lived in a shallow excavation. Other ellipsocephaloids do not show this form of the anterior axial rings, and as a consequence the horizontally extended body suggests a life on the surface of the sediment.

Flexure of the body was essential to activity on the substrate, and the presence of coaptative structures in the exoskeleton of trilobites suggests that complete enrollment was a characteristic habit. It has long been urged that such enrollment was a protective reaction to attack by a predator and that a spiny exoskeleton when enrolled made an awkward target or an unwieldy mouthful. An elegant example in support of this idea is the restoration of the enrolled *Burmeisterella* by Wenndorf (1990, fig. 47). Clarkson and Henry (1973) also emphasized the function of coaptative devices in strengthening the exoskeleton against lateral shear by a predator. In studies of enrolled specimens of *Phacops* and *Greenops* from the Middle Devonian of New York State, Babcock and Speyer (1987) and Speyer (1988) discussed morphology, musculature, and enrollment behavior. They emphasized the role of rapid burial in the preservation of enrolled specimens and stressed that such enrollment was a response to such adverse conditions as a toxic environment or rapid influx of sediment. The possible musculature involved in enrollment and extension of the body has been discussed above (p. 101). A long-standing view (Raymond, 1920, p. 99) is that some trilobites used a rapid partial enrollment (i.e., a downward flick of the pygidium) to dart backward in an escape reaction. Campbell (1975), however, argued for the opposite action, rapid outrolling, as a swimming or righting action in *Cryptolithus.* Probably the ability of trilobites to flex the body into a dorsally concave curve was necessary to right the animal if accidentally overturned; a long, median, thoracic or pygidial spine may have aided in such an activity. Rapid, complete enrollment, alternating with partial outrolling (i.e., clapping the isopygous pygidium and cephalon together) has been suggested as a possible swimming mechanism. For *Agnostus pisiformis* this mode of locomotion is considered unlikely (Müller & Walossek, 1987), and it appears improbable for larger trilobites such as asaphids.

Babcock and Speyer (1987) emphasized that the complete encasement of the soft parts in tightly enrolled *Phacops* and *Greenops* protected the animal in conditions of sudden environmental change such as deoxygenation. As noted above in the discussion of enrollment in some dalmanitids, complete enrollment left a gap in the exoskeleton, and in *Symphysurus* (and possibly some other trilobites) minute passages remained. It is argued that such gaps aided in respiration while the animal was enrolled. By no means all trilobites had the soft parts sealed from the outside when enrolled,

because those in which the outer portion of the pleura was spinose did not fit closely (cylindrical enrollment of Bergström, 1973a, p. 14). Complete enrollment may have been largely protective in function, but the protection was against different kinds of external factors.

The range of sculpture on the external surface of the exoskeleton and the transitions between types has been described in the section on microstructure and sculpture (p. 74–84). Prominent sculpture that thickened the exoskeleton may have strengthened it: for example, strong terrace ridges, closely spaced symmetrical ridges in an anastomosing or reticulate arrangement, or large tubercles that were not accompanied by any thinning of the cuticle. Sensory devices associated with sculpture have been described above. Miller (1975) argued that asymmetrical terrace ridges comprised a current monitoring system, while Stitt (1976) and Schmalfuss (1981) argued for the role of such ridges in burrowing and in gripping sediment. Fortey (1985, 1986) criticized aspects of these interpretations. Terrace ridges are present on the doublure of trilobites that may not have been benthic; on the other hand, such groups as cheirurids, encrinurids, calymenids, and dalmanitids lacked terrace ridges on the doublure, although probably many species were benthic. Terrace ridges and other forms of external sculpture may have had a different function in relation to behavior in different portions of the exoskeleton of species.

TRACKWAYS, TRAILS, AND BEHAVIOR

Traces of activity are a source of information on behavior, if they may be attributed to trilobites with some confidence. The trackway produced by a trilobite walking in the manner described above (Fig. 99), however, would have had no distinctive features and been difficult to assign to its originator. More distinctive trackways were ascribed by Seilacher (1955, fig. 1; cf. Osgood, 1970, p. 351–352, fig. 17b, 20a, etc.; Seilacher,

1959, p. 390–391, fig. 2b) to trilobites walking in fashions that I have regarded as unlikely (Whittington, 1980a, p. 194–195, fig. 12). These doubts concerned the proposed relative lengths of the limbs, the suggestion that all the limbs moved in a single metachronal wave, and the idea that part of the body was dragged along. Traces that include groups of parallel scratches have been also attributed to trilobites (Osgood, 1975, p. 98–100), including the sideways raking reported by Seilacher (1955, p. 349–355, fig. 3, pl. 17, fig. 2). The manner in which such tracks were made and the supposition that they recorded a feeding activity are also open to question (Whittington, 1980a, p. 202).

The trace fossil *Rusophycus* is a bilobed hollow commensurate with a trilobite, which may show transverse or obliquely, forwardly directed grooves across the hollows. In the remarkable examples figured by Osgood (1970, pl. 57, fig. 6, pl. 58, fig. 4–5), the complete exoskeleton of *Flexicalymene meeki* closely overlies the bilobed trace and hence appears to have been its maker. Other examples of *Rusophycus* (e.g., Osgood, 1970, pl. 57, fig. 1, pl. 58, fig. 7–8; Hofmann, 1979, pl. 9) show impressions of the cephalic and pygidial doublures, genal spine, and hypostome, as well as paired impressions beside the midline. The latter are considered to have been made by the proximal portions of the appendages, the coxae. These excavations may have been made by flexure and extension of alternate limbs (Fig. 130), enabling the animal to dig vertically downward. Examples of *Rusophycus* from the Lower Cambrian of Sweden (Jensen, 1990), which intersect worm burrows, are considered to be traces of hunting burrows as trilobites dug down to capture worms. It has also been suggested that burrowing may have afforded protection from predators, for example, to trilobites that had the eye on the highest part of the gena or raised on a stalk, so that it was above the concealing sediment. Ingham (1968) and Hammann (1985) pointed out that the abilities to flex the body
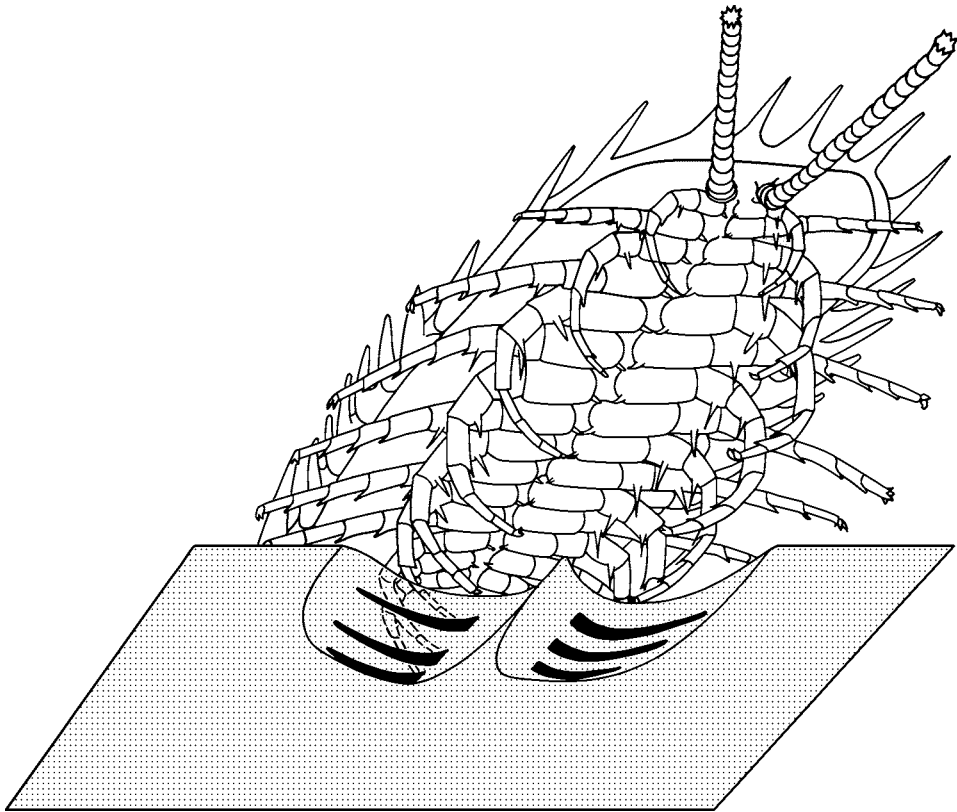
FIG. 130. Diagrammatic oblique ventral view of *Olenoides serratus* (ROMINGER) as it alternately flexed and extended pairs of limbs. Coxae and leg branches I to XV and their major ventral spines are shown; outer branches are omitted. During flexure the limbs dug into the sediment and excavated a shallow depression. Lower part of drawing shows surface of sediment (*coarse stipple*) from below, including that part of the bilobed excavation below the first seven pairs of appendages. The grooves in the excavation made by the flexure of limb pairs I, III, and V are shown in *black,* and on the left side *dashed lines* show the concealed distal portions of these limbs. Antennae assumed to be forwardly extended; cerci incomplete. Ventral integument *stippled* (Whittington, 1980a, fig. 14).

into a curve concave upward or to tilt the cephalon down may have aided in covering the dorsal surface with sand and that spines may have helped in digging and in giving stability. It may be reasonable to suggest that forward walking (Fig. 131) by a trilobite in wet sand, with the cephalon slightly lowered, may have been a form of plowing employed in search of food. Such an activity would have left a nondescript trace, since the footprints at the margins of the furrow are not likely to have been preserved. The resistance to such furrowing would have been greater the deeper the cephalon. It has been urged (SDZUY, 1957; HAMMANN, 1985) that the

wedge-shaped form, high eye lobe, shovel-like anterior border of the cephalon, semicircular cross section, and smooth exterior of homalonotids are adaptations for burrowing. It seems reasonable to suggest that this form was an adaptation to making a deeper furrow. Study of trace fossils associated with Homalonotinae in the Lower Devonian led WENNDORF (1990, p. 15–21, fig. 7–12) to suggest the presence of grazing and hunting trails.

An undescribed trace fossil that shows a series of paired imprints repeated at intervals led MANTON (1977, p. 48) to suggest that a trilobite could launch itself off the bottom
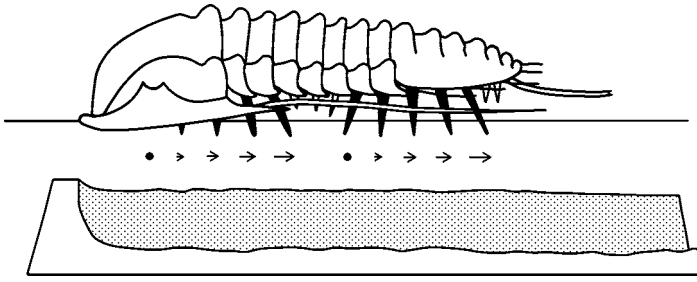
FIG. 131. Diagrammatic left-lateral view of *Olenoides serratus* (ROMINGER) in gait shown in Figure 99 but with cephalon inclined downwards and plowing shallowly into sediment; antennae curved back. *Horizontal line* shows position of sediment surface; left half of furrow (*stippled*) shown in oblique lateral view in panel below. Other symbols as in Figure 99 (Whittington, 1980a, fig. 15).

and drift or swim before sinking again (Fig. 125). An asymmetrical Upper Cambrian trackway (BRIGGS & RUSHTON, 1980) in which scratches on one side are deep and transverse and on the other side are short or absent has been interpreted as probably having been made by a trilobite hopping in the manner suggested (Fig. 125) but under the influence of a current. This detailed description offers an alternative interpretation for dimorphic tracks of the type described by SEILACHER (1955) and OSGOOD (1970). Thus, walking on the bottom, digging and plowing shallowly in it, launching off the bottom and drifting or swimming, and oblique progress against a current are reasonable activities to suggest for benthic trilobites and appear to have been recorded by trace fossils.

The trace fossil *Cruziana* extends straight or curved for up to a meter or more, may be 5 to 6 cm wide, and is characterized by a V-shaped pattern of grooves directed forward and outward. Varied forms of the trace have been illustrated by SEILACHER (1970), CRIMES (1970), BIRKENMAJER and BRUTON (1971), and BERGSTRÖM (1976). Outside the deeper, V-shaped grooves may be a narrower zone with finer scratches, and outside these may lie a continuous, longitudinal groove. A large slab showing straight and curved trails crossing one another and associated with a bilobed *Rusophycus* excavation was figured by SEILACHER (1985, fig. 4), and the same asso-

ciation was earlier shown by CRIMES (1970, pl. 12a,b). *Cruziana* has been ascribed to the activities of trilobites because it is commensurate with them, is abundant in Cambrian and Ordovician shallow-water sediments, and the longitudinal groove suggests a trail left by the genal spine. A curved trace, such as might have been left by the anterior border of the cephalon, is apparently not known in *Cruziana* but is recorded from apparently similar Triassic trails, which were ascribed to xiphosurids (SEILACHER, 1985, fig. 2i). The large (maximum width 23 cm), *Cruziana*-like trail from the Triassic of South Africa may have a similar origin (SHONE, 1979); these post-Paleozoic examples lack the characteristic V-form of the grooves. The view that the early Paleozoic *Cruziana* trails were made as an open furrow in mud and subsequently cast by silt and sand (CRIMES, 1975; BALDWIN, 1977) was opposed by SEILACHER (1955, 1970, 1985) and BIRKENMAJER and BRUTON (1971). These latter authors considered that it was a furrow plowed in loose, wet sand and silt overlying a mud layer. The investigation by GOLDRING (1985) suggested that the latter view is a more likely mode of origin and emphasized the complex nature of the casting of the track.

The production of a *Cruziana* track required considerable expenditure of energy (cf. BERGSTRÖM, 1976, p. 1618) in what was presumably a search for food. A problem I find baffling (WHITTINGTON, 1980a, p. 200–

202, fig. 16) is the nature of the limb movements required to produce the V-shaped grooves, sets of which overlap each other in succession (BIRKENMAJER & BRUTON, 1971, fig. 10). Pairs of limbs would have to have been directed forward and outward and flexed in toward the midline to produce the grooves. Such a method of dragging itself forward, through a layer of sand, would have been clumsy and inefficient because of the heavy demand on energy. It would have been far more efficient for the animal to have plowed a shallow furrow in the manner shown in Figure 131, but this activity would not have produced *Cruziana*. These considerations lead me to doubt whether the *Cruziana* trail was made by a trilobite. Diagrams such as that of BIRKENMAJER and BRUTON (1971, fig. 10) imply that a trilobite could plow or even tunnel into a mud layer. The trilobite limb, however, was inserted at the base into an apparently uncalcified ventral integument, the coxa not having been joined to a calcified sternite that was linked to the dorsal exoskeleton. Thus any push on the substrate by the limbs could not have been directly transferred to the dorsal exoskeleton, only indirectly by the extrinsic limb muscles. The implication is that the animal's power to push through sediments was severely limited. Thus I remain skeptical of the ability of the trilobite to plow deeply and consider it most unlikely that it could have made a tunnel. GOLDRING (1985) did not observe tunnels in his study.

The very limited sample we have of trilobite appendages makes speculations on modes of life and habits hazardous. This is especially so in considering the function of the outer branch. In *Agnostus pisiformis* (MÜLLER & WALOSSEK, 1987) the long, outer branches of the first two cephalic limbs are considered to have been used in swimming and those of more posterior limbs in creating respiratory currents. In *Olenoides* (WHITTINGTON, 1975) and *Triarthrus* (WHITTINGTON & ALMOND, 1987) the shaft of the outer branch was apparently rigidly attached to the coxa, the long sheets of filaments directed backward and those of the successive limbs forming an overlapping series beneath the ventral integument of the pleural region. No specimen of either *Olenoides* or *Triarthrus* shows the filaments directed in an alternating series between the inner branches in what would have been a downward direction of the filaments. Nevertheless, it has been claimed (CRIMES, 1970; BERGSTRÖM, 1973a; CAMPBELL, 1975; SEILACHER, 1985) that fine scratch marks in some trace fossils, including those in the outer portion of *Cruziana* tracks, were made by the tips of the filaments of the outer branch. I have argued (WHITTINGTON, 1980a, p. 189) that this activity was unlikely, particularly by *Olenoides,* which has fine hairs at the tips of the filaments, but also for other trilobites. It appears probable that the outer branches, their sheets of filaments forming an overlapping series beneath the ventral integument, moved up and down as the limbs swung about a transverse axis and were respiratory in function (WHITTINGTON & ALMOND, 1987, p. 40). Respiration by *A. pisiformis* (MÜLLER & WALOSSEK, 1987, p. 37) may have been via the club-shaped projections from podomeres of the inner branches and possibly also via the ventral integument. Respiration through the ventral integument has been suggested for other trilobites, but there is as yet no evidence for or against this idea. JELL (1978a) has argued that the anastomosing genal caeca and the similar structures of the thorax and pygidium aided in respiration, rather than having been branches from the alimentary canal (ÖPIK, 1961a).

It has been stated frequently that some trilobites, or even most, were filter feeders (SCHMALFUSS, 1981; SEILACHER, 1985). It is thought that the trilobite was partially buried in sediment, and a filter chamber was maintained beneath the animal, extending from the frontal cephalic arch to the tip of the pygidium. GEYER (1990b, p. 60, fig. 36) suggested that in *Kingaspis* the downward flexure of the body posteriorly, which gave the small pygidium a downward and forward inclination, closed the filter chamber
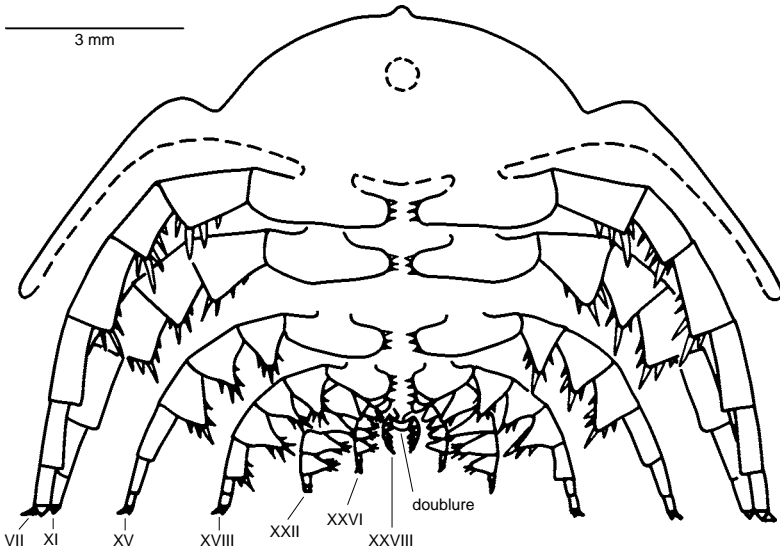
FIG. 132. *Triarthrus eatoni* (HALL), Upper Ordovician, New York, USA. Restoration of coxae and inner branches of selected appendages from the series I to XXVIII. Each pair vertical, shown looking posteriorly from cross section at fourth thoracic segment (beneath which is appendage VII). Stance as in Figure 86.2; median portion of doublure of pygidium visible in midline (Whittington & Almond, 1987, fig. 43).

posteriorly. In a cross section of a reconstructed trilobite, SCHMALFUSS (1981, fig. 7) portrayed the outer branch of the limb with the filaments vertical and held entirely above a small inner branch; the filaments are considered to have trapped particles drawn through the chamber. This reconstruction is misleading, for in no known example could the outer branch be held in this position (if we accept the evidence of taphonomy) and the downwardly directed attitude of the relatively small inner branch appears unlikely. Furthermore, the manner in which particles trapped by the sheet of filaments could be gathered and carried to the mouth is not explained. The array of spinose endites on the inner branches of the more posterior limbs of *Triarthrus* (Fig. 132) appears to constitute a food trap situated toward the rear of the animal. It is thought that this species and others displaying similar structures were predators and scavengers, as well as deposit feeders, food being carried forward in the midline to the mouth. The hypostome in some Cambrian and in most post-Cambrian trilobites was rigidly braced against the rest

of the cephalon. It must have helped to guide food into the mouth and may have acted also as a plate against which the anterior coxae could scrape food (e.g., in odontopleurids). Until we have a greater knowledge of trilobite appendages, our understanding of the mode of life of these animals will remain inadequate.

EXUVIATION AND THE FUNCTION OF SUTURES

Like other arthropods, trilobites molt. In extant arthropods, molting (HENNINGSMOEN, 1975; SKINNER, 1985) includes the processes of preparation for withdrawal from the old integument, the withdrawal and casting of the remains (exuviation or ecdysis), and the subsequent stages of growth. Presumably in trilobites the sequence of events was similar. Their relative duration is unknown, but as in living animals the stage with the fully developed exoskeleton and high activity may be assumed to have occupied a large portion of the time. Thus there presumably was a relatively short, immediately postecdysial stage

when the integument was soft and rapid growth was possible. Secretion of the principal layer of the new exoskeleton followed. Support for such a sequence of events is found in two kinds of evidence.

(i) Miller and Clarkson (1980) and Speyer and Brett (1985) have described rare specimens of *Phacops* in which the exoskeleton was thin, fragile, and light colored. These specimens have the typical outer, prismatic layer of normal thickness, but the principal layer is thin, as thin as 25 μm compared to 500 μm in other specimens. The thin exoskeleton is interpreted as being postecdysial, the likelihood being that the principal layer was thickened inwardly to the final intermolt stage.

A specimen of *Olenoides serratus* from the Middle Cambrian Burgess Shale with appendages appears to be an example of an early postecdysial trilobite (Fig. 133). In contrast to other specimens from the same deposit (Fig. 85), this one shows little relief, and the surface is wrinkled (Whittington, 1975, 1980a). There is no mineralized exoskeletal layer; the pleural furrows and portions of the axial furrow are absent; and no eye lobe, eye ridge, or sutures can be seen. Thus the exoskeleton is preserved in a different manner from those of the intermolt specimens from the Burgess Shale, but the appendages are preserved in a similar manner.

(ii) Occurrence of a trilobite exoskeleton arranged in a particular pattern that involves inversion of certain portions can hardly have been chance, and the arrangement is interpreted as resulting from a manner of exuviation.

The earliest recorded example (Sowerby in Sedgwick & Murchison, 1840, p. 693, pl. 57, fig. 30; Salter, 1864a; Richter, 1937, 1942) is the arrangement in the holaspid phacopid *Trimerocephalus,* the inverted cephalic exoskeleton (excluding the hypostome) lying with the posterior edge facing forward with respect to the outstretched **thoracopygon.** The dissociated hypostome may be situated anterior to and

Fig. 133. *Olenoides serratus* (Rominger), Middle Cambrian, Canada. Photograph of specimen immersed in water; the thin, flattened, and wrinkled exoskeleton shows a trace of the alimentary canal beneath the right pleural region; portions of appendages project beyond the right side, ×2 (Whittington, 1980a, pl. 19, fig. 1).

beneath the first thoracic segment. This arrangement is the so-called Salterian mode of molting. In genera of phacopids with large eyes, the facial suture (the anterior branches joined along the outer edge of the anterior border) was apparently fused; in well-preserved specimens of holaspides (Campbell, 1967, pl. 15; Haas, 1969, pl. 82) their course is only faintly visible. This fusion and the arrangements of portions of the exoskeleton suggest that exuviation may have been initiated by the opening of the hypostomal suture and facilitated by a split between cephalon and thoracopygon, enabling the newly molted animal to emerge anteriorly.

SPEYER (1985) has suggested (Fig. 134.8–12) that this split resulted from sharp flexure of the body anteriorly in an upright position.

In studies of ontogenetic series of species of *Trimerocephalus* (MAXIMOVA, 1955; OSMÓLSKA, 1963) that lacked eyes, adult molt assemblages are in the Salterian mode. In meraspides, however, molt assemblages have the dorsal exoskeleton articulated or only slightly displaced, the detached cephalic doublure lying beneath the cephalon or the anterior portion of the thorax. In these meraspides the facial suture, which crossed the lateral border and continued forward in the border furrow, was functional, so that it and the hypostomal suture opened to facilitate ecdysis. The change in mode of molting in holaspides resulted from fusion of the facial suture, and as OSMÓLSKA pointed out, this change seems to have occurred in a number of phacopid genera. Growth stages of different Phacopina (CHATTERTON, 1971, 1980; H. ALBERTI, 1972) show that the suture was functional in meraspides. SPEYER's (1985) studies on molt assemblages of holaspid *Phacops rana* show that the Salterian mode was rare, arrangements in which the thoracopygon was inverted and the cephalon in various attitudes being more common. He also suggested the behavior from which such arrangements resulted (Fig. 134.1–7). Molt arrangements of other Phacopina, in which the facial suture was apparently fused, are those of *Greenops* (SPEYER, 1985) and *Toxochasmops* (MCNAMARA & RUDKIN, 1984). WENNDORF (1990, p. 28–30, fig. 15) found that the remains of Homalonotinae in Lower Devonian sandstones were current-sorted, separated exoskeletal parts, the conjoined cranidium, free cheeks, and rostral plate being rarely present. In shales, however, the remains included the cranidium, free cheeks, and rostral plate joined together and the articulated thoracopygon minus the anterior two or three segments. The inverted cephalon (lacking the hypostome) lay adjacent to or under the thoracopygon, rotated 180° in relation to it. This suggested that the Salterian mode of molting occurred in

Homalonotinae in addition to a mode in which the facial suture opened.

It has long been stated that in the odontopleurid *Ceratocephala* (BARRANDE, 1852, p. 125; WHITTINGTON & EVITT, 1954, p. 53; BRUTON, 1968b, p. 49; CHATTERTON & PERRY, 1983, p. 32, 39, 48) the facial suture was fused in larger individuals. CHATTERTON and PERRY's studies show that such fusion took place in the holaspid period in species of several genera. In the larger specimens of these species, the cranidium and librigena are preserved fused together, but the rostral plate and hypostome are detached. Thus rostral, connective, and hypostomal sutures were functional; and, as HENNINGSMOEN suggested (1975, p. 197), opening of these sutures may have initiated exuviation and enabled the freeing of the cephalon from the old exoskeleton. The silicified growth stages of odontopleurids (WHITTINGTON, 1956b; CHATTERTON & PERRY, 1983) strongly suggest that the facial suture was functional. Hence, in odontopleurids, as in certain Phacopina, exuviation in meraspides was in a mode different from that in large individuals.

A presumed molt configuration of a specimen of *Paradoxides,* originally described by MCNAMARA and RUDKIN (1984), has been shown (WHITTINGTON, 1990) to consist of the **axial shield** with the librigenae and rostral-hypostomal plate inverted beneath it. I have suggested (Fig. 135) maneuvers in exuviation that would have resulted in this arrangement. I follow HENNINGSMOEN (1975) in considering that the primary purpose of the cephalic sutures was to provide an anterior opening for exuviation. This opening freed the vital soft parts of the cephalon—the eye surface by the circumocular suture or the connective sutures, allowing the librigenae to be pushed outward by the emerging cephalon, the attached hypostome freed, and the backward facing mouth released. Egress forward was also essential to allow the newly molted animal to withdraw the genal and pleural spines and the appendages from the discarded cuticle. The dragging forward of
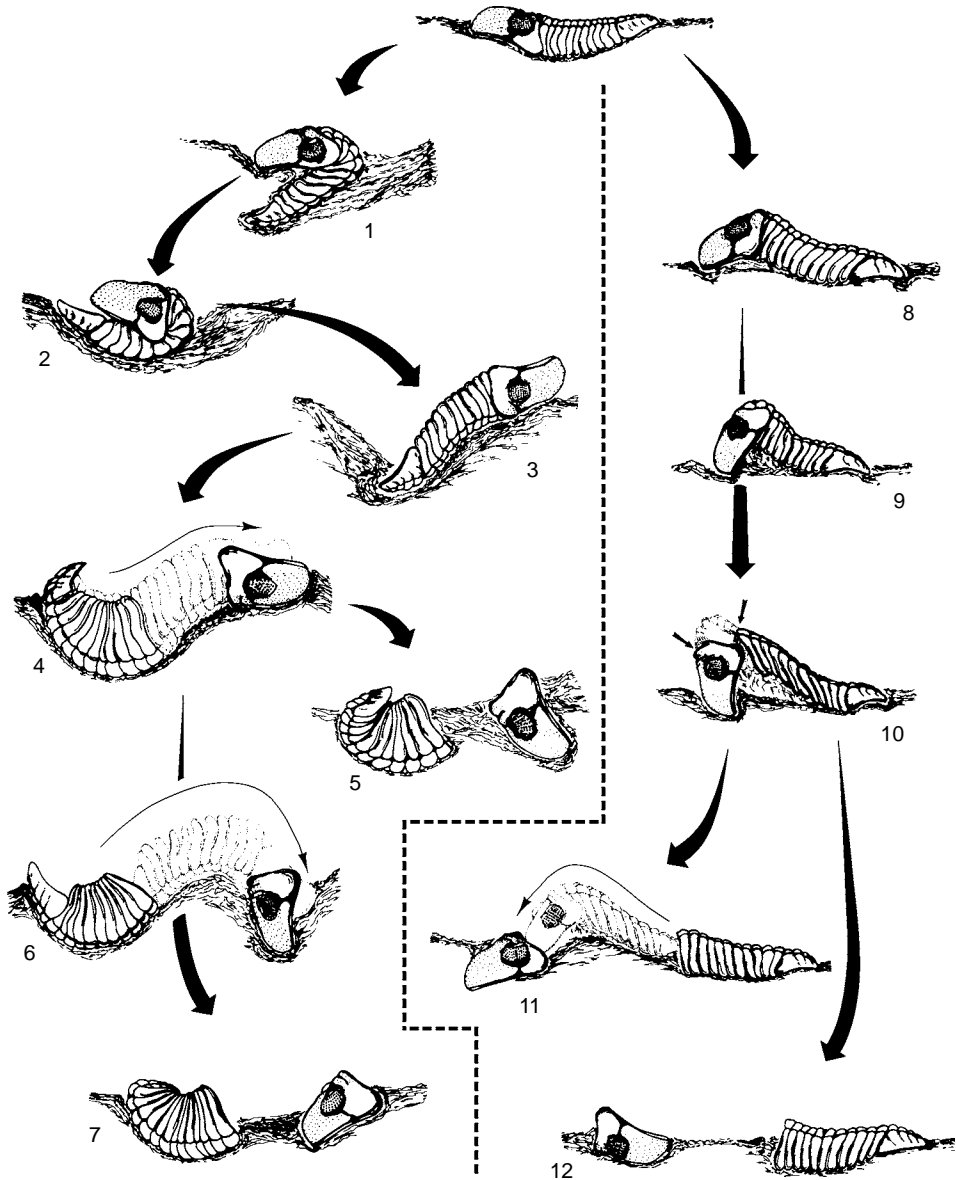
FIG. 134. Manner of exuviation in *Phacops rana* (GREEN). *1–7,* Body inversion procedure. Thoracic flexure (*1,2*) resulted in inversion of the body (*3*). Erratic contraction and expansion of longitudinal muscles (*3,2,3*) resulted in opening of sutures (*4*). As the animal withdrew from the molted exoskeleton, the cephalon may have remained inverted (*5*), or extreme arching of the body may have resulted in the cephalon lying dorsal side uppermost (*6,7*). *8–12,* Body upright procedure. The cephalon is flexed downward as the anterior portion of the thorax is arched (*8,9*) and a suture opens between cephalon and thorax (*10*). Emergence of the newly molted animal may (*12*) or may not (*11*) have inverted the cephalon (part 12 is the so-called Salterian mode). Reproduced by permission of the Royal Society of Edinburgh and S. E. Speyer (Speyer, 1985, fig. 7).

the exuviae in this withdrawal is thought to have overturned the rostral-hypostomal plate

and librigenae. I consider that a split between cranidium and first thoracic segment
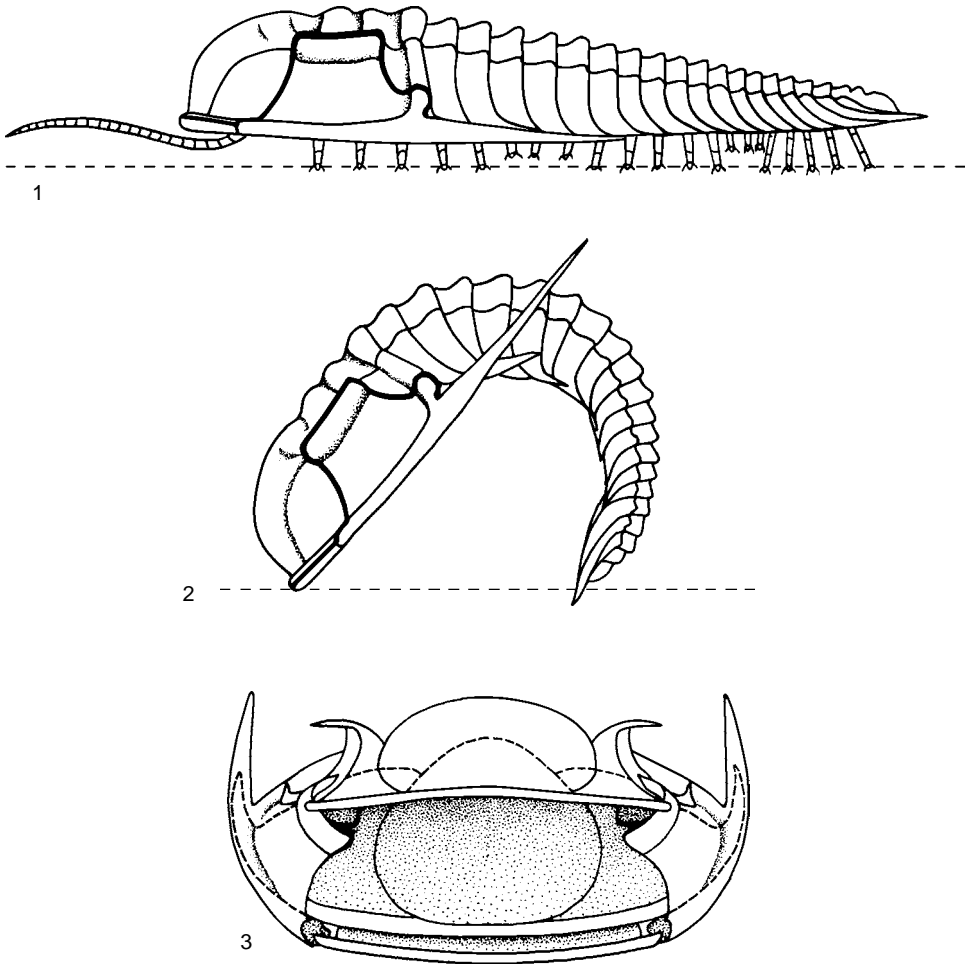
Fig. 135. Suggested maneuvers during exuviation of *Paradoxides* sp.; *1,* left lateral view, showing assumed appendages, with suture line *thick; 2,* flexure of body above substrate, with the pleural spines of thoracic segments 15 to 17 used to dig into sediment (limbs omitted); *3,* anterior view as sutures opened and cephalon of molted animal (*stippled with dashed outline*) began to withdraw from old exoskeleton and emerge; *4,* left lateral view of molted animal (*stippled, dashed outline of cephalon,* three anterior walking legs indicated) as it emerged from exuviae, which included rostral-hypostomal plate and appendages shown diagramatically; *5,* exuviae after emergence of molted animal (includes mineralized exoskeleton, cast ventral cuticle, and cuticle covering appendages), portrayed perched on substrate, the librigena and rostral-hypostomal plate having been rotated back from position shown in part 4 (Whittington, 1990, fig. 2–6).

(advocated by McNamara and Rudkin) was not necessary and hence reject the sharp downward flexure of the body anteriorly that they suggested (McNamara & Rudkin, 1984, fig. 11). Their proposals were made with reference to a species of *Ogygopsis,* but in this example, as well as those of *Oryctocephalus* they studied, I consider that

maneuvers like those shown in Figure 135 may explain the specimens. A specimen of *Olenellus* (Whittington, 1989, fig. 8) has the perrostral plate inverted beneath the thorax, the posterior tips of the plate lying directly beneath their original position. I regard it as a molt configuration resulting from similar maneuvers. I agree with Hennings-
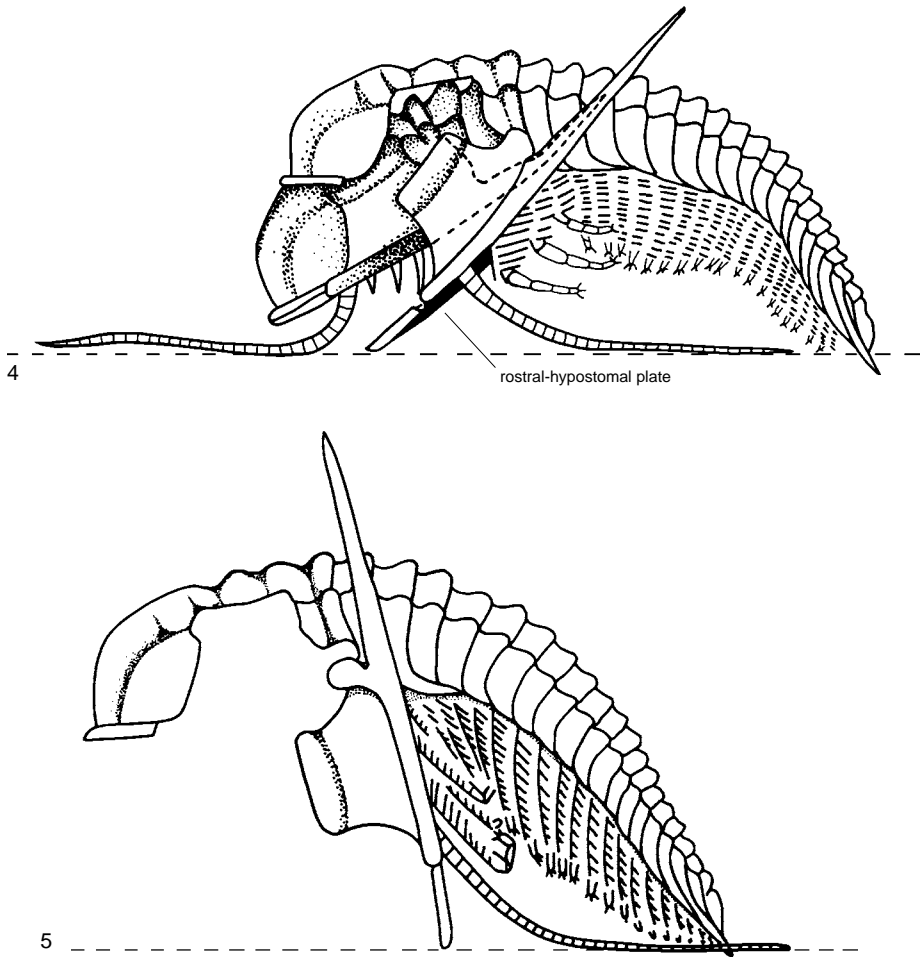
FIG. 135. *For explanation, see facing page.*

MOEN (1975) that emergence forward at exuviation was normal for most trilobites in which the sutures were functional and that it was important to have no hindrance to such egress. As was pointed out in describing the course of sutures, some species with a frontal cephalic process (e.g., *Spathacalymene* or certain asaphids or dalmanitids) have sutures that would have aided in freeing these processes. While inversion of parts of the exoskeleton may have taken place in the course of exuviation, it may have occurred rarely rather than commonly.

HENNINGSMOEN (1975) discussed aspects of molting, and descriptions and discussions of many supposed molt configurations have followed (FORTEY, 1975b; LUDVIGSEN, 1979a, 1979b; MCNAMARA & RUDKIN, 1984; SPEYER, 1985; MCNAMARA, 1986c; WHITTINGTON, 1990). The exuviae (Fig. 135.5) were presumably abandoned on the surface of the substrate and consisted of the mineralized exoskeleton held together by articulatory membranes and ventral cuticle, including that which had sheathed the limbs. Decay of the unmineralized cuticle would lead to progressive dismemberment of the exuviae. The weakest link was that between cranidium and first thoracic segment, so that the large cranidial sclerite was likely to have

been detached first and may have been inverted nearby or carried farther away. Separation of librigena, rostral plate, and hypostome and then dismemberment of the thoracopygon may have followed. Such a decay series of exuviae, at whatever point it was interrupted by burial, could be invoked to explain some specimens thought to be exuvial configurations. Rapid burial would have been essential to preserve exuviae, and I find it difficult to accept that burial could take place without some disturbance of the remains. I do not assume that portions of the old mineralized exoskeleton were carried away on the newly molted animal, but rather that exuviae were normally complete. Distinguishing between the complete (or almost complete) exoskeleton derived from a carcass and that from exuviae poses problems. Symmetrical inversions of portions of the exoskeleton beneath the axial shield may be indicative of exuviae. I have questioned (WHITTINGTON, 1990), for example, whether the specimens of *Redlichia* described by MCNAMARA (1986c) are to be regarded as derived from a decay series of exuviae or at least in part from carcasses. Because the exoskeleton of the genal spine was an elongate cone, it appears that in molting the animal must have emerged forwards in order to withdraw this spine (Fig. 135.3–4). The opening of the cephalic sutures provided the means of egress and made superfluous an opening between cephalon and first thoracic segment.

In exuviation the cephalic sutures played an essential and primary role, for even in holaspides of those species in which facial sutures were fused the connective, rostral, or hypostomal sutures were functional. Opening of a joint between cephalon and thorax was probably a secondary procedure. For most species the ability to enroll the body was necessary to the process and probably also the ability to flex the body in a concave-upward arch. CHATTERTON and PERRY (1983, p. 17) commented that the function of the preannulus in odontopleurids and other trilobites was to facilitate such arching. The

remopleuridid *Hypodicranotus* (WHITTINGTON, 1952b) was unable to enroll because of the long, forked hypostome, so that opening of the cephalic sutures must have begun the process of exuviation. The role of sutures in this process has not been denied, but it has been argued that the sutures may have been lines of movement in the exoskeleton, especially the hypostomal suture. In trilobites with a conterminant hypostome, such movement about the hypostomal suture does not appear to have been possible (WHITTINGTON, 1988a, 1988b). There is thus no evidence that cephalic sutures served any purpose other than exuviation. The claim that any suture was fused needs careful consideration, for it may have been that in trilobites with a fully developed exoskeleton (between molts), the sutures were closed. A fossil from that stage would show a fused suture, but a molted exoskeleton would not.

It is widely assumed (e.g., HENNINGSMOEN, 1975) that most fossils of trilobites, which are disarticulated portions of the exoskeleton, are dissociated portions of exuviae. The less common, entire exoskeletons, extended or enrolled, are the remains of dead animals or in some cases derived from exuviae. Both types of fossils may have thick exoskeletons, up to 0.5 mm, which may include the calcified lenses of the eye (MILLER & CLARKSON, 1980). It may have been, therefore, that trilobites did not resorb the inorganic salts before ecdysis, as many living crustaceans do. MILLER and CLARKSON pointed out the considerable effort in renewal of calcite that this would imply. Measurements by PALMER (1957) on *Olenellus,* and by HUNT (1967) on *Trinodus,* have shown the large number of instars during development, more than the number of thoracic segments. HUNT noted that growth of *Trinodus* terminated after a fixed number of instars, but it is doubtful if this was true for non-Agnostida. It is usual when collecting such trilobites to find fragments of far larger individuals than any represented by entire cranidia or pygidia, for example. Continued growth would have provided many exuviae.

CLUSTERS AND MONOSPECIFIC OCCURRENCES

Considerable numbers of well-preserved, entire, or only partially disarticulated trilobite exoskeletons occurring close together have been remarked on by authors. One such example, a large slab from the Ordovician Bromide Formation of Oklahoma, contained some 111 complete exoskeletons of the asaphid *Vogdesia bromidensis* (LAUDON, 1939; LOEBLICH, 1940; SHAW, 1974). The individuals are similar in size, about half are inverted, and other slabs (BRANSON, 1965) show that the hypostome is present in many. The remains may be of carcasses, not of molted exoskeletons. Another occurrence of many complete, similar-sized exoskeletons of *Dalmanitina socialis* in Upper Ordovician sandstones in the former Czechoslovakia (PŘIBYL & VANĚK, 1976, pl. 8, fig. 1) is attributed to mortality following rapid burial during a storm. Different is the thin dolomitic layer from the Ordovician Maquoketa Group in Missouri (BREZINSKI, 1986a), in which 97 individual exoskeletons of the raphiophorid *Ampyxina bellatula* were found. These specimens exhibited a size range, and the absence of the librigena suggested that they were molts. BREZINSKI demonstrated size clusters in his sample and related them to instars. He interpreted this monospecific occurrence as that of an opportunistic species. These conclusions, however, have been criticized by SHELDON (1988).

Studies by SPEYER and BRETT (1985) and SPEYER (1985) draw attention to another example in Middle Devonian rocks from New York. These are considered to be *in situ* assemblages of the Phacopina *Phacops rana* and *Greenops boothi* and of the proetid *Dechenella rowi*. Each cluster is of three or more exoskeletons of a single species that are close together, of similar size, and considered to be of two types. *Body clusters* appear to be of corpses, while *molt clusters* are of thoracopyga in close proximity to corresponding cephala. The two types of clusters are of individuals of similar size and occur in close lateral proximity along a common stratigraphical horizon. It is considered that such clusters represent a related phenomenon. An analogy with living marine arthropods is drawn, suggesting that the clusters resulted from a behavioral pattern of a species gathering at a particular age (as indicated by the size), prior to synchronized ecdysis and reproduction.

The occurrence of complete enrolled holaspid Agnostina in siliceous nodules from the Ordovician of Czechoslovakia (PEK, 1977) packed closely together in a line has been interpreted as resulting from the adults having lived attached to algal strands. No trace of such strands remains, but the linear orientation is striking.

ABNORMALITIES OF THE EXOSKELETON

Abnormalities in a single exoskeleton may include such features as a lack of symmetry between paired structures (one of the eyes or one of the major spines larger than the other), or in the pleural region of thorax or pygidium an irregularity of the segments or furrows of one side, or a marginal embayment or projection on one side. Figure 136 is a selection of examples from OWEN's review (1985); additional occurrences were described by RUDKIN (1985), ŠNADJR (1985), HESSIN (1988), and BABCOCK (1993). The latter author described healed injuries and malformation and discussed the evidence for behavioral asymmetry. Abnormalities in the anterior axial region are extremely rare, but many have been recorded in the pleural region and axis of the pygidium (e.g., RUDKIN, 1985). This may be a reflection of the greater vulnerability of the peripheral parts of the animal to injury by accident or predation and the fact that abnormalities are most readily recognizable in thorax and pygidium. The possibilities of injury from predation by other arthropods (WHITTINGTON & BRIGGS, 1985), cephalopods (ŠNADJR, 1981b; RUDKIN, 1985), sea anemones (ALPERT &
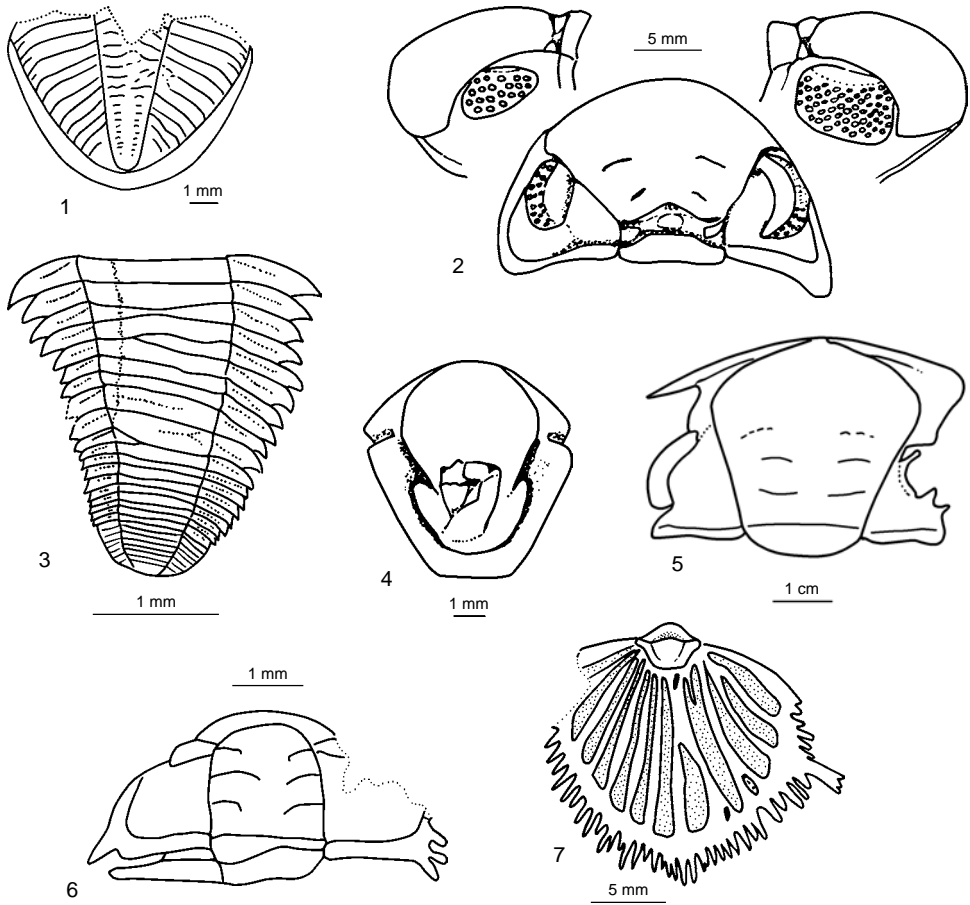
FIG. 136. Abnormalities in the exoskeleton. *1, Dechenella maclareni* ORMISTON, irregular furrows of axis and pleural field of pygidium; *2, Phacops rana* (GREEN), abnormal left gena and eye lobe; *3, Emuella polymera* POCOCK, part of thorax showing additional half segments; *4, Ceraurinella* sp., broken and partially cicatrized median body of hypostome; *5, Paradoxides gracilis* (BOECK), damaged right fixigena; *6, Rossaspis superciliosa* (ROSS), anterior two thoracic segments fused and partially incorporated into cephalon; *7, Scabriscutellum speciosum* (HAWLE & CORDA), irregular pleural spine and rib development on one side of the pygidium. Reproduced by permission of the Royal Society of Edinburgh and A. W. Owen (adapted from Owen, 1985, fig. 1b,e,g,j, 3b, 4a,h).

MOORE, 1975), starfish, and fish have been discussed; but as OWEN (1985) noted, many abnormalities may have resulted from damage sustained during or immediately after exuviation, either in the process of shedding the old exoseleton or by accidental damage or predation when the exoskeleton was thin. It is difficult to distinguish between the effects of any such injury and those that may have been caused by genetic or developmental malfunction. The unique, damaged hypostome in Figure 136.4, which shows fracture and disarrangement of fragments externally and callus internally, appears to be a clear instance of injury and repair in the same intermolt period. OWEN (1985) suggested stages over a series of molts of repairs to the trinucleid fringe. On the other hand, OWEN attributed abnormality in a cephalon of *Phacops* (Fig. 136.2) to genetic or developmental malfunction rather than to injury. Abnormalities resulting from infestation by parasites might be manifested by swellings on or borings in the exoskeleton. Exoskeletal

swellings have been described (Šnadjr, 1978) and were formed during life, but it is difficult or impossible to decide whether, in a shed exoskeleton or in a carcass, borings were made when the animal was alive. As Owen (1985) pointed out, while it may be difficult to establish the causes of abnormalities, their study may shed light on paleoecology.

DIMORPHISM

The presence of two forms, one relatively long and the other relatively broad, was noticed by Barrande (1852, p. 102–104) in many species in his collections. He suggested that these differences were not an expression of individual variation but of sexual dimorphism. Salter (1865, p. 127; 1866a, p. 132) followed this lead, regarding supposedly long (male) and broader (female) specimens as evidence of sexual dimorphism in certain asaphids, for example. Measurements by C. P. Hughes (1979, p. 126, 142), however, showed no evidence for this distinction. As Kielan (1960, p. 41–42) and Henningsmoen (1960, p. 207–210) have pointed out, these supposed differences are the result of deformation, such deformation being common in finer-grained, terrigenous, clastic sediments. When the deformation is asymmetrical it is more readily observed, but when symmetrical, either lengthening or broadening the specimen, it is less obvious; and there are many examples of its having been used as a specific distinction. Trilobites in limestones are preserved in full relief, without distortion, and supposed long and wide forms have been noted, for example of the illaenid *Stenopareia glaber* (Owen & Bruton, 1980, p. 16). In this instance, however, measurements of a larger sample (Bruton & Owen, 1988, p. 243) have shown no dimorphism. Differences between specimens in a single character, rather than in shape, have been used to discriminate dimorphs. One example is the presence or absence of the posterior doublure of the pygidium in *Redlichia* (see earlier section on the pygidial region, p. 59). While Öpik (1958) regarded this as an example of sexual dimorphism, Sdzuy (1959) attached little significance to it. More information is needed on the exact morphological differences between specimens of *Redlichia* and on their occurrence. In specimens of Ordovician *Selenoharpes* and *Bathyurellus,* the prolongation posteriorly of the genal region has been shown to differ in length and shape (Whittington, 1963, p. 23), the sample in the former case being large enough to suggest that the difference may not be merely an expression of individual variation. In *Platycalymene duplicata* C. P. Hughes (1969) noted that although wide and narrow forms could not be distinguished, the cephala could be divided into those with and without an occipital tubercle. The occurrence of specimens in the same stratum that may be separated into two distinct groups on a number of characters presents the problem of whether to regard them as dimorphs of a single species or two separate species (e.g., Hintze, 1953, p. 150; Whittington, 1965, p. 298). Hu (1964a, 1964b, 1968, 1969, 1971, 1981, 1983, 1984, 1985b, 1986) developed his views on sexual dimorphism in trilobites as a result of studying large collections and by a general analogy with such dimorphism in extant arthropods. However, the data presented on characters demonstrating the occurrence of dimorphs, in the form of drawings, photographs, and ratios of dimensions (Hu, 1968, fig. 2; 1969, fig. 2) are inadequate. A more detailed study of the eye of a Carboniferous species of *Paladin* by Clarkson (1969a) was thought to show dimorphism, but this is no longer considered to be the case (Clarkson & Zhang, 1991). The claims of dimorphism or even of polymorphism in species of phacopids (Eldredge, 1973; Campbell, 1977) were rejected by Ramsköld and Werdelin (1991), mainly on the grounds that the collections used were from more than one locality or not from a single horizon. If dimorphism in the exoskeleton of a species of trilobite does occur, it has not yet been satisfactorily demonstrated. If it is
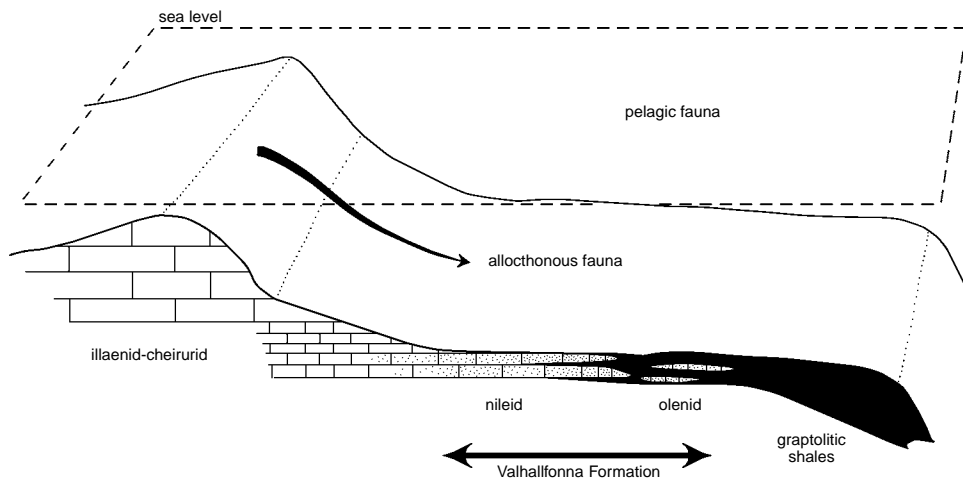
FIG. 137. Paleogeographical model showing disposition of communities of trilobites (illaenid-cheirurid, nileid, and olenid) across an Early Ordovician shelf sea. The communities are preserved in Spitsbergen in the Valhallfonna Formation, which accumulated in the area shown by the *heavy black arrow.* Remains of the shallow water illaenid-cheirurid community were brought into the area as shown by the *curved arrow.* Rock types graded from massive, light-colored limestones on the left to platy, black limestone and graptolitic shales on the right (Fortey, 1975a, fig. 3).

shown, the decision on whether to regard it as evidence of sexual dimorphism or to rank it as a subspecific or specific difference will be arbitrary.

DISTRIBUTION IN ROCK TYPE, TIME, AND SPACE

It is clearly recognized that particular taxa occur commonly in one kind of rock; for example, olenid trilobites occur in dark shales (HENNINGSMOEN, 1957a) and trilobites with relatively smooth exoskeletons in pure, white limestones (LANE, 1972). A study of the abundance of trilobites in a section of Lower Ordovician rocks in Spitsbergen led FORTEY (1975a) to distinguish communities, each with a characteristic suite of genera. Each assemblage of species occurs in a different rock type, considered to be related to environments in shallow to deeper water (Fig. 137). The olenids occur in black, graptolitic limestones and shales, and articulated exoskeletons and growth series are preserved. These and other evidences suggest an autochthonous assemblage, and FORTEY

(1989, p. 339) favored the view that olenids were adapted to the dysaerobic environment in deeper water. Dark, flaggy limestones and shales enclose nileids, raphiophorids, and other genera of the nileid community; olenids are absent; and the associated fauna more varied. The evidence suggests an environment of quiet, well-oxygenated waters. The illaenid-cheirurid assemblage occurs in thin bands of lighter limestone, the broken and disarticulated exoskeletons being part of the evidence for this being an allochthonous assemblage swept in from shallower waters. In addition to these faunas, species of *Carolinites* occur throughout the section in equal abundance in the different communities. The worldwide distribution of *Carolinites* and the unlikelihood of its having been a benthic trilobite of wide tolerance suggest that its habit was pelagic. The existence of a fourth, pelagic community is thus argued, which included other trilobites and graptolites. In other parts of the world, for example the contemporaneous rocks of southern Wales (FORTEY & OWENS, 1978, p. 237–240), the shallower-water shelf faunas were different, the deeper-water ones being more
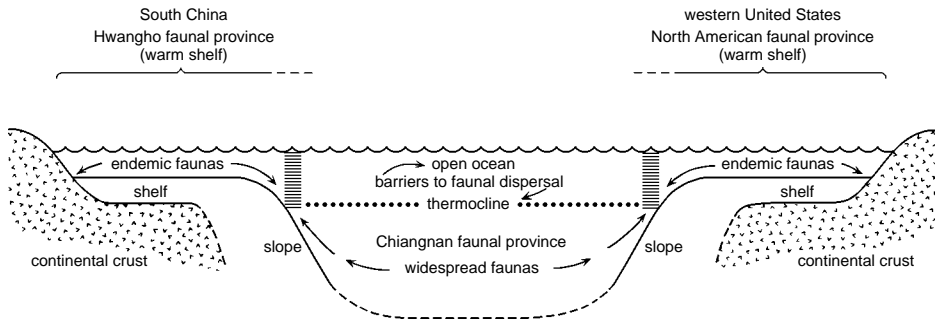
FIG. 138. Inferred habitat relationships between Upper Cambrian trilobite faunal provinces in South China and the western United States (Cook & Taylor, 1975, fig. 4).

similar to those of Spitsbergen. The contrasts are explained in terms of paleogeographical position and presumed water temperatures.

Another study (COOK & TAYLOR, 1975; TAYLOR, 1976, 1977) of autochthonous slope and allochthonous shelf trilobites of late Cambrian age from Nevada showed that some of the former were also known in China, Korea, and Alaska. From analogy with distribution of living isopod crustaceans (TAYLOR & FORESTER, 1979), it was argued that the slope faunas in lower latitudes were inhabitants of cooler water below the thermocline and hence of wide geographical distribution (Fig. 138). Similarly, it was argued by BABCOCK (1994b) that Middle Cambrian trilobites of Baltic type inhabited the cooler waters of the outer shelf facies of northern Greenland, typical Laurentian faunas occurring in contemporaneous shallow-water shelf facies. These slope faunas may also have inhabited the cold, shallow waters of high latitudes.

Associations or assemblages of trilobites in Cambrian (JAGO, 1973; REPINA, 1979; LUDVIGSEN & WESTROP, 1983a; THEOKRITOFF, 1985), Ordovician (BERGSTRÖM, 1973c; APOLLONOV, 1975; PŘIBYL & VANĚK, 1976; LUDVIGSEN, 1978b; HENRY, 1989; HAVLICEK & VANĚK, 1990; HENRY & DESTOMBES, 1991), Silurian (THOMAS, 1980; MIKULIČ & WATKINS, 1981; CHLUPAČ, 1987), Devonian (CHLUPAČ, 1983; WENNDORF, 1990), and Carboniferous (PRENTICE, 1967; BREZINSKI, 1986b, 1988a, 1988b) rocks of different fa-

cies have been discriminated as a result of detailed stratigraphical studies and the making of large, new collections. Authors emphasized the importance of the latter, to overcome the bias present in older collections that may be poorly localized. The terms *association, assemblage,* or *biofacies* are preferred to *community* because trilobites were only a portion of the original organic community. Parallels between associations of different age are commented on, particularly well-known being the similarities in composition and general morphology of trilobites found in carbonate buildups of Paleozoic age (MIKULIC, 1981). CHLUPAČ (1983, p. 64) referred to assemblages in deeper, outer, low energy to stagnant environments in which phacopids and proetids with small or no eyes were prominent. This assemblage is widespread in geosynclinal belts of the Devonian. A similar facies in Carboniferous shales and cherts (PRENTICE, 1967; cf. HAHN & HAHN, 1981; HAHN, 1990; OWENS & TILSLEY, 1995) contains small, thin-shelled proetids in which the eye was small or absent. In shallow-water, calcareous facies, species with large eyes, thick exoskeleton, and coarse tuberculation are characteristic but not universal, as BREZINSKI (1988a) showed. A benthic association in Lower Ordovician rocks that is possibly analogous to the deeper-water Devonian and Carboniferous facies, is the assemblage (FORTEY & OWENS, 1987, p. 106) of blind or nearly blind trilobites named by these authors an atheloptic (shrunken-eyed)
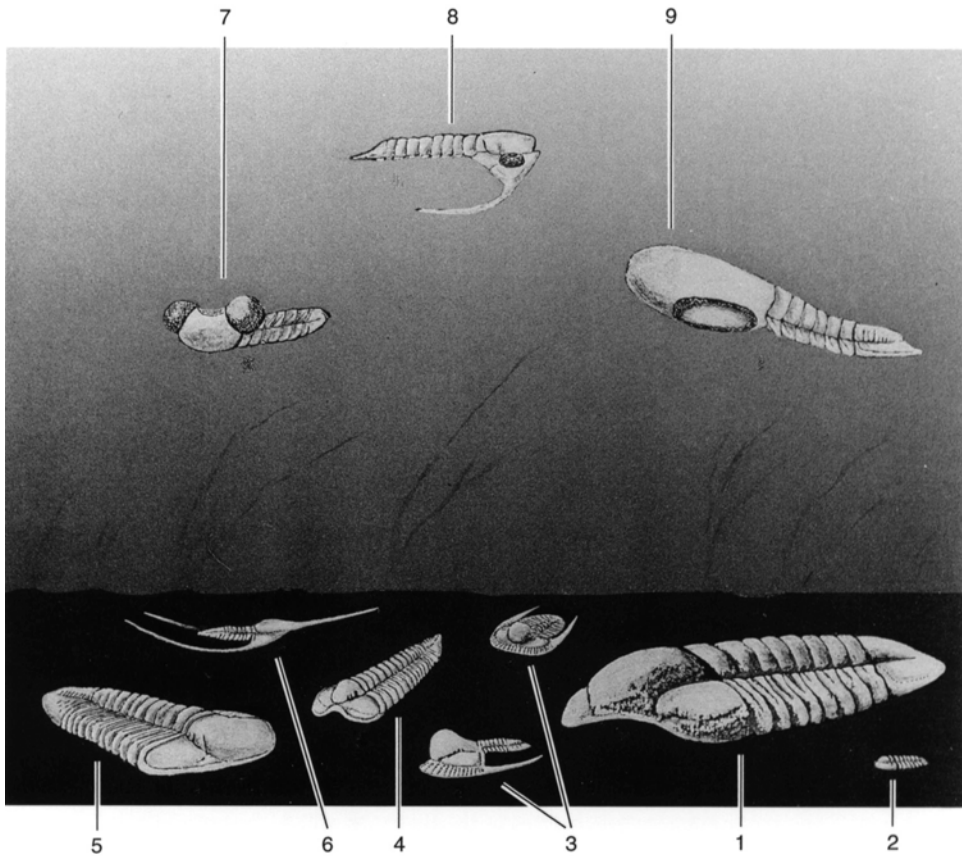
Fig. 139. *1–6,* Atheloptic assemblage of blind or nearly blind benthic trilobites; *1, Illaenopsis; 2, Shumardia; 3, Bergamia; 4, Colpocoryphe taylorum* Fortey & Owens; *5, Ormathops nicholsoni* (Salter); *6, Ampyx. 7–9,* Large-eyed, mesopelagic, free-swimming forms; *7, Pricyclopyge; 8, Bohemilla (Fenniops); 9, Degamella* (Fortey & Owens, 1987, fig. 13).

assemblage (Fig. 139). Also occurring in it are large-eyed cyclopygids, considered to have been mesopelagic in habit. In describing a nautiloid assemblage from Upper Ordovician shales in Ohio, Frey (1989) remarked that species of the trilobites *Flexicalymene* and *Isotelus* are the most abundant. Attention is drawn to this and other examples of a possible predator-prey relationship between nautiloid cephalopods and trilobites.

The recognition of lateral facies changes, the problems they pose in correlation, and the need for separate zonal schemes in adjacent facies are illustrated by examples from western North America (Robison & Rowell, 1976) and other continents (Palmer, 1977). Palmer (1965a) also proposed the name *biomere* for a regional stratigraphic unit, the boundaries of which were defined by an abrupt, nonevolutionary change in the dominant members of a single phylum, in this case trilobites of the Upper Cambrian pterocephaliid biomere in the Great Basin (Palmer, 1965b). In his original definition, Palmer remarked that the change at the base of a biomere was not necessarily related to any break in sedimentation and might be diachronous. Further study (Palmer, 1984) has not revealed evidence of lithological

change or diachroneity at the abrupt faunal change, and the advent of cooler or anoxic waters on to the shelf is regarded as a possible cause of change. That some faunal changes occurred is admitted, but it has been argued (BRIGGS, FORTEY, & CLARKSON, 1988, p. 187) that the change may have been exaggerated by the taxonomic treatment employed. The three Upper Cambrian biomeres have been proposed as stratigraphic stages by LUDVIGSEN and WESTROP (1985). These authors (1983a) have used cluster analysis to differentiate trilobite facies faunas at generic and family level in Upper Cambrian and Lower Ordovician rocks. As a result of this analysis they concluded that a catastrophic event was not required to explain the faunal change between Cambrian and Ordovician trilobites (cf. FORTEY 1983; WESTROP & LUDVIGSEN, 1987). A subsequent examination of this faunal change by FORTEY (1989) and of that at the Ordovician-Silurian boundary suggested that the data indicating such a change may have been influenced by how the trilobites had been classified. The importance of mode of life and possible oceanic events was assessed in relation to the faunal change. LUDVIGSEN and others (1986) have discussed stratigraphical problems, including zones and facies, in a wider context.

Consideration of the geographical distribution of families and genera led to the idea of faunal provinces or realms, areas to which particular taxa were limited (WALCOTT, 1890b, 1910; GRABAU, 1931; KOBAYASHI, 1944b). RICHTER and RICHTER (1941b) portrayed a *Redlichia* sea extending from the Middle East to Australia, and WILSON (1957) linked the worldwide occurrence of Upper Cambrian and Lower Ordovician olenids to a dark shale and limestone facies situated in and near the borders of troughs that were the sites of Paleozoic mountain belts. These ideas of a link between facies, tectonics, and faunas were applied to the distribution of North American Cambrian trilobites by LOCHMAN-BALK and WILSON (1958), who explained the differences between faunas of similar ages as related to

three different realms—a cratonic, shallow-shelf realm; an intermediate realm at the margin of the craton; and an extracratonic realm coinciding with the mobile belt. The biogeography of Cambrian and Ordovician trilobites in relation to Tethys was discussed by SDZUY and DEAN (in ADAMS & AGER, 1967) and in relation to the Atlantic ocean by WILSON (1966). The distributions of trilobites on a present-day world map were given for the Cambrian by COWIE (1971) and PALMER (1972) and for Ordovician trilobites by WHITTINGTON (1966; in HALLAM, 1973). Meanwhile, studies on paleomagnetism and the fit of continents around the Atlantic (BULLARD, EVERETT, & SMITH, 1965) were beginning to be widely appreciated, and speculations on possible early Paleozoic paleogeography, pole positions, and climate could be compared with past distributions of animals. From such studies came the reconstructions for the Cambrian by JELL (1974) and BURRETT and RICHARDSON (1980) and for the Ordovician by WHITTINGTON and HUGHES (1972, 1973, 1974). Faunal realms are seen to have been associated with the seas around continental masses, the barriers between realms being the deeper waters between these masses, and the temperature that was determined by latitude and water depth. The influence of ocean currents on these distributions was considered by ROSS (1975), and the distribution of the cold-water, shallow-shelf *Neseuretus* fauna of the Lower Ordovician was described by FORTEY and MORRIS (1982). WILDE (1991) considered the oceanographic conditions during the Ordovician in more detail. Studies of Lower Paleozoic trilobite faunal realms are by W. ZHANG (1989) on the Cambrian, Zhiyi ZHOU and DEAN (1989) on the Ordovician, SCHRANK (1977) on the Silurian, and COCKS and FORTEY (in McKERROW & SCOTESE, 1990) on the Ordovician and Silurian. Phanerozoic world maps, compiled using data from paleomagnetism and tectonics, were provided for a symposium on biogeography by SMITH, BRIDEN, and DREWRY (1973). Newer versions of such

maps are by SCOTESE and others (1979), SMITH, HURLEY, and BRIDEN (1981), and SCOTESE and McKERROW (1990). The data on biogeography were derived independently and so provide a test of these maps. However, an unusual fauna found in an area of structural complexity on the margin of a continental block, such as that of SAMSON and others (1990), may provide problems. Is it unusual because it belonged to a (supposedly) distant faunal realm, or does its distinctive character result from facies change at a continental margin?

TAPHONOMY

Over the past 50 years, an increased understanding of sedimentary processes has enabled a more detailed picture to be drawn of the burial events that led to preservation. The abundance and variety of trilobites, the molting process as size increased, and the thickness of the cuticle shed caused large quantities of skeletal debris to be produced. The preservation of entire exoskeletons, of appendages, of particular arrangements of exoskeletal parts, or of exoskeletons in a characteristic orientation gives clues to the type of sedimentary process that operated as well as to behavior. Relationships between the various processes are complex (SPEYER, 1987; 1991); the processes and their interactions were discussed by BRIGGS and CROWTHER (1990, p. 213–297).

DISARTICULATED REMAINS

In a study of the taphonomy of trilobites in Middle Devonian rocks in New York, SPEYER and BRETT (1986) used indices of fragmentation, orientation, and occurrence of articulated, enrolled, or molted exoskeletons. From these they derived divisions termed *taphofacies* that are related to type of sediment, rate of sediment supply, and water depth. This study has many parallels with the earlier studies by FORTEY (1975a) and TAYLOR (1976), which also recognized the distinctions between rocks containing assemblages of disarticulated parts of exoskeletons

(some broken) and those containing complete exoskeletons and related these distinctions to depth and type of sediment.

Disarticulation and fragmentation of trilobite exoskeletons probably took place rapidly after death or exuviation if the exoskeletons were exposed at the sediment-water interface and subjected to decay, scavenging, and currents. Currents may have resulted in sorting by size, shape, and resistance to fragmentation. Assemblages recovered at different localities from a single zone in Upper Cambrian strata in western Canada (WESTROP, 1986a) show a gradation in abundance of species of two genera. Individuals of *Ellipsocephaloides* are small (having a maximum cranidial length of 12 mm) and include early ontogenetic stages, while those of *Ptychaspis* are twice this size, and early ontogenetic stages are rare or absent. The *Ellipsocephaloides* assemblage occurs in relatively fine-grained beds, the *Ptychaspis* in relatively coarse-grained strata. These beds are considered to have been generated by storms and the intergrading assemblages to be the effect of size sorting. Thus, as WESTROP pointed out, the end-members of the series might be thought to represent different facies or to be depth-related but are the outcome of taphonomic processes. Another example of sorting is from Lower Cambrian rocks in northwestern Vermont (SPEYER, 1987). Randomly oriented cephala of *Olenellus* (with or without the hypostome and perrostral plate) occur in a quartz arenite. It is thought that the relatively fragile thoracic segments and pygidium were broken down, and the cephala survived because of greater resistance to mechanical breakdown. In siltstone beds a few meters higher in the section are accumulations of either cephala or pygidia of *Billingsaspis*. These segregations appear to be examples of size sorting and breakage and are related to grain size of the sediments. The effects of fragmentation and sorting on exoskeleton parts in Middle Devonian rocks in New York (SPEYER, 1987, fig. 3) were revealed by counts of specimens in strata of different facies. Fragmentation was greatest

in current-sorted deposits in which cephala of *Greenops* are rare because of their susceptibility to damage. In contrast, cephala and pygidia of *Phacops* are roughly equally represented in different types of strata. The pygidium and cephalon of *Phacops* were of similar convexity, and convex-up and convex-down specimens occur in similar numbers. In *Greenops* these two sclerites responded differently to hydrodynamic conditions. In contrast is the study of mainly disarticulated exoskeletal remains of *Dikelocephalus* from the Upper Cambrian of the northern Mississippi Valley (N. C. HUGHES, 1993). In these predominantly fine-grained rocks, transportation has been minimal, but compaction has cracked and deformed sclerites, producing shapes that are artifacts and hence not characters of taxonomic significance.

Experiments by HESSELBO (1987) using models of the *Dikelocephalus* cephalon and pygidium showed that these sclerites differed in behavior, both when falling through still water and when entrained in flowing water. Similar experiments by LASK (1993) showed that the most stable attitude for the cephalon or pygidium of *Flexicalymene* was concave-side down; enrolled exoskeletons were moved more readily than isolated sclerites. Evidently the hydrodynamic properties of sclerites need to be take into account and may be useful as paleocurrent indicators. SPEYER (1987, p. 211) considered that in the Devonian strata of New York, the occurrence of sclerites oriented randomly, obliquely, or perpendicularly to the bedding, indicated deep bioturbation. Such orientations have been recorded in coarse-grained glauconitic limestones (BOHLIN, 1949), and it was argued that burial was rapid, a settling out from a suspension of sedimentary particles and organisms or parts of skeletons.

Disarticulated parts of trilobite exoskeletons may be broken. COURTESSOLE, HENRY, and VIZCAÏNO (1991, p. 13) remarked that the exoskeletons of *Neseuretus* and *Pradoella* are never found entire in sandy, platform sediments, and the fragile free cheeks and

thoracic segments rarely occur. Cranidia and pygidia found in nodules were in most instances broken before burial. It was also suggested that abrasion may have removed the external sculpture from convex portions of some exoskeletons and even the inner portion of glabellar furrows. On the other hand illustrations of silicified specimens or of those in limestones show that surface sculpture may be preserved in remarkable detail in dissociated exoskeletal parts. WILMOT's study of fragments of proetids (1991) exemplified such perfection of preservation, and she remarked that the use of sculptural detail in characterization of species is limited because of destruction of detail during diagenesis (not as a result of abrasion).

ARTICULATED REMAINS

The occurrence of outstretched, complete exoskeletons (FORTEY, 1975a; TAYLOR, 1976) or of molt configurations (see section on exuviation and the function of sutures, p. 152) is taken to indicate burial of an autochthonous assemblage of species, and the type of rock in these examples suggests accumulation in deeper, quiet, offshore waters. Burial of entire exoskeletons does not occur only in deeper water. Those of *Dalmanitina socialis* in the Ordovician of Czechoslovakia (PŘIBYL & VANĚK, 1976, p. 20, pl. 8) are in quartzites considered to be a nearshore deposit. The occurrence of the librigenae united by a narrow strip of doublure (FORTEY, 1974b, pl. 3, fig. 1) or of the hypostome beneath the glabella (TAYLOR, 1976, pl. 2, fig. 7; FORTEY, 1990a, pl. 1) is indicative of the lack of disturbance of the remains and suggestive of rapid burial. In an analysis of articulated remains SPEYER (1987, fig. 6) drew attention to the importance of behavior in ecdysis and to burial in anaerobic or dysaerobic conditions. Thus molting behavior may account for preservation in an inverted and partly disarticulated condition (Fig. 134). Aggregations, some of them monospecific, of many complete or almost complete exoskeletons (see section on clusters and monospecific occurrences, p. 159),

were discussed by SPEYER (1987), who favored the view that decay of a carcass and accumulation of gas beneath the exoskeleton caused overturning prior to burial. Complete, enrolled trilobites have been collected from pure and muddy limestone and from a wide range of terrigenous, clastic rocks; hence, the conditions under which they were preserved may have differed considerably. In the Hamilton beds of New York, enrolled trilobites are abundant in some deeper-water sediments, and the lateral persistence of horizons yielding them suggests burial during such widespread events as storms (BABCOCK & SPEYER, 1987; SPEYER, 1987). As BABCOCK and SPEYER remarked, essential conditions for preservation were rapid burial combined with reducing conditions at or just below the sediment-water interface. The manner in which specimens of *Olenoides serratus* are preserved in the Burgess Shale (WHITTINGTON, 1975; 1980b) indicates that similar factors operated—catastrophic burial and reducing conditions after entombment.

Conditions of burial and preservation of the trilobites in the Upper Ordovician Frankfort Formation with pyritized appendages (CISNE, 1973a; BRIGGS & EDGECOMBE, 1993) were similar. CISNE commented on the orientation of the specimens, noting that some were entombed in an attitude oblique to the bedding. Examples of such specimens of *Triarthrus eatoni* have been illustrated by WHITTINGTON and ALMOND (1987). The famous pyritized fossils from the Devonian Hunsrück Shale of Germany are oriented in different directions and were preserved under similar conditions (STÜRMER & BERGSTRÖM, 1973). Authors have referred to the compaction that has taken place in these fine-grained sediments in the course of lithification. Its effects on obliquely oriented specimens (WHITTINGTON, 1980b, fig. 3) were considerable, shifting the entire suite of appendages relative to the exoskeleton and greatly changing the alignment of and distance between appendages of the two sides. Such compaction also affected the exoskeleton, and in finer-grained, terrigenous clas-

tic rocks the flattening and cracking, resulting in reduction of the original convexity, is familiar. Tectonic deformation may also have affected the exoskeleton, distorting the shape and also leading to the so-called long and broad forms (see section on dimorphism, p. 161).

The effects of diagenesis on the exoskeleton are most obvious in the dissolution that resulted in preservation as casts and molds and in replacements. Silicification of exoskeletons in limestones has enabled exceptional specimens to be extracted for morphological and ontogenetic studies; the silica may be in the form of quartz (WHITTINGTON & EVITT, 1954) or beekite in some of the trilobites from the Permian of Texas. In some specimens from the Frankfort Formation (WHITTINGTON & ALMOND, 1987), the exoskeleton is replaced by pyrite; in the Burgess Shale (WHITTINGTON, 1980a) replacement of the exoskeleton was by clay minerals of the illite group. The external sculpture of the exoskeleton has been preserved with remarkable fidelity in the course of these replacements. Decay and diagenesis of enrolled trilobites from Devonian strata was discussed by SPEYER (1987). Studies of the microstructure of the cuticle (see section on microstructure and sculpture, p. 74) reveal in detail the effects of diagenesis. Preservation of appendages was by different diagenetic processes (ALLISON & BRIGGS in DONOVAN, 1991). In the Burgess Shale the appendages are flattened and preserved as an exceedingly thin, dark film that is reflective. This film was thought to be of calcium aluminosilicate (WHITTINGTON, 1980b), but the work of BUTTERFIELD (1990) suggested that it may be composed of carbon, which may have acted as a template for diagenetic silicate minerals. The reinvestigation of the appendages of *Triarthrus eatoni* has suggested (WHITTINGTON & ALMOND, 1987) that pyrite was deposited as an infilling or lining of the cavity within the cuticle covering the limbs. How pyrite formed in such fine-grained sediments, rich in organic matter, was reviewed by ALLISON and BRIGGS (in DONOVAN, 1991);

the conditions that obtained in the beds containing pyritized *Triarthrus* have been investigated by Briggs, Bottrell, and Raiswell (1991). The phosphatization of appendages, as either a replacement or coating of the cuticle, of *Agnostus pisiformis* from Upper Cambrian strata of Sweden, has been discussed by Müller (1985), Müller and Walossek (1987), and Allison and Briggs (in Donovan, 1991). The importance of gaining some understanding of diagenesis in order to interpret what is preserved has been emphasized by authors. It makes a difference in the appearance of an appendage, if the cuticle has been infilled by mineral matter, or whether it has been replaced or coated.

USE OF NUMERICAL AND CLADISTIC METHODS

H. B. Whittington

Linear dimensions and counts of numbers of segments, of axial rings, tubercles, and ribs of the pygidium, for example, have long been used to show the range in size of species, variation between individuals, and aspects of growth and evolution (e.g., Barrande, 1852; Hupé, 1950, 1953c; Whittington, 1957b; Palmer, 1957, 1958; Best, 1961; Hunt, 1967; Ramsköld, 1986; Sheldon, 1988; Foote, 1989, 1991). There have also been attempts to introduce greater precision into the description of species by measurements, for example, Jaanusson (1953a, 1953b), Shaw (1956, 1957, 1959), C. P. Hughes (1969, 1971, 1979) and Owen (1981). The difficulties in discriminating between species are made evident by the detailed study of material of *Dikelocephalus* from the Upper Cambrian of the Mississippi Valley (Labandeira & Hughes, 1994). Orientation of specimens (see section on size, form, and orientation, p. 1) when they are not flattened in one plane presents problems, and standardization of procedures in orientation and measurement has been discussed (Temple, 1975). Numerical methods have not been widely adopted in descriptions of species, even for well-preserved specimens in limestones or those freed from the matrix with acid. An exception is the trinucleids, because the number and arrangement of pits in the fringe may be investigated in detail. Since the pioneering work of Bancroft (1929), numerical methods have been employed generally on trinucleids (C. P. Hughes, 1970; C. P. Hughes, Ingham, & Addison, 1975; Owen, 1987a, 1987b). Distinct species and subspecies have been distinguished by analysis of the arrangement and number of the pits in specimens from small samples. Larger samples, however, have shown that two or three of such forms may be present in a single, polymorphic population. This enabled Owen (1980) to characterize some species or subspecies of the Upper Ordovician *Tretaspis* by the relative abundance of two or more forms or morphs. In their study of *Cryptolithus,* Shaw and Lespérance (1994) have found similar polymorphism in large samples from Middle and Upper Ordovician rocks in eastern North America. Morphs, originally considered to be distinct species, occur in different proportions in successive populations and appear to constitute a single polymorphic species. Species of what is thought to be a distinct genus occur in western areas and have been shown to have hybridized in the south, in Oklahoma (Shaw, 1991), with populations of *Cryptolithus.* Thus, numerical work on larger samples has radically altered earlier views on taxonomy and raised problems regarding supposed evolutionary mechanisms.

Special methods were applied to Encrinurinae (Temple & Tripp, 1979; Temple & Wu, 1990) and to Trinucleidae (Temple, 1980), the aim having been to define each species as objectively as possible by the use of a local sample, which is of necessity assumed to be monospecific. A list of morphological attributes (e.g., presence and length of mucro, presence of particular tubercles, numbers of tubercles in encrinurinids, or characters of glabella and fringe in trinucleids) was coded for each species, based on either published descriptions or topotype collections. Each species was thus analyzed and characterized numerically, and relationships between the species were examined. Suggestions of evolutionary relationships and taxonomic groupings emerged. Important in these studies are the attempts to select attributes and to define precisely characters that may be coded. In using cladistic methods, characters must be clearly defined, be homologous for all taxa coded, and show discontinuous states, i.e., be present or absent, long or short relative to some standard, or, in the case of a furrow, be deeply impressed, weak, or absent (cf. Ramsköld, 1991a). A taxon, of whatever rank, is considered to be monophyletic if it includes the

stem species (the latest common ancestor of the group) and all those species derived from it (e.g., JEFFERIES, 1986, p. 2–16). In some cladistic treatments a character is determined to be either primitive for a particular taxon or derived from it and hence advanced. Such determinations have been made by comparison with closely related taxa (out-groups), by use of the premise that similarities in early ontogeny reflect a common ancestry, and from stratigraphical evidence (FORTEY & JEFFERIES, 1982). The classification arrived at is based exclusively on those characters considered to be advanced. Examples of the application of these methods include a study of encrinurid protaspides and their relevance to family and subfamily groupings (EDGECOMBE, SPEYER, & CHATTERTON, 1988), diagnosis of new encrinurid genera (EDGECOMBE & CHATTERTON, 1990a, 1990b), classification of Asaphina (FORTEY & CHATTERTON, 1988) and trilobites at a higher level (FORTEY, 1990a), and evolution in odontopleurids (RAMSKÖLD, 1991a, 1991b) and phacopids (RAMSKÖLD & WERDELIN, 1991). As many as 30 or 40 characters have been used, some of which involve measurements of length or width. Cladograms have been constructed using computer programs to examine the character data. There is considerable current debate on methodology in cladistic analyses, as a recent examination of relationships between species of *Odontopleura* shows (ADRAIN & CHATTERTON, 1990); a review of cladistics in paleontology was written by YOUNG (1995).

Relationships between assemblages of genera of trilobites occurring at particular localities and in relation to the enclosing rock type have been analyzed using different methods (ROWELL & MCBRIDE, 1972; ROWELL, MCBRIDE, & PALMER, 1973; SHAW & FORTEY, 1977; LUDVIGSEN, 1978b; LUDVIGSEN & WESTROP, 1983a). The merits and demerits of the various methods are discussed, cluster analysis appearing to be useful in discriminating biofacies in time and space (LESPÉRANCE, 1990). Studies of biogeography and faunal provinces (WHITTINGTON & HUGHES, 1972; BURRETT, 1973; JELL, 1974; BURRETT & RICHARDSON, 1980) have used other procedures, particularly those designed to assess differences between faunal assemblages.

ONTOGENY

BRIAN D. E. CHATTERTON and STEPHEN E. SPEYER

Trilobites molted their exoskeletons at regular intervals in ontogeny. Growth and change in external form occurred when the trilobites were soft-shelled, following molting and before secretion of the next hard exoskeleton. We know little of trilobite behavior during this period. It is likely that the animals were relatively inactive because of the changes taking place in their bodies and the importance of the exoskeleton in providing leverage for proper action of many of their muscles (LOCKWOOD, 1968; REYNOLDS, 1980).

The postembryonic part of the trilobite life cycle has been divided into three main intervals, the protaspid, meraspid, and holaspid periods (Fig. 140–141). These have been subdivided into a number of stages that are usually synonymous with molts or instars (Fig. 140). The existence of an uncalcified preprotaspid stage after hatching is purely speculative; calcification probably took place very soon after emergence from the egg.

Because each calcareous exoskeleton was carried essentially unchanged for a short period during the life cycle of each trilobite animal, an excellent record is available of most of the external form. Different individuals of the same species apparently molted the same or a similar number of times during a complete life cycle, usually at similar sizes. Individuals with exoskeletons that are approximately the same size cluster as instars. As a rule, instars are more distinct early in the life cycle than later (Fig. 142), since individual variability in growth rates usually causes later instars of the same specices to overlap in size. Some species, perhaps associated with more stable environments or a stronger genetic relationship between size and onset of molting, allow the recognition of distinct instars on the basis of size late in ontogeny (Fig. 143). Instars are more easily recognized in collections taken from a single bed (or block of rock) and in samples that show little or no distortion.

Little opportunity occurred for wear, solution, or attachment of epiphytic organisms during life, since the the exoskeleton was carried by the animal only for the period between two ecdyses (a period of a few weeks to a year in modern horseshoe crabs, depending mainly upon the age of the animal; see SEKIGUCHI, SESHIMO, & SUGITA, 1988). Following molting or death, the exoskeleton was subjected to normal taphonomic processes. Some arrangements of sclerites have been regarded as the result of molting rather than death (see earlier section on exuviation and the function of sutures, p. 152).

We do not know how many molts occurred during the life cycles of most trilobites. Clearly there was considerable variation between taxa. Very large trilobites and those with many thoracic segments presumably molted a greater number of times than those that were small or had few thoracic segments. HUNT (1967) demonstrated that the Agnostina *Trinodus elspethi*, which had only two thoracic segments, had at least nine instars (three meraspid, six holaspid) during its life cycle and thus must have molted at least eight times (Fig. 143). Probably this is close to a minimum number for the class. The number of thoracic segments released into the thorax following each molt during the meraspid period was usually one, sometimes two (CHATTERTON, 1971), and rarely greater than two. This suggests that some Early and Middle Cambrian Redlichiida may have molted more than 30 times.

Small growth stages are often very different from the adults of the same species, being usually simpler in form and more conservative. Hence, considerable disparity exists between different trilobite larvae. Metamorphosis during the life cycle or radical, growth-related allometry often eliminated features present in larval stages. Larvae of closely related taxa are more similar than those of distantly related taxa (CHATTERTON & others, 1990) so that the larval stages
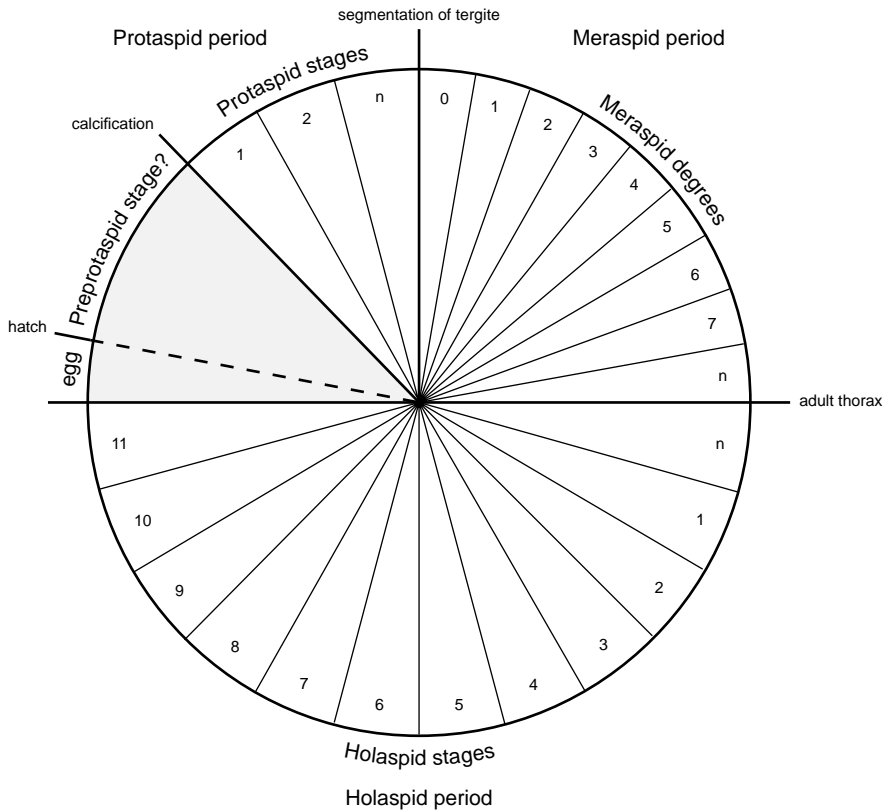
FIG. 140. Trilobite life history (adapted from Speyer & Chatterton, 1989).

contain morphological information vital for understanding trilobite taxonomy, systematics, and phylogeny.

HISTORY OF RESEARCH

BARRANDE (1852) described the ontogeny of *Agnostus, Blainia, Paradoxides, Sao,* and *Trinucleus.* In doing so, he put into synonymy a number of taxa (10 genera and 18 species) that had been erected by HAWLE and CORDA (1847), recognizing these specimens as different growth stages of a single species, *Sao hirsuta.* BARRANDE also suggested a method for numbering growth stages during the meraspid period that is still in use today (meraspid degrees, distinguished by the number of free segments that have been released into the thorax).

BEECHER (1893a) was the first to describe the silicified larvae of trilobites, although silicified adult trilobites had been obtained from limestones earlier by RATTE (1886). Two years later, BEECHER (1895a) provided a general discussion of trilobite ontogeny and proposed the term protaspis (plural protaspides) for early growth stages where the head and tail parts of the trilobite are still fused. He subdivided the protaspid period, which often included several instars, into ana-, meta-, and paraprotaspides. These subperiods were not defined and are of limited practical value, having been used inconsistently, and lack biological meaning (see discussion of morphology and terminology, p. 183).

JAEKEL (1909) was the first to suggest heterochrony as the cause of origin of a major group of trilobites by proposing that the
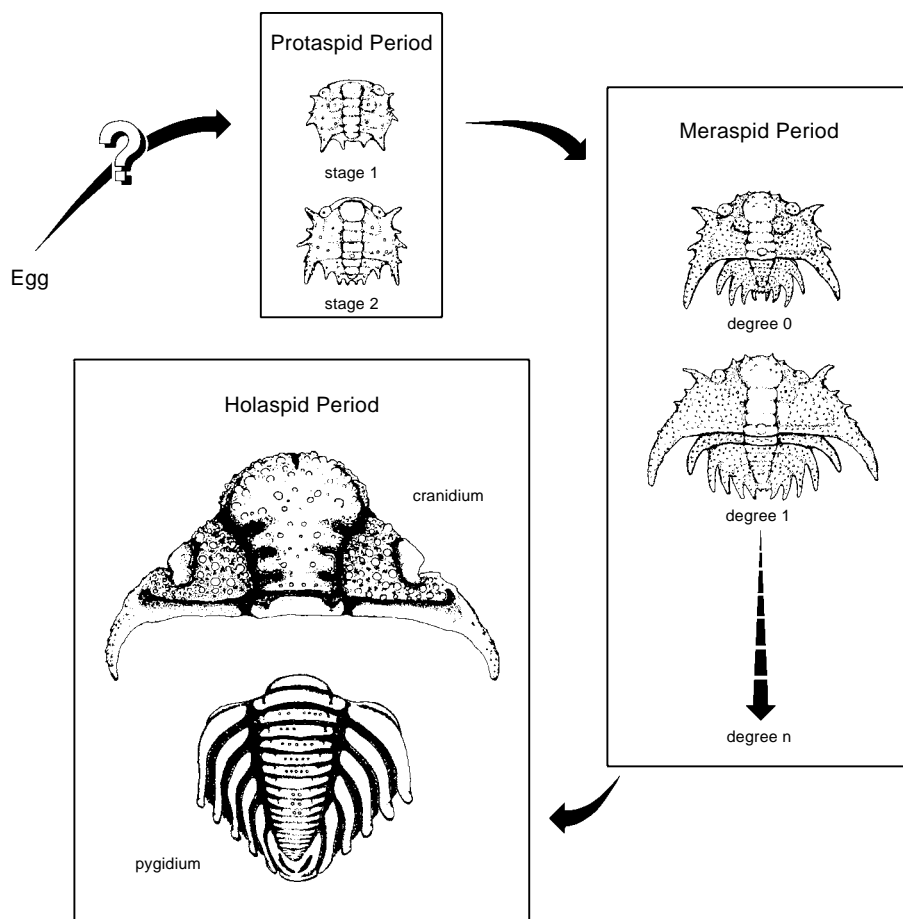
FIG. 141. Growth stages of the life history of a typical trilobite, *Encrinuroides rarus* (WALCOTT) (adapted from Speyer & Chatterton, 1989).

Agnostida, which he called miomerids, arose from polymerid trilobites through paedomorphic evolution (see section on heterochrony, p. 199). RAW (1925) added the terms meraspis and holaspis to BEECHER's term protaspis, dividing the life cycle of most trilobites into three periods. Later summaries of trilobite ontogeny include works by RAW (1927), STØRMER (1942), HUPÉ (1954), WHITTINGTON (1957a, 1959b), HU (1971), CHATTERTON (1980), MCNAMARA (1986b), CHATTERTON and SPEYER (1989, 1990), and SPEYER and CHATTERTON (1989, 1990).

STUBBLEFIELD (1926) described the addition of new segments in the trilobite thorax, originating near the back of the pygidium and migrating forward during the ontogeny of *Shumardia (Conophrys) salopiensis.* New material was described by FORTEY and OWENS (1991) but did not include protaspides. STUBBLEFIELD showed furrows crossing the axis of the protaspis, but these are not evident with SEM examination of his original material in the Natural History Museum, London.

STØRMER (1942) discussed the pattern of somitic organization of trilobites and provided additional data on growth series of *Liostracus* and *Olenus* in particular. He also discussed ontogenetic information available
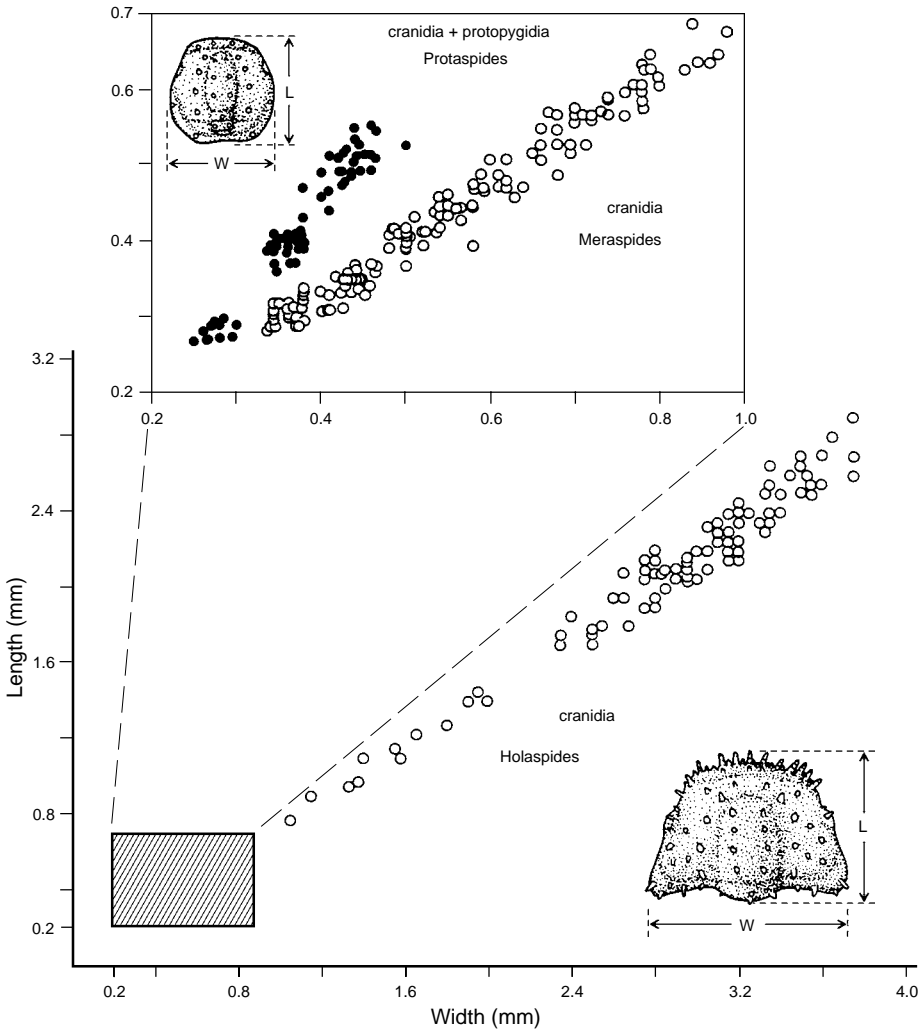
FIG. 142. Growth and recognition of instars of *Dimeropyge* (see Fig. 160) from the Middle Ordovician Esbataottine Formation in northwestern Canada. Due to individual variation in growth rates in meraspides and holaspides, recognition of instars is easier in protaspides (*solid circles*) than in later growth stages (*open circles*). This figure shows data for protaspides and cranidia; those for protaspides and transitory pygidia and pygidia are similar (new).

for higher taxa and considered the use of larval attributes in classification and understanding homologies.

Papers describing silicified trilobite larvae have substantially increased the number of known trilobite growth series and the amount of morphological information available (WHITTINGTON, 1941, 1956a, 1956c, 1956d, 1959a; EVITT, 1961; WHITTINGTON & EVITT, 1954; ROSS, 1951a, 1951b, 1953;

PALMER, 1957, 1958, 1962b; HUNT, 1967; SHAW, 1968; WHITTINGTON & CAMPBELL, 1967; HU, 1971, 1974a, 1974b, 1975a, 1975b, 1976, 1985a, 1985b, 1986; CHATTERTON, 1971, 1980; CHATTERTON & PERRY, 1983, 1984; EVITT & TRIPP, 1977; TRIPP & EVITT, 1981, 1983, 1986; EDGECOMBE, SPEYER, & CHATTERTON, 1988; CHATTERTON & others, 1990; CHATTERTON & others, 1994). Larvae preserved in other manners
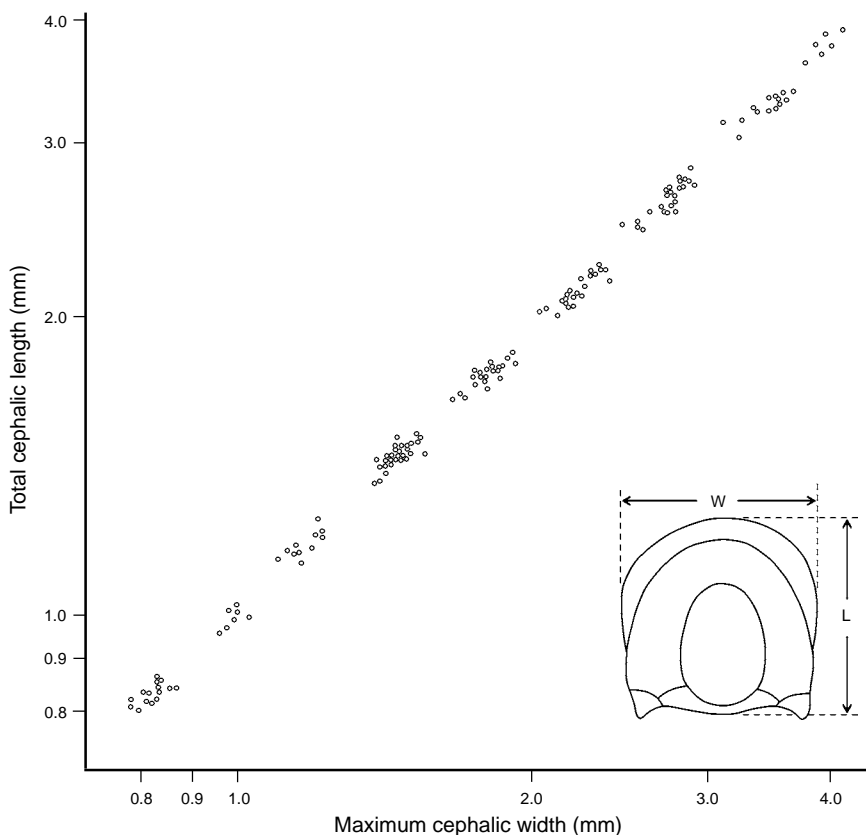
FIG. 143. Growth increments and instars in the life cycle of *Trinodus elspethi* (RAYMOND). Nine instars have been recognized, three in the meraspid period and six in the holaspid period (adapted from Hunt, 1967).

seldom provide as much morphological information, especially for the ventral surfaces of the larvae.

In recent years, phosphatized fossil collections from Australia (JELL, 1970), Spitsbergen (FORTEY & MORRIS, 1978; FORTEY & CHATTERTON, 1988), and China (X. ZHANG, 1987, 1989) have yielded well-preserved skeletons and internal molds of Cambrian and Early Ordovician trilobites.

Since 1950, studies of incremental growth and ontogenetic statistics of various taxa have provided data that are discussed below in the section on trilobite growth and population dynamics (see SHAW, 1956, 1957; BRIGHT, 1959; HUNT, 1967; PALMER, 1957; CISNE, 1973b; ROMANO, 1976; KOPASKA-MERKEL, 1981; BUSCH & SWARTZ, 1985; BREZINSKI, 1986a; SHELDON, 1988; CHATTERTON & others, 1990; CHATTERTON & SPEYER, 1990).

Since GOULD's (1977) work on ontogeny and phylogeny, paleontologists have re-examined relationships between ontogeny, phylogeny, and ecology in the context of heterochrony. Because trilobites grew by increments, they are particularly apt subjects for such studies (McNAMARA, 1978, 1981a, 1981b, 1983, 1986a; LUDVIGSEN, 1979a; FORTEY & RUSHTON, 1980; WHITTINGTON, 1981; EDGECOMBE & CHATTERTON, 1987; RAMSKÖLD, 1988; and CHATTERTON & SPEYER, 1990).

Early growth stages have been used to solve taxonomic problems ever since BARRANDE's (1852) synonymy of HAWLE and

CORDA's (1847) taxa. In the last 40 years, larval attributes have become an important source of information critical to our understanding of trilobite taxa at the ordinal level. WHITTINGTON (1954c) suggested that the Phacopida have a distinctive protaspid stage, and this criterion was used in the diagnosis of that order by HENNINGSMOEN (in HARRINGTON, MOORE, & STUBBLEFIELD, 1959). FORTEY and OWENS (1975), likewise, used the similarity among early growth stages (meraspid cranidia) in erecting the Proetida. FORTEY and CHATTERTON (1988) regarded the distinctive asaphoid protaspis as an important synapomorphy (uniting character) of the Asaphina. FORTEY (1990a, 1990b) has discussed the general relationships of ontogeny to trilobite classification. In accordance with von Baer's rule (see GOULD, 1977, p. 56), related taxa display a greater morphological similarity among larval stages than among adults. These larval stages are more similar to each other than to those of distantly related taxa. A number of workers have investigated the relationships and similarities of larvae of trilobite taxa that share a recent, common ancestor (WHITTINGTON, 1956a, 1959a, 1959b; EVITT & TRIPP, 1977; CHATTERTON, 1980; EDGECOMBE, SPEYER, & CHATTERTON, 1988; and CHATTERTON & others, 1990).

Few studies have addressed questions of larval autecology, functional morphology, and mode of life, most having concentrated on adults (e.g., CLARKSON, 1969c; WHITTINGTON, 1975; STITT, 1976; HAMMANN, 1985; FORTEY, 1985). WHITTINGTON (1956d), however, suggested that some protaspides were pelagic but offered little evidence to support his conclusion. CISNE (1973b) argued for pelagic mode of life solely on the basis of size. More recently, CHATTERTON (1980), FORTEY and CHATTERTON (1988), and SPEYER and CHATTERTON (1989, 1990) have discussed trilobite larval ecology and functional morphology in more detail; and CHATTERTON and SPEYER (1989) have examined the relationship between extinction, survivorship, and different trilobite life-history patterns during the Ordovician (see discussion of life-history strategies below).

PRESERVATION AND OCCURRENCE

Early growth stages are preserved in several ways. Most commonly they are preserved in their original calcite (Fig. 144.1; WHITWORTH, 1970), have been silicified (Fig. 144.3–4), or occur as molds or casts in a matrix resistant to solution or weathering (Fig. 144.2; BARRANDE, 1852; HU, 1971; LU & WU, 1982). Calcium phosphate may replace the calcareous exoskeleton (Fig. 144.6; JELL, 1970; FORTEY & MORRIS, 1978), fill in the shell to provide an internal mold (Fig. 144.5; FORTEY & CHATTERTON, 1988), or even, in rare instances, replace the appendages of small growth stages (MÜLLER & WALLOSEK, 1987). Sclerites may be replaced by pyrite or other such minerals, but usually the crystals of the replacing mineral are too coarse to permit the preservation of morphological details. No pyritized appendages of juvenile stages have been described from the Lower Devonian Hunsrück Shales of Germany or the Ordovician Frankfort Shales of New York, for example (WHITTINGTON & ALMOND, 1987; STÜRMER & BERGSTRÖM, 1973).

The type of preservation constrains the amount and type of information available. Larvae preserved in their original calcareous material can seldom be prepared to permit analysis of their concave ventral surfaces. They may, however, display the surface sculpture in exquisite detail (FORTEY & CHATTERTON, 1988; CLARKSON & ZHANG, 1991). In contrast, it is often possible to eliminate all excess matrix from diagenetically replaced larval remains during preparation (G. A. COOPER & WHITTINGTON, 1965) to permit examination of all preserved details. Unfortunately, the original shell material of early growth stages is often lost preferentially during diagenesis. Indeed it is common in many sedimentary rocks to find
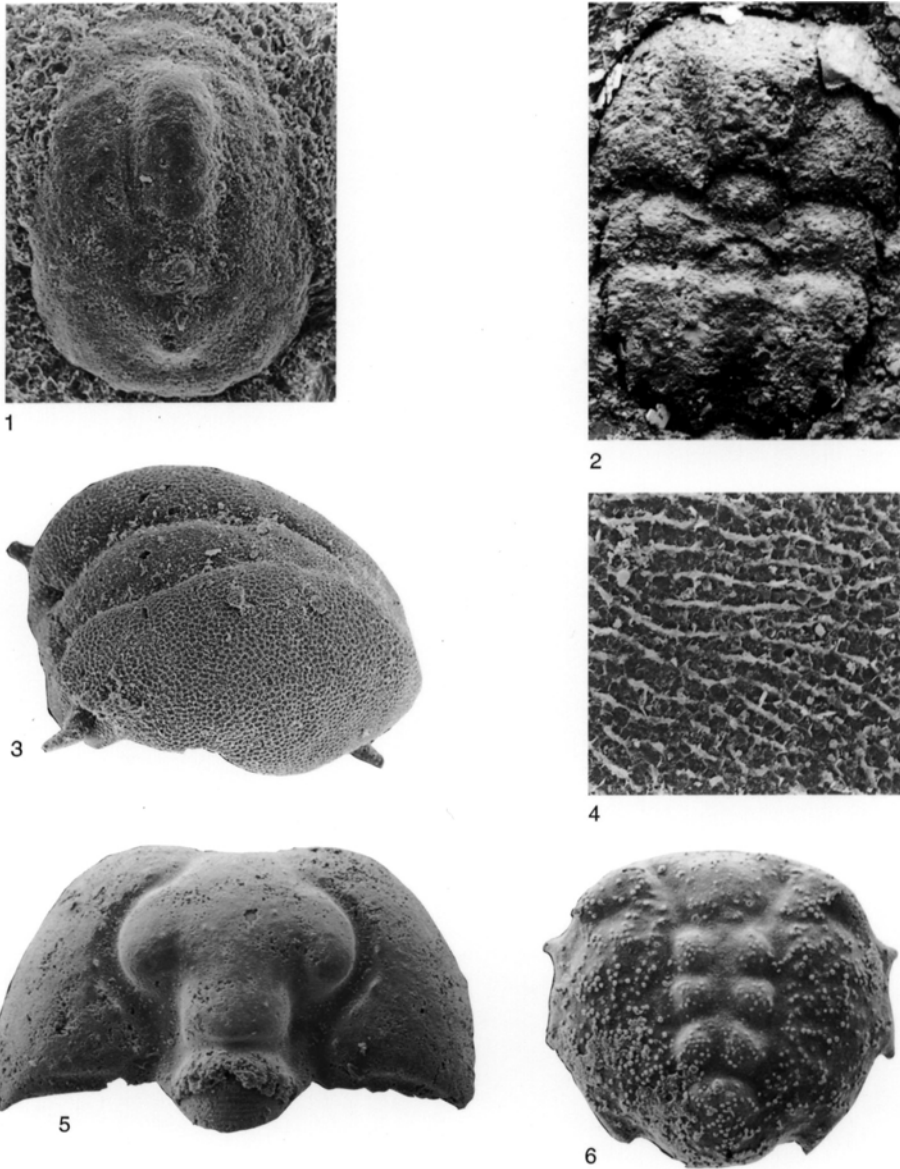
FIG. 144. Preservation of small growth stages. *1,* Preserved in original calcite, proetid protaspid from the Viola Formation, Ordovician, Oklahoma, NYSM 16296, ×115 (new, specimen courtesy of P. J. Lespérance). *2,* Preserved as a mold in shale, meraspid degree 1 of *Conophrys pusilla* (STUBBLEFIELD) from the Shineton Shale, Lower Ordovician, England, BMNH In 26812, ×94 (new, original of Stubblefield, 1926). *3,* Silicified specimen, asaphoid protaspis of *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York, NYSM 16297, ×62.4 (new). *4,* Silicified sculpture from asaphoid protaspis of *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York, NYSM 16029, ×2150 (new). *5,* Calcium phosphate steinkern of *Shumardia acuticaudata* FORTEY from the lower part of the Profilbekken Member, Valhallfonna Formation, Lower Ordovician, Spitsbergen, BMNH It 21250, ×190 (new). *6,* Phosphatized protaspis of *Cybelurus brutoni* FORTEY from the lower part of the Profilbekken Member, Valhallfonna Formation, Lower Ordovician, Spitsbergen, BMNH It 21251, ×93 (new).

numerous specimens of large trilobites and no larval stages at all (SHELDON, 1988). Many of these situations are clearly not the result of current sorting or other mechanical, biostratinomic processes, because articulated exoskeletons are common in the same strata.

Replacement by silica may be coarse, preserving little detail (H. ALBERTI, 1972), or fine enough to preserve exquisite details of the sculpture (Fig. 144.4, 145.5; SPEYER & CHATTERTON, 1989, fig. 11). Calcium phosphate may also preserve very fine detail (Fig. 144.5; FORTEY & MORRIS, 1978).

As a general rule, the best three-dimensional preservation occurs where the exoskeleton has been replaced by quartz or calcium phosphate in fairly pure limestone or early diagenetic calcareous concretions. Specimens preserved in shales are usually flattened as a result of postdepositional compaction, and details of marginal spines and the ventral surfaces of such specimens are rarely shown in published illustrations. Techniques for making high-quality casts of small fossils preserved in fine, indurated, siliciclastic rocks (ZAPASNIK & JOHNSTON, 1984) may, however, provide an important source of information in the future.

Larval sclerites are usually disarticulated. The chances of discovering articulated stages, particularly those belonging to the meraspid period, are greater when specimens have been cracked from limestone or shale. However, some silicified specimens have been discovered with one or both free cheeks attached in life position (Fig. 145.3, 146.1–3; SPEYER & CHATTERTON, 1989, fig. 3c), and even more rarely the rostral plate or hypostome may also be preserved in their original positions (Fig. 146.3; see Fig. 150.7–9; SPEYER & CHATTERTON, 1989, fig. 9e). These latter specimens probably represent examples of infant mortality. Much more common are specimens with the hypostome, rostral plate, or free cheeks attached to the ventral side of the protocranidial-protopygidial fused sclerite (Fig. 145.4,6, 146.4–6). The free cheeks are likely to be located posteromedial of their life positions, and the hypostome occurs be-

hind its life position (Fig. 145.4,6, 146.4–6; SPEYER & CHATTERTON, 1989, fig. 4e, 8a, 8b). The samples in which all of the sclerites are present could represent either carcasses (where the sclerites were dislodged after death, perhaps by shrinking of the ventral integument) or molts, where the trilobites molted while lying on their backs, and the smaller sclerites fell into the empty shell as the animal left its molted exoskeleton. Specimens where only some of the sclerites are present could be examples of either of the above but are more likely to have resulted from the latter. We note that protaspid specimens with the hypostome, free cheek, or rostral plate still attached, either in place or out of place, are rare but are much more common in some rock units (e.g., the Middle Ordovician Crown Point Formation of the Chazy Group of New York) than in others (e.g., the Middle Ordovician Esbataottine Formation of northwestern Canada).

Association of different larval sclerites must be done on the basis of their size, morphology (including sculpture), and spatial distributions (including co-occurrence). Co-occurrence of similar sclerites or larvae at a number of different localities and horizons is often important to determine correct associations, particularly where the trilobites passed through radical metamorphoses in their ontogenies. This problem is made worse by the small number of distinctive, morphological features and broader, ecological (stratal) distributions of the globular, immature, planktonic forms that usually precede metamorphosis. A number of incorrect assignments of larvae to trilobite taxa have been published. It is important that researchers give complete faunal lists of trilobite taxa occurring with larvae that they describe, but we know of instances where the diversity of trilobite larvae exceeds that of the adults in the same samples. Articulated specimens or partly fused specimens are, of course, particularly valuable in associating different parts of a particular stage. They do not, however, provide a correct association of all of the growth stages of a taxon.
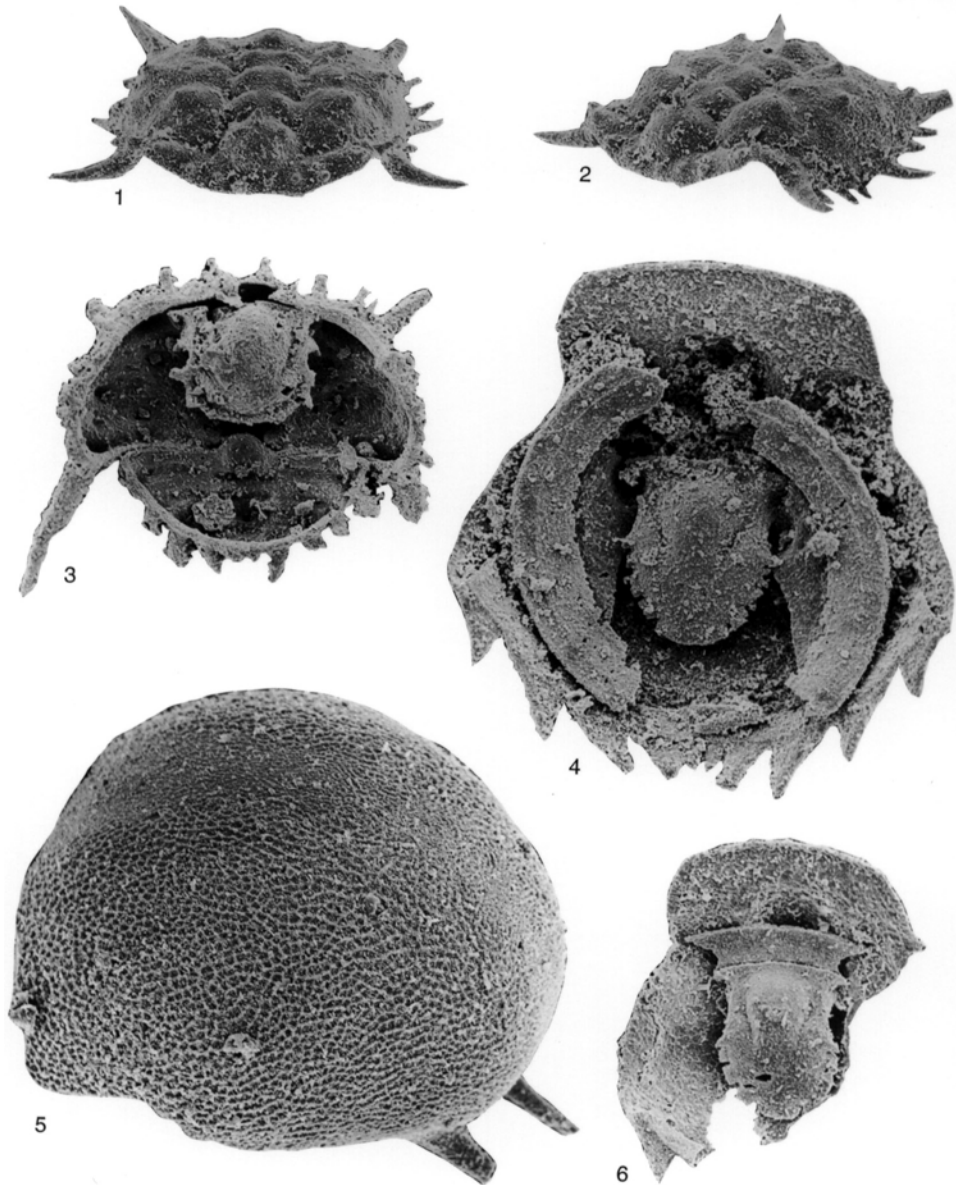
FIG. 145. Larval morphology. *1,2,* Anterodorsal and oblique anterolateral views of protaspis of the encrinurid *Physemataspis insularis* (SHAW) from the Crown Point Formation, Middle Ordovician, New York (locality PB 81), NYSM 16298, ×81 (new). *3,* Ventral view of meraspid degree 0 of encrinurid *Balizoma* sp. from the Wenlock Delorme Formation of northwestern Canada (locality AV 2 248.8); sclerites are in life position, except rostral plate, which is missing, UA 7831, ×51.25 (new). *4,* Ventral view of lichid *Hemiarges* aff. *H. turneri* CHATTERTON & LUDVIGSEN from the Crown Point Formation, Middle Ordovician, New York (locality PB81); free cheeks and hypostome are attached to ventral surface but not in life position, NYSM 16014, ×88 (new). *5,* Dorsolateral view of protaspis of asaphid *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York (locality PB 81); sculpture of polygonal ridges is weaker in region of axis than on genae, NYSM 16299, ×97.5 (new). *6,* Ventral view of broken, small adult-like protaspis of lichid *Hemiarges* aff. *H. turneri* CHATTERTON & LUDVIGSEN from the Crown Point Formation, Middle Ordovician, New York (locality PB81); rostral plate and hypostome are attached to ventral surface, NYSM 16300, ×83 (new).
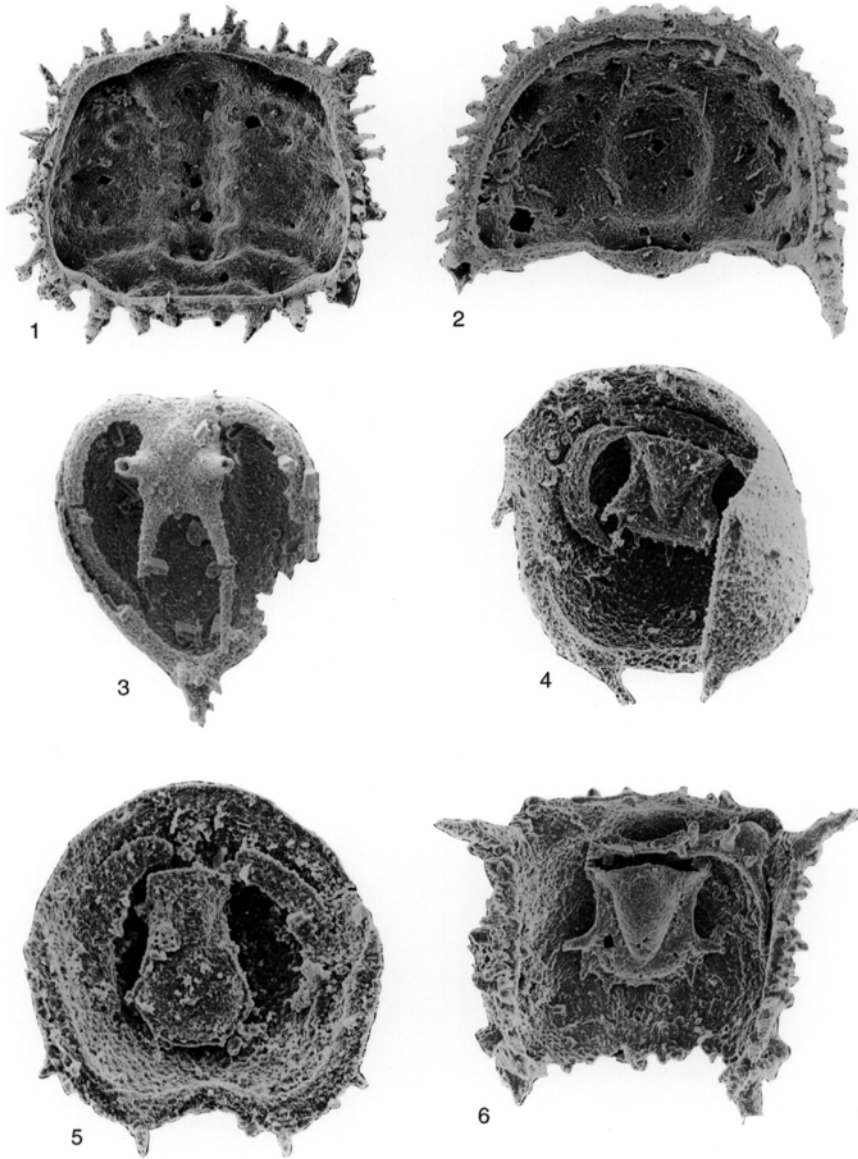
FIG. 146. Association of larval sclerites. *1,* Ventral view of protaspis of the encrinurid *Balizoma* sp. from the Delorme Formation, Mackenzie Mountains, Silurian, northwestern Canada, with attached free cheeks and rostral plate, UA 7824, ×67.25 (new). *2,* Ventral view of small meraspid cranidium of the bathyuroid *Dimeropyge* sp. from the Esbataottine Formation, Middle Ordovician, northwestern Canada, with free cheeks and rostral plate (fused to one another), UA 8420, ×94 (new). *3,* Ventral view of second protaspid stage of the trinucleid *Cryptolithus tesselatus* Green from the Martinsburg Formation, Middle Ordovician, Virginia, with free cheeks and hypostome almost in place, NYSM 16301, ×75 (new). *4,* Subventral view of smallest protaspid instar of the dalmanitoid *Calyptaulax annulata* (Raymond) from the Crown Point Formation, Middle Ordovician, New York; note free cheeks, rostral plate, and hypostome attached to ventral surface, NYSM 16302, ×123 (new). *5,* Ventral view of first protaspid stage (probably of *"Otarion" spinicaudatum* Shaw) from the Crown Point Formation, Middle Ordovician, New York; note free cheeks and hypostome attached to ventral surface, NYSM 16303, ×190 (new). *6,* Ventral view of protaspis of cheiruroid *Cybeloides* sp. from the Whittaker Formation, Mackenzie Mountains, Upper Ordovician, northwestern Canada, UA 7764, ×81 (new).

MORPHOLOGY AND TERMINOLOGY

There is some controversy about whether the protaspid period of some trilobites was preceded by a calcified stage called the **phaselus** (see section on phaselus stage below). The phaselus lacks sutures, has an entire doublure, and is not known to have had a hypostome.

There is general agreement that the prefix *proto* should be used to denote a part of the larval stage that is homologous with a discrete sclerite in the adult. Thus the terms **protocranidium** (in protaspides) and **protothoracic segments** (in protaspides and meraspides) refer to parts of the trilobite that will ultimately become the separate cranidium and the thoracic segments, respectively. The term **protopygidium** refers to that part of the protaspis from which the thorax and pygidium subsequently develop. During the meraspid period, the corresponding tergite is called the **transitory pygidium.**

We do not advocate the usage of the terms **anaprotaspis, metaprotaspis,** and **paraprotaspis** for all trilobites. These terms were proposed by BEECHER (1895a) as subdivisions of the protaspid period (in developmental order). We feel that *paraprotaspis* should be discarded because it is undefined and little used. We also have serious reservations about *anaprotaspis* and *metaprotaspis,* which BEECHER used to describe the stages before and after a recognizable pygidial portion can be distinguished from the protocranidium, usually by the presence of a small furrow behind the head. HU's (1971, p. 49–50) definitions of these terms were based on size and morphology. They differed from those of earlier workers (HU, 1971, fig. 23), however, and are limited to only some trilobite protaspides. Many specialists judge that two separate events must occur for trilobites to develop from anaprotaspis to metaprotaspis: (1) development of enough somites, either in volume or in number behind the head for a future pygidial portion to be apparent and (2) the formation of a furrow to mark the posterior margin of the head. In some taxa the first event occurs some time before the second; in others both events occur almost simultaneously. EDGECOMBE, SPEYER, and CHATTERTON (1988) summarized many of the objections to this classification. In short, these terms bear little biological reality and confuse rather than clarify.

Although the timing of the first appearance of a distinct furrow between the protocranidium and the protopygidium may be a useful marker of ontogenetic stages of closely related trilobites, it is merely one of a number of different developmental events that may be used to monitor heterochronic changes among taxa. Large, supposedly pelagic protaspides (which usually lack such a furrow, e.g., Remopleuridioidea) are remarkably different from much smaller, supposedly benthic protaspides (which may possess such a furrow, e.g., Proetida). The possession of a differentiating furrow, then, is less of a developmental marker denoting relative maturity than a probable ecological correlate. (See discussion of ecological differences between adult-like and nonadult-like trilobite larvae below.) Some pelagic protaspides clearly possess portions that are homologous with what will later become the transitory pygidium. These parts of the protaspis are, however, quite different in form from the transitory pygidium and not delineated from the protocranidium by a distinct furrow. Should they be called anaprotaspides or metaprotaspides? While we accept that the time of origin of a distinct furrow between the protopygidium and the protocranidium can be a useful marker of a stage in the maturity of an individual (for instance in heterochronic studies), the terms *anaprotaspis* and *metaprotaspis* cannot be applied in a homologous fashion for all trilobites. They should be restricted taxonomically and used purely descriptively (perhaps as a synonym for adult-like protaspis). There is little need for retaining the term *paraprotaspis.*

Some of our criticisms of the terms *anaprotaspis, metaprotaspis,* and *paraprotaspis* could also be applied to the three periods

(protaspis, meraspis, and holaspis), whose boundaries may occur in widely different ages and degrees of morphological maturity in distantly related trilobites. With very few exceptions, however (e.g., PALMER, 1958; X. ZHANG, 1989), all students of trilobite ontogeny have recognized these divisions and used them in the same fashion. These boundaries are based on individual rather than multiple developmental events, and herein lies the potential problem (see SPEYER & EDGECOMBE, 1989).

CHATTERTON and others (1990; see Fig. 179) used a system in which different protaspid instars were labelled informally with a letter prefix (P for planktonic subperiod; B for benthic subperiod) and a number suffix (1 for first instar within subperiod, 2 to *n* for later instars within the same subperiod), a convention derived from SPEYER and CHATTERTON (1989) where planktonic and benthic larvae were charted according to ecological criteria. The problem with this system is that discovery of new, earlier instars of a taxon requires renumbering of previously labelled, later instars within the same subperiod. For instance, since the earlier paper was written, new (smaller) P1 instars of the Silurian *Calymene* species described in that work have been discovered so that these growth series now consist of P1, P2, B1, and B2 (not the published P1, B1, and B2, which are equivalent to the new P2, B1, and B2). This system is stable, however, once all protaspid instars of a species are known.

Some trilobite larvae have prominent marginal, submarginal, or dorsal spines on the protocranidia. Some of these have been identified by such terms as anterior fixigenal spine, **midfixigenal spine,** and **posterior fixigenal spine** (see Fig. 148) (PALMER, 1962b). Others have been provided with a more or less formal system of terms, letters, and numbers by various authors (WHITTINGTON, 1956d; CHATTERTON, 1971) according to particular groups of trilobites (see Fig. 149; see also EDGECOMBE, SPEYER, & CHATTERTON, 1988 for terminology of encrinurid

larvae). These systems can be applied to some but certainly not all trilobite early growth stages, even within the groups for which they have been invented.

Prominent spines in early growth stages are frequently lost and sometimes reemerge as a consequence of heterochronic displacement. The basic spine pattern is very conservative; and while particular spines are often lost, prominent new spines are seldom added to the basic pattern. Thus, the patterns of these spines are useful for some levels of phylogenetic analysis.

Prominent pairs of spines evident in larval stages may disappear through ontogeny or may grow at a rate consistent with the overall increases in body size. They may also be displaced or incorporated by other structures of the trilobite (i.e., cranidial lobes). Since these pairs of spines are believed to be homologous with segments of the body, they may provide important evidence for determining the homologies of structures that displace or incorporate them.

LIFE HISTORIES

GROWTH

Growth may occur through auxetic growth (growth of individual cells), multiplicative growth (increase in cell number but not size), and accretionary growth (some special groups of cells retaining their ability to divide mitotically after most others have ceased to do so). The balance between these different types of growth probably changed during ontogeny, perhaps entering the largely accretionary pattern at sexual maturity. Changes in balance may be apparent through changes in allometric growth curves or in the proportional increments between adjacent instars.

REPRODUCTION

We consider that trilobites probably reproduced sexually, as do most arthropods. Certainly the extensive discussion of whether sexual dimorphism occurs in trilobites (see p.

161) would imply that this view is shared by others (e.g., HU, 1971). Clusters and monospecific occurrences (see p. 159) have been described or illustrated for a wide range of trilobite taxa (Cambrian *Asaphiscus wheeleri* in frontispiece of GUNTHER & GUNTHER, 1981; Ordovician *Cyamops stensioei* on cover of CLARKSON, 1979b; Ordovician *Cryptolithus tesselatus* on pl. 139 and *Ampyxina bellatula* on pl. 140 of LEVI-SETTI, 1975; Silurian *Dalmanites limulurus* in LUDVIGSEN, 1979a, fig. 43a; and Devonian *Greenops boothi* in T. T. JOHNSON, 1985, p. 147). SPEYER (1985) and SPEYER and BRETT (1985) compiled biostratinomic details of modern taxa with clustered assemblages associated with molting or reproductive behaviors (limulid xiphosurans, varied crustaceans, and nereid polychaetes).

EMBRYOLOGY

BARRANDE (1852, pl. 27, fig. 1–3) described some small structures as trilobite eggs (disputed by RAYMOND, 1931) and later illustrated a cephalon and six thoracic segments of *Parabarrandia crassa* with egglike structures under the cephalon (BARRANDE, 1872; see also HORNÝ & BASTL, 1970). The arguments that these and similar structures under articulated *Ceraurus pleurexanthemus* (described from thin sections by WALCOTT, 1881, pl. 4, fig. 8) and under *Flexicalymene meeki* (described by BILLINGS, 1870, p. 485) are trilobite eggs was refuted by RAYMOND (1931). RAYMOND reviewed all published examples of trilobite eggs and commented (p. 172) that the larger structures described are definitely not trilobite eggs (we concur), "and the smaller ones, even if correctly identified, have furnished no information of any value."

It is not known whether fertilized eggs were brooded. Egg masses are often seen attached to the undersides of extant marine crustaceans. Few of the morphological features suggested by various authors to be sexually dimorphic in trilobites (see p. 161 on dimorphism) can be correlated to brooding strategies. (An exception could be degree of vaulting or width of pygidium.) If these are really examples of sexual dimorphism, the functions may be any one of a number, and further comment would be sheer speculation. Some of the morphological features considered to be dimorphic are now known to be apparent quite early in the ontogeny of the trilobites, a considerable time before the probable time of onset of sexual maturity. The case would be stronger if these features developed rapidly immediately prior to the time of sexual maturity. If sexual dimorphism occurred and the dimorphs show extreme morphological differences, however, the differences would need to appear quite early in the ontogeny if one or both morphs were not to undergo a radical metamorphosis immediately prior to sexual maturity. In some ostracodes, however, brood pouches appear in heteromorphic individuals quite suddenly during the latter part of ontogeny.

X. ZHANG (1987, fig. 8) illustrated some spheroidal, phosphatized supposed egg cases and trilobites from the Lower Cambrian of China, which he assigned, with question, to a bradoriid or trilobite. These specimens are larger than the protaspides of the eodiscid *Neocobboldia* occurring with them, but at a diameter of 0.35 mm to 0.5 mm they may have been small enough to house the embryos of polymerid trilobites (he assigned protaspides with a length of 0.36 mm to the polymerid *Ichangia ichangensis* LEE, from the same rock unit). Thus, although we assume that trilobites did produce eggs, no undoubted examples are known from the fossil record.

The size and morphology of the first calcified (protaspid) stage are highly variable between but not within different trilobite taxa. This suggests that some trilobites with large protaspides may have passed through more growth as embryos within the egg than others (Fig. 147). There is also the possibility that trilobites passed through one or more growth stages between emerging from the egg and secreting the first calcareous exoskeleton, although there is no evidence for the existence of such free, uncalcified stages.
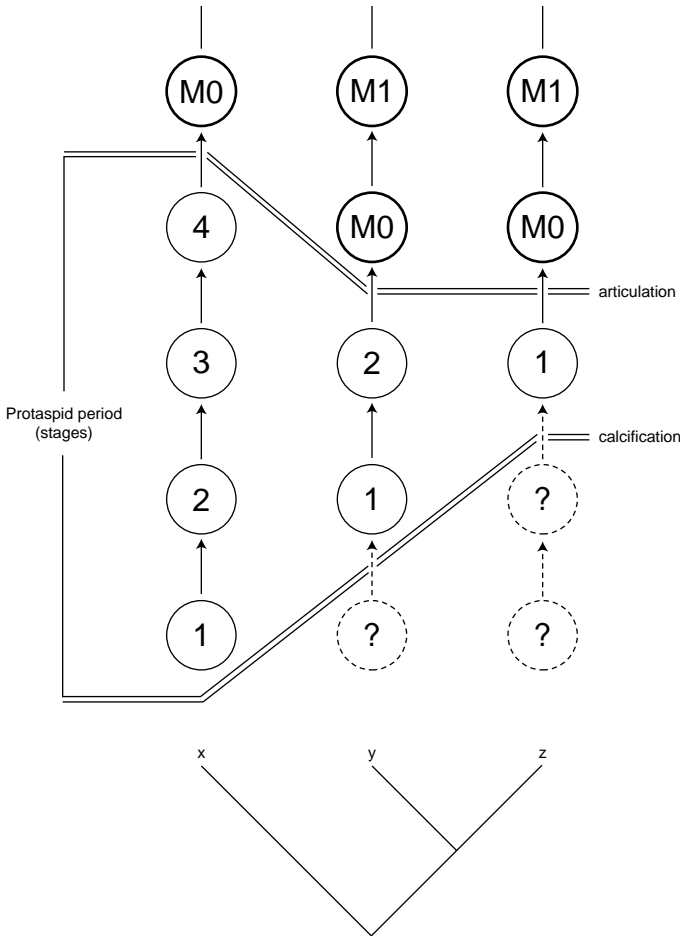
Fig. 147. Calcification and articulation may occur at different times in the life cycles of different trilobites, perhaps as a result of brooding of early instars. *Circled numbers* (or letters and numbers; M = meraspid) are discrete instars in the life cycle of three different hypothetical trilobites: x, y, and z. The *double lines* leading to calcification and articulation represent, respectively, the hypothetical timing of the first calcification and the timing of separation of the head and tail portions of the trilobites (onset of meraspid period). The small cladogram below shows hypothetical evolutionary relationship between these taxa, implying that later calcification and earlier articulation may be derived characters in some groups of trilobites (adapted from Speyer & Chatterton, 1990).

The metabolism required for calcification is not likely to be a secondary derivative within the Trilobita, such as might be argued for some heavily calcified Crustacea (e.g., brachyuran crabs, lobsters). Crustacea add carbonate into a pre-existing organic matrix that is entirely lacking in trilobite cuticle. Therefore, all free-living trilobites may have possessed a calcified exoskeleton. Speyer and Edgecombe (1989) argued that calcification and hatching coincided.

PHASELUS STAGE IN TRILOBITES

Small ovoid, phosphatized exoskeletons were described by Fortey and Morris (1978) from the Lower Ordovician of Spitsbergen. These minute exoskeletons, 0.1–0.3 mm in diameter, are complete dorsally, open ventrally, and have a narrow, entire doublure. They show no sign of a facial suture, rostral plate, or hypostome. They come from two members of the Lower Or-

dovician Valhallfonna Formation of Spitsbergen and were assigned to *Cybelurus.* [These specimens would now be assigned to both *Cybelurus* and *Lyrapyge* (see FORTEY, 1980b).] FORTEY and MORRIS (1978) proposed that these specimens were a calcified preprotaspid stage, termed a phaselus, that they regarded as equivalent to the crustacean nauplius. They discussed the arguments for and against the phaselus being homologous with the crustacean nauplius and noted that the nauplius may be present in different crustaceans, since it is often passed in the egg stage. These arguments centered around the size of the phaselus, its form, its possible appendage number, and its position within the ontogeny of a trilobite (if it is a trilobite). They also noted on the best phaseluses the presence of a surface sculpture of cell polygons typical of early arthropod growth stages. However, they noted that with such early growth stages, similarity in size and form could be more a function of simplicity than of homology. HU (1971, p. 50) believed that early trilobite protaspides have fewer segments visible in the head than later stages, but our own observations indicate that in many taxa protaspides do not have fewer segments.

Some workers (SCHRAM, 1982; ROY & FÅHRAEUS, 1989) have considered FORTEY and MORRIS's (1978) claims to be unjustified. We have discovered (work in progress) silicified phaseluses in six formations ranging from the Middle Ordovician to the Lower Devonian. None of the hundreds of specimens recovered contains any evidence of facial sutures or hypostomes. All of the occurrences of silicified phaseluses are in beds containing numerous silicified trilobites and ostracodes as well as many other silicified fossils. In a few instances, they occur with definite protaspides that are as small as the largest phaseluses (see Fig. 150.1–2) and with bivalved ostracodes that are smaller than the phaseluses. In some instances, however, the smallest definite protaspides present are almost five times the size of the phaseluses. It is not certain that phaseluses

are trilobites and not naupliuses of crustaceans or an extinct group of arthropods that has yet to be recognized. One problem confounding their correct assignment is that their minute size precludes common preservation and discovery. They are found only in exceptionally well-preserved faunas, and they may occur in one bed but not in the beds above and below, which may contain silicified protaspides and later growth stages of trilobites.

HU illustrated three specimens, which he assigned to *Norwoodia halli* RESSER from Upper Cambrian strata in Missouri, that are similar in form to Ordovician phaseluses (1963, pl. 19, fig. 18–24). These are slightly larger than most of the phaseluses that we have found to date (0.38 mm long and 0.32 mm wide, versus 0.1 to 0.2 mm in size for the phaseluses we have examined).

PROTASPID PERIOD

Morphological terms for different protaspides are provided in Figure 148, and number and letter designations for the prominent cranidial spines of odontopleurid and lichid trilobites are given in Figure 149. These terms may be applied with varying confidence in homology to similar spines present on the cranidia of protaspides and early meraspides of the Illaenina, Phacopida, and some Ptychopariida.

The overall body plan of trilobite protaspides has been characterized as either adult-like or nonadult-like by SPEYER and CHATTERTON (1989). This distinction is based upon the dichotomy that exists among all studied stages that is neither taxon specific nor exclusive. The nonadult-like protaspides are usually more globular and three dimensional in form. The adult-like forms are more disk-shaped, with a lower profile and more planar ventral surface in lateral view, a prominent doublure, and a posteriorly tapered hypostome (Fig. 148, 150, 151). The differences would be even more apparent in Figure 150 if the free cheeks and hypostomes were present in lateral views (Fig. 150.3,9). In many nonadult-like forms, the hypo-
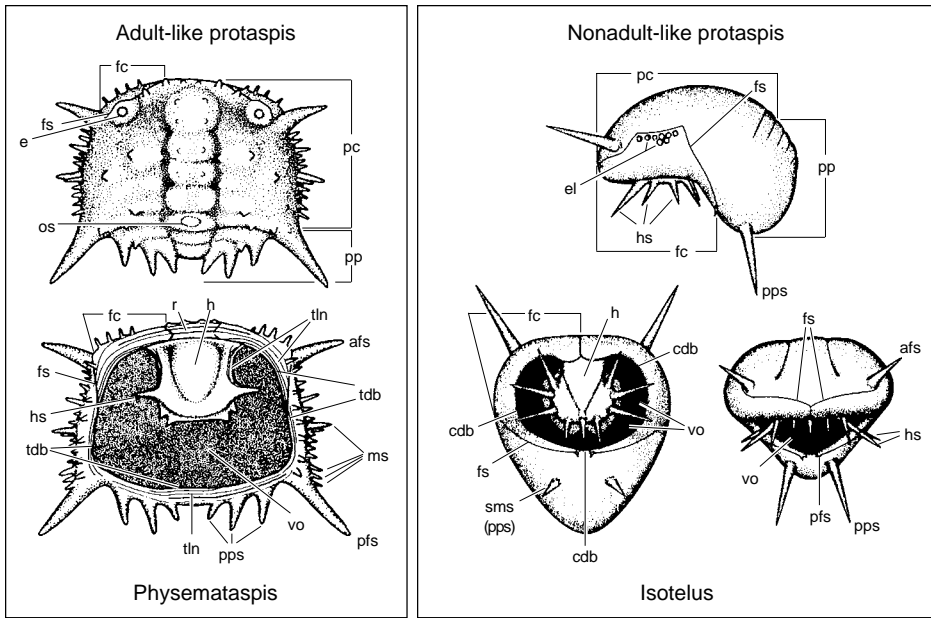
Fig. 148. Morphological terms applied to adult-like (probably benthic) and nonadult-like (or asaphoid) protaspides, based on drawings of the encrinurid *Physemataspis* and the asaphid *Isotelus*. Abbreviations: *afs,* anterior fixigenal spine; *cdb,* incurved doublure; *e,* eye; *el,* eye lens; *fc,* free cheek; *fs,* facial suture; *h,* hypostome; *hs,* hypostomal spine; *ms,* marginal spine; *os,* occipital spine (lobe); *pc,* protocephalon (protocranidium + free cheeks); *pfs,* posterior fixigenal spines; *pp,* protopygidium; *pps,* protopygidial spines; *r,* rostral plate; *sms,* submarginal spine; *tdb,* inturned doublure; *tln,* terrace ridges; *vo,* ventral opening (adapted from Speyer & Chatterton, 1989).

stomal spines extend obliquely downward well below the doublure.

EVITT and TRIPP (1977), in describing the ontogenies of encrinurid and staurocephalid trilobites, coined several terms, including **torulus** for a rounded fixigenal swelling alongside the glabella of small stages. They also applied the system of notation for glabellar tubercles introduced by TRIPP (1957) to larval stages (followed by EDGECOMBE, SPEYER, & CHATTERTON, 1988).

Ontogenetic events (as time or maturity markers) during the protaspid period may be useful for examining heterochronic relationships between rate of growth, morphological change, and timing of appearance or disappearance of specific morphologies. These include the appearance of a furrow between the protocranidium and the protopygidium, the appearance of distinct axial furrows rather than a pair of pits that were probably associated with attachment of the hypostome, the appearance of connective sutures,

the appearance of a hypostomal suture, the fusion of connective sutures, a movement of the genal spine from the fixigena to the librigena (in only some taxa), the timing of a major metamorphosis (e.g., change from nonadult-like to adult-like), and a change from a concave to a convex posterior margin.

Some groups of trilobites have larval instars that are particularly diagnostic. For instance, the first benthic instar of a lichid trilobite always appears to have three pairs of marginal spines on the protopygidium, and the second instar has five pairs of marginal spines (see Fig. 183.1,5). These features of lichid larvae not only make them recognizable, but may also be useful time markers for identifying heterochronic changes occurring early in the life cycle.

Some features of protaspides are fairly general among trilobites, and others show a considerable degree of variation. For example, Figure 152 shows protaspid and early meraspid hypostomes. Most of these show
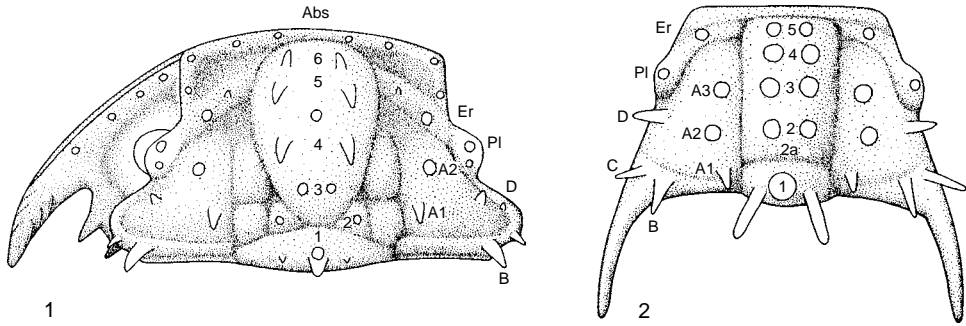
FIG. 149. Sytems for labelling prominent pairs of spines on the dorsal surfaces of meraspid cranidia; *1,* the lichid *Acanthopyge bifida* EDGELL (adapted from Chatterton, 1971); *2,* the odontopleurid *Apianurus barbatus* (adapted from Whittington, 1956d). Spines are labelled *1–6* on glabella forward from the occipital ring, *A* on the fixed cheek; *Abs* on the anterior border; *B, C* on the posterior border; *D* on fixed cheek behind palpebral lobe; *Er* on eye ridge; and *Pl* on palpebral lobe.

marginal spines. Even though the number and shape of marginal spines vary within some groups, they may be useful to characterize some taxa. As a general rule, early protaspides are more likely to have marginal spines on the hypostome than later growth stages, and those spines are more likely to be sharply conical. The presence of these marginal spines is probably a synapomorphy of trilobites (FORTEY & WHITTINGTON, 1989). Such distinctive shapes of marginal spines as the blunted, distal ends of the marginal spines of lichid and styginid, adult-like protaspides or the reduction in size or loss of marginal spines in the odontopleurids and proetids may be derived, apomorphic features. SPEYER and CHATTERTON (1989) pointed out that the marginal spines of hypostomes of nonadult-like, pelagic protaspides are generally much longer and sharper than those of adult-like benthic growth stages in the same species (contrast Fig. 152.11 with 152.7), and the hypostomes of nonadult-like protaspides cover a much greater proportion of the ventral surface than those of adult-like protaspides (Fig. 145.3, 146.3, 148).

The width of the rostral plate relative to the front of the hypostome also varies among different groups of trilobites. In some taxa the rostral plate is narrower than the hypostome (Phacopida, Fig. 152.1,3), in others it is the same width (Lichidae, Fig. 145.6;

Odontopleuridae, Fig. 152.2), and in others it is much wider (Olenellina, see PALMER, 1957).

MERASPID PERIOD

This period incorporates the growth stages in which the cephalon is separate from the thorax or the pygidial portion (transitory pygidium) but lacks a full (adult) complement of thoracic segments.

Number of Meraspid Instars

Typically, a single thoracic segment is released into the thorax between adjacent instars, and meraspid degree numbers increase by increments of 1 during the life cycle of a trilobite. Thus the number of meraspid instars equals the number of adult thoracic segments (Fig. 153). In certain species, however, the number of meraspid instars differs from the number of adult thoracic segments. CHATTERTON (1971), for example, demonstrated that for *Dentaloscutellum campbelli* two thoracic segments are released into the thorax between instars, so the meraspid degrees mainly increased in increments of 2 (0, 1, 3, 7, and 9). Thus, there are only five meraspid instars, although there are ten thoracic segments in the adult, holaspid trilobite. Some Early and Middle Cambrian trilobites with numerous thoracic segments must either have passed through a very large
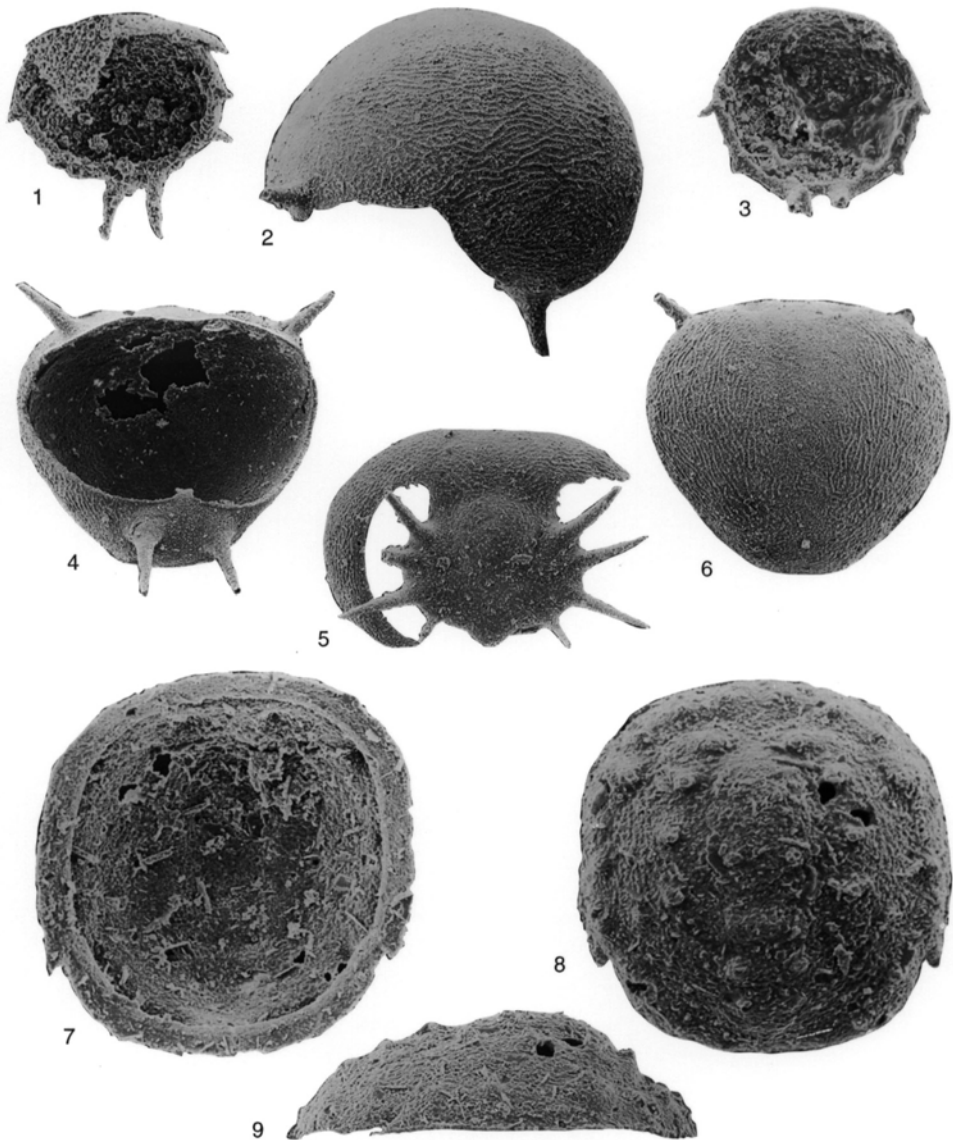
FIG. 150. Larval morphology and ecology. The smallest protaspides are shown together with adult-like and nonadult-like protaspides. *1,3,* Ventral views of two very small protaspides of uncertain assignment (possibly belonging to the Cheirurina) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16304, 16305, ×136 (new). *2,4–6,* Nonadult-like protaspides assigned to the asaphid *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York; *2,* lateral view of NYSM 16306, ×60; *4,* ventral view of NYSM 16307, ×45; *5,* ventral view of fused hypostome and free cheeks, NYSM 16308, ×60; *6,* dorsal view of NYSM 16309, ×45 (new). *7–9,* Ventral, dorsal, and right lateral views of adult-like, benthic late protaspis of bathyuroid *Dimeropyge* n. sp. from the Esbataottine Formation, Middle Ordovician, northwestern Canada, UA 7900, ×113 (new).

number of instars or released several segments into the thorax between instars (PALMER, 1957). If the number of instars of *Neocobboldia chinlinica* that X. ZHANG (1989) recognized is correct (they are not very distinct on his diagrams), and if his boundary between meraspid and holaspid stages is correct (as it appears to be on
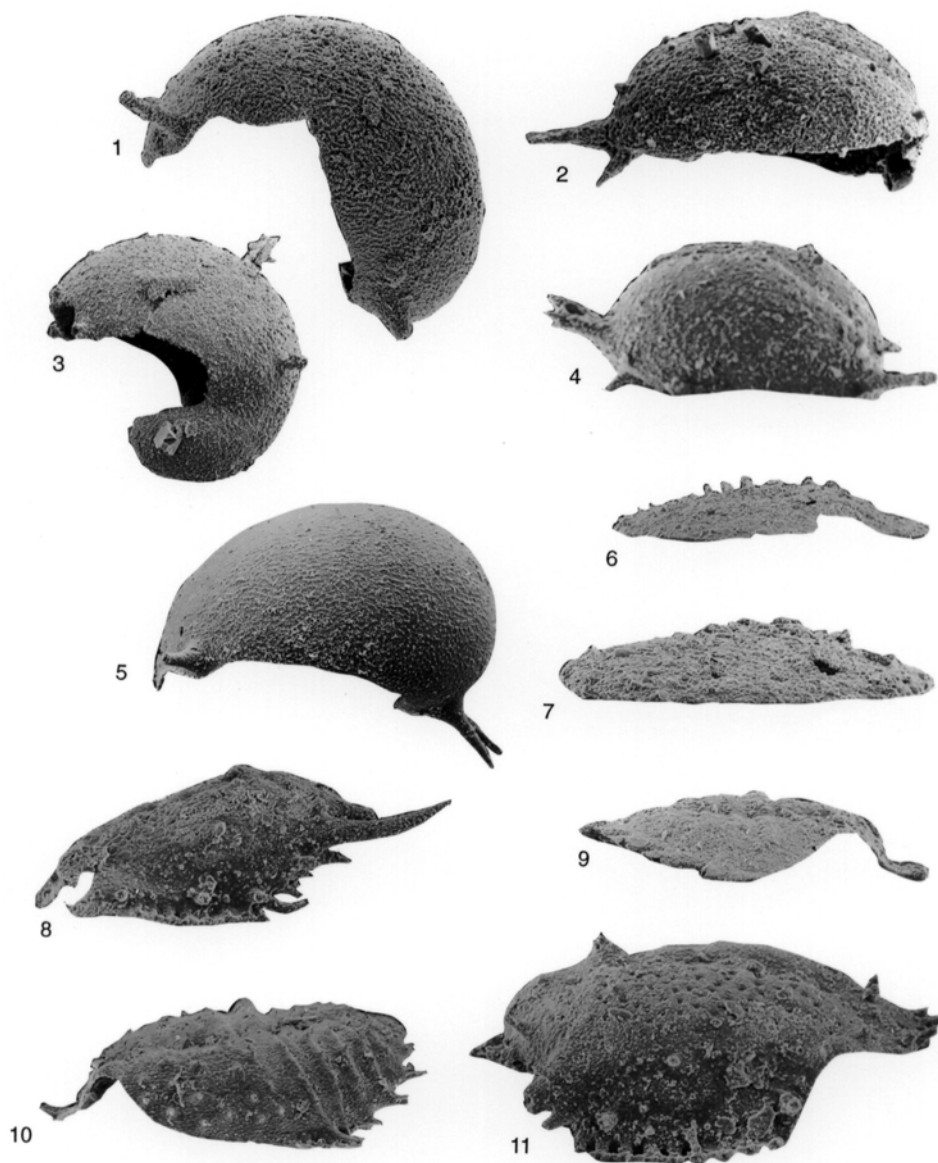
FIG. 151. Lateral views of protaspides. *1–5,* Nonadult-like, probably planktonic protaspides of Asaphida; *1, Isotelus?* sp., an asaphid, from the Crown Point Formation, Middle Ordovician, New York, NYSM 16310, ×49; *2, Cryptolithus tesselatus* (GREEN), a trinucleid, from the Martinsburg Formation, Middle Ordovician, Virginia, NYSM 16311, ×83; *3, Remopleurides* sp., a remopleuridid, from the Edinburg Formation, Middle Ordovician, Virginia, NYSM 16312, ×60; *4, Lonchodomas chaziensis* SHAW, a raphiophorid, from the Crown Point Formation, Middle Ordovician, New York (locality PB81), NYSM 16313, ×92; *5, Isotelus* sp., an asaphid protaspis from the Crown Point Formation, Middle Ordovician, New York, NYSM 16314, ×60 (new). *6–11,* More adult-like, probably benthic protaspides; *6,7,* aulacopleurid *Scharyia* sp. from Wenlock part of the Delorme Formation, northwestern Canada; *6,* UA 8421, ×38; *7,* UA 7902, ×56; *8,* encrinurid *Cybeloides prima* (RAYMOND) from the Crown Point Formation, Middle Ordovician, New York (locality PB81), NYSM 16315, ×76; *9,* lichid *Hemiarges* aff. *H. turneri* CHATTERTON & LUDVIGSEN from the Crown Point Formation, Middle Ordovician, New York, NYSM 16316, ×38; *10,* homalonotid *Brongniartella* sp. from the Martinsburg Formation, Middle Ordovician, Virginia, AMNH 43959, ×41; *11,* pterygometopid *Calyptaulax annulata* (RAYMOND) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16317, ×108 (new).
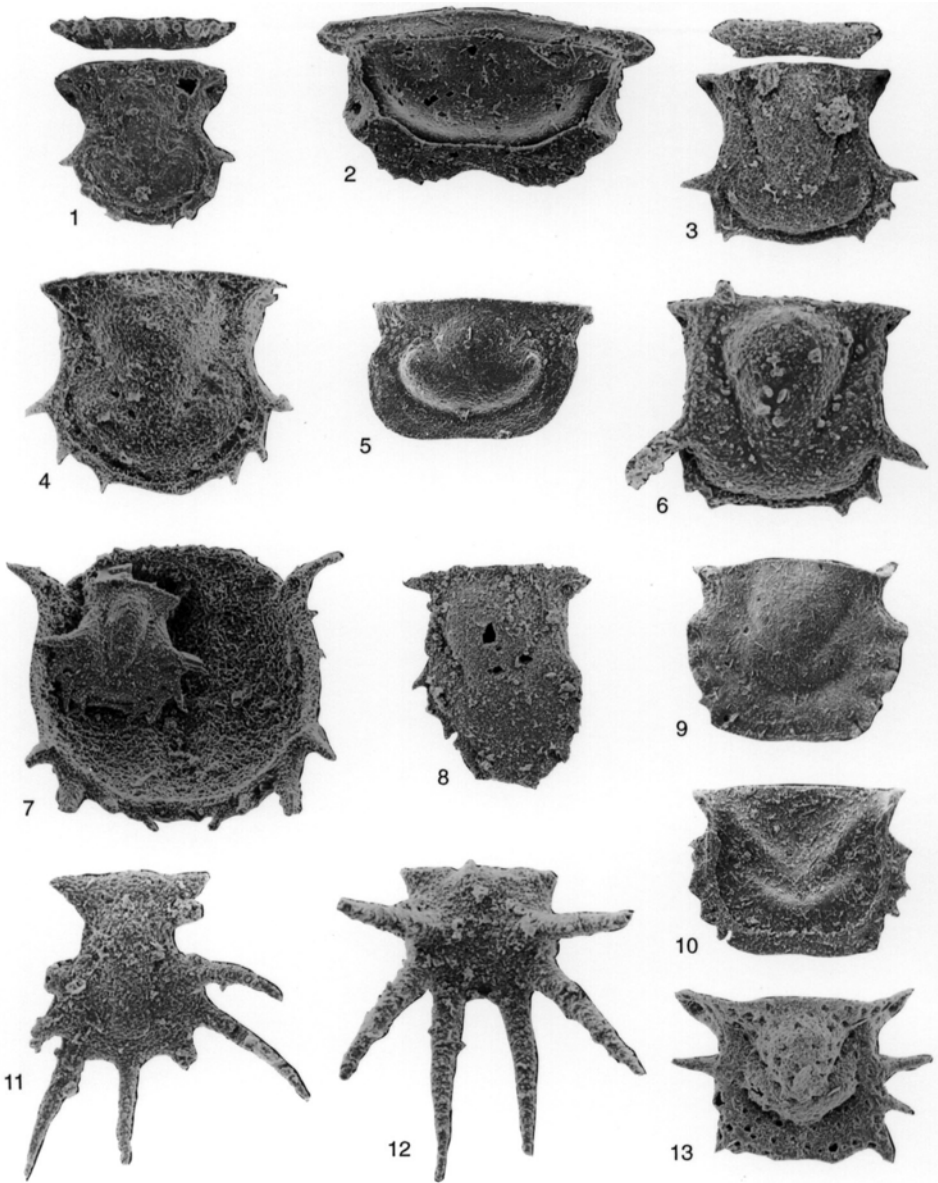
FIG. 152. Hypostomes and rostral plates. *1,* Ventral view of hypostome and rostral plate from same protaspis of pterygometopid *Calyptaulax annulata* (RAYMOND) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16318, ×119 (new). *2,* Dorsal view of hypostome and rostral plate (meraspid?) of odontopleurid *Ceratocephala triacantheis* WHITTINGTON & EVITT from the Esbataottine Formation of the Mackenzie Mountains, Middle Ordovician, northwestern Canada, UA 8422, ×60 (new). *3,* Ventral view of hypostome and rostral plate from underside of same protaspis of encrinurid *Physemataspis insularis* (SHAW) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16319, ×129 (new). *4,* Ventral view of small hypostome of pterygometopid *Calyptaulax annulata* (RAYMOND) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16320, ×132 (new). *5,* Ventral view of small hypostome of odontopleurid *Acidaspis lesperancei* CHATTERTON & PERRY from the Wenlock Delorme Formation, northwestern Canada, UA 4550, ×46.25 (new). *6,* Ventral view of hypostome of encrinurid *Physemataspis insularis* (SHAW) from the Crown Point Formation, Middle Ordovician, New York, NYSM
(Continued on p. 193.)
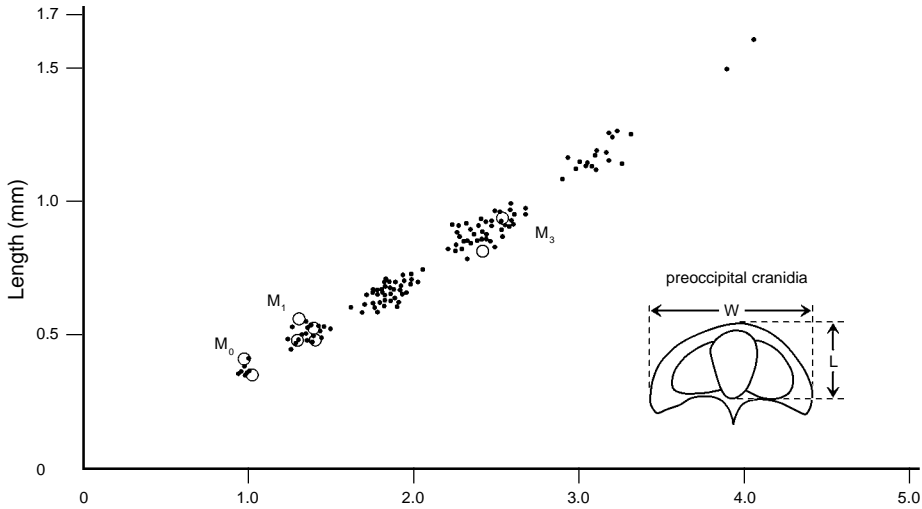
FIG. 153. Meraspid instars of trinucleid *Cryptolithus tesselatus* GREEN. *Open circles* represent articulated specimens that can be demonstrated to belong to meraspid degrees 0, 1, or 3 (M0, M1, M3). No articulated specimens were found with two free thoracic segments, representing meraspid degree 2 (M2). However, a distinct size cluster of cranidia was found between those that apparently represent meraspid degrees 1 and 3, suggesting that there was a meraspid degree 2 instar in the life cycle of *C. tesselatus,* and that each meraspid degree of this species was represented by a single instar. All articulated specimens are from a single block of the Middle Ordovician Martinsburg Limestone from north of Spring Hill, Virginia (processed by G. D. Edgecombe, collected by M. Kay); other specimens are from this locality and from locality 12 of WHITTINGTON, 1959a (processed by A. S. Hunt)(new).

morphological grounds), there are six instars during the meraspid period. Since eodiscid trilobites release only three segments into the thorax, the number of instars is twice the number of meraspid degrees; i.e., no thoracic segments were released between some instars. A similar pattern was found by HUNT (1967) for the metagnostid *Trinodus elspethi,* in which he identified three meraspid instars in a species that has only two adult thoracic segments, and by MÜLLER and WALOSSEK (1987,

p. 20) for the agnostid *Agnostus pisiformis.* This similarity could be regarded as a synapomorphy for eodiscoids and Agnostina (see FORTEY, 1990a, 1990b, for more discussion); or, alternatively, it could have resulted from convergence among taxa with a reduced number of thoracic segments.

PALMER (1958, p. 165) divided the meraspid period into three subperiods, based on characters of the head. In the first, the early meraspid stage, "the glabella is continuous

FIG. 152. *Explanation continued from facing page.*

16321, ×163 (new). *7,* Ventral view of third protaspid stage of calymenid *Flexicalymene senaria* (CONRAD) from the Martinsburg Formation, Middle Ordovician, Virginia, AMNH 43931, ×62.5 (new). *8,* Ventral view of hypostome of protaspis of lichid *Hemiarges* aff. *H. turneri* CHATTERTON & LUDVIGSEN from the Crown Point Formation, Middle Ordovician, New York, NYSM 16322, ×98 (new). *9,10,* Ventral and dorsal views of small hypostomes of illaenid *Failleana calva* CHATTERTON & LUDVIGSEN from the Crown Point Formation, Middle Ordovician, New York; *9,* UA 2717, ×36; *10,* UA 8423, ×37.5 (new). *11,* Fused hypostome and rostral plate of second protaspid stage of calymenid *Flexicalymene senaria* (CONRAD) from the Martinsburg Formation, Middle Ordovician, Virginia; most of hypostomes of this species have an extra, small pair of marginal spines between the median spine and the third pair, NYSM 16323, ×91 (new). *12,* Ventral view of hypostome of protaspis type P2 (see Fig. 174) of raphiophorid *Lonchodomas* sp. from the Crown Point Formation, Middle Ordovician, New York, NYSM 16324, ×125 (new). *13,* Ventral view of hypostome of cheirurid *Sphaerocoryphe goodnovi* RAYMOND from the Crown Point Formation, Middle Ordovician, New York, NYSM 16325, ×62.5 (new).

with the eye ridge and reaches to the anterior margin of the cranidium." In the middle meraspid stage "the glabella is separated from the border by a frontal area composed only of the brim." In the late meraspid and holaspid stage, "the frontal area is divided by a shallow marginal furrow onto [*sic*] a brim and border." He believed that these stages are "recognizable in the development of most non-olenellid trilobites with a brim and border." This may be true for a number of Cambrian ptychoparioid trilobites, but it is not applicable to most non-Olenellina. Although it may be useful in studies of heterochrony among some Cambrian trilobites, we do not advocate the use of this scheme.

KOPASKA-MERKEL (1987) divided the meraspid period into two subperiods, depending on whether the number of dorsally expressed protothoracic segments is increasing (**accumulation phase**) or decreasing (**shedding phase**) between adjacent instars. Early in the meraspid period, in the accumulation phase, new segments usually form near the back of the transitory pygidium at a rate faster than they are released into the thorax at the front. Towards the middle of the meraspid period, new segments may differentiate at the back of the transitory pygidium at about the same rate as they are released into the thorax. In the later shedding phase of the meraspid period, usually all of the segments have formed, including a protopygidium; and as segments are released into the thorax, the number of segments in the transitory pygidium is reduced. These stages can be recognized for most if not all trilobite growth series. KOPASKA-MERKEL recognized an accumulation phase of five to seven instars for the pliomerid *Hintzeia* and a shedding phase of four instars. He also noted that unpublished data of LUDVIGSEN on the cheirurid *Gabriceraurus* reveal an almost identical pattern. While speculating on the value of these data in determining relationships, he noted the apparently aberrant pattern of other cheirurids, *Ceraurinella typa* and *Ceraurinella chondra,* in which the first

meraspid transitory pygidium found apparently contains all of the protothoracic segments as well as those that will become the pygidium. In other words, the entire accumulation phase occurs during the protaspid period or at least before meraspid degree 1 and perhaps involves a number of instars (see reconstruction by WHITTINGTON, 1957b, fig. 27; see also *Ceraurinella* protaspis in Fig. 178.1–2, which appears to be an intermediate state). Whether the shedding phase occurs in these two species over a number of instars as small steps or as a cascade in a very few instars is not yet known. Considering the very large size of these transitory pygidia, the latter is possible. This is not so for some other species of *Ceraurinella* such as *C. nahanniensis* (see CHATTERTON & LUDVIGSEN, 1976; CHATTERTON, 1980), where the pattern is more typical.

A substantial amount of trilobite growth, from less than 25 to as much as 30 to 40 percent, probably took place during the meraspid period (WHITTINGTON, 1957a; CHATTERTON, 1971; HUNT, 1967; X. ZHANG, 1989). There is surprisingly little reliable, numerical information in the literature on the proportion of the life cycle taken up by the meraspid period. This suggests that most workers have not considered this information to be important or that it is difficult to ascertain, certainly in contrast to proportional growth increments between instars. We also know of no data that may be used to mark the end of a trilobite's life due to old age other than the size of the largest specimens discovered in any collection.

During the meraspid period the trilobite was undergoing major reorganization, the production of new segments posteriorly and their release into the thorax. Thus, the length of the meraspid period, measured by the number of instars or the amount of growth, may have been an important constraint on the life-history strategy of a trilobite. A progenetic, paedomorphic pattern could have reduced the length of the meraspid period in a trilobite switching from a K-

selective towards an r-selective life-history strategy of MacArthur and Wilson (1967; see also Gould, 1977).

HOLASPID PERIOD

In the holaspid period all of the thoracic segments have been released. Most trilobites undergo considerable growth, probably most of their growth, during the holaspid period, although the exact amount has been documented for very few trilobites (Hunt, 1967; Whittington, 1957a; Chatterton, 1971; Chatterton & Ludvigsen, 1976). Considerable allometric growth may take place during the holaspid period; however, no major metamorphoses are known. Some of these allometric changes may be useful in diagnosing heterochronic evolution (see below). The number of instars that occurred during the holaspid period is usually very difficult to determine because of variations in the rate or amount of growth or even the timing of instars between individuals. These variations, which may be minor between any two instars, are compounded through the lives of the trilobites. Thus instars may be easy to distinguish in protaspid stages, more difficult to separate upon the basis of size during the meraspid period (but often possible on the basis of morphology), and impossible to discriminate in the holaspid period. Some authors have attempted to determine the number and sizes of holaspid instars for various taxa by using such growth rules as Dyar's rule or Przibram's rule. Where the instars cannot be distinguished clearly on the grounds of size or morphology, however, the use of these rules must be teleological.

Some trilobites appear to have exercised a closer genetic control over the sizes of their instars, and these can be distinguished even in holaspid stages. One such example is the metagnostid *Trinodus elspethi* (see Hunt, 1967). This species is small, however, with only nine recorded instars in the meraspid and holaspid periods. If the number of instars is correlated with age, a greater number of instars should increase the chance that

individual variation will blur the boundaries between adjacent instars in later growth stages. Thus, the factors of (1) genetic variation and control (through release of hormones), (2) the age of the trilobite (or number of instars as a measure of age), and (3) the complexity of ecology or overall morphology may determine whether holaspid instars may be discriminated. It is also easier to discriminate instars in a collection made from a single bedding plane or from a single block of limestone than from a collection obtained from a number of beds. There are exceptions even to this rule, however; and Chatterton and others (1990) found that it was possible to discriminate instars in at least very early growth stages in collections of *Flexicalymene* made from more than one locality. Another factor, well documented among modern insects, is that the type or availability of food may affect the rate of growth and the number of molts (Bernays, 1986; Bernays & Hamai, 1987). This is also documented for many long-lived crustaceans, including crabs and lobsters (Travis, 1954; Hartnoll, 1969; Lipcius & Herrnkind, 1982; Ginatzy & Romer, 1984), and for chelicerates (Jegla, 1982; Laverock, 1927; Shuster, 1982).

Indications of sexual maturity are difficult to find in trilobites. Some of the morphological features that have been suggested as sexually dimorphic appear relatively early in their life cycles, presumably before the animals reached sexual maturity. Speyer and Brett (1985) have suggested that aggregations of adult individuals of similar size were for the purpose of reproduction and that, therefore, the study of the sizes of a number of individuals composing such aggregations may provide information on the size of trilobites at the onset of sexual maturity. A change in growth allometry during ontogeny may mark the time of onset of sexual maturity (Hartnoll, 1969). This could be apparent from an inflection on a growth curve or a change in the proportional growth increment between instars. However, as noted
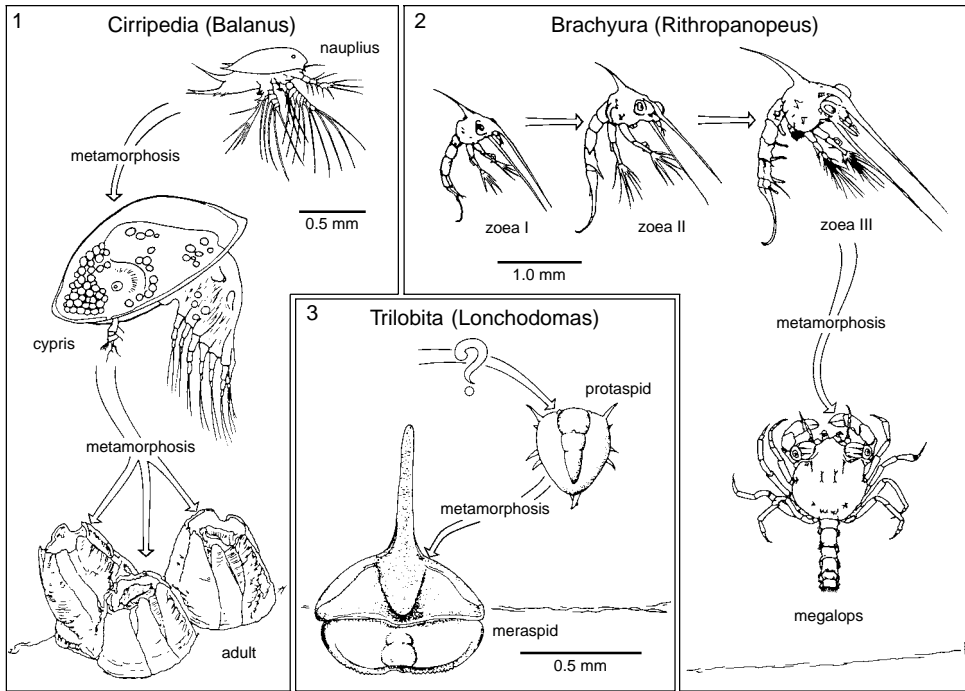
FIG. 154. Metamorphosis among marine arthropods. *1,* Barnacles (Cirripedia) undergo two ecology-related metamorphoses during development: the nauplius, a feeding and free-swimming larva transforms into a bottom-seeking nonfeeding cypris, which then transforms into a very specialized adult. *2,* Decapod crabs have an active, feeding zoea that passes through several molts before changing into a bottom-seeking megalops. *3,* The raphiophorid *Lonchodomas* passes through two protaspid instars before undergoing a metamorphosis between protaspid and meraspid periods, which, by inference, we consider to be related to a change in ecology (planktonic to benthic) (adapted from Speyer & Chatterton, 1989, fig. 12).

above, instars are usually very difficult to discriminate late in ontogeny.

LIFE-HISTORY STRATEGIES

CHATTERTON and SPEYER (1989) have noted the more common life-history strategies, considering the larvae as either benthic or planktonic and most as heterotrophic, lecithotrophic, or planktotrophic. Some life cycles included a radical metamorphosis early in the ontogeny, usually accompanied by a change from a planktonic to a benthic mode of life, as is the case for many modern arthropods (Fig. 154). The size of the smallest known exoskeleton in the growth series of different trilobites varies greatly (from less than 0.2 mm to greater than 1.0 mm). Some trilobites passed through stages and size classes as embryos or free-swimming, uncalcified individuals that other taxa passed through calcified (Fig. 140, 147). The four life-history strategies listed below are predicated on the thesis that some larvae were planktonic and others were not. Figure 155 shows hypothetical appendages and life positions for a nonadult-like, planktonic larva and an adult-like, benthic larva. Recognition of the mode of life of larvae is based on their overall morphology (the nonadult-like being unconstrained in three dimensions, without ventral apertures and muscle attachment sites that would be expected for efficient operation of appendages that might be used for locomotion on or digging in a sedimentary substrate), their separation from more adult-like later stages by a radical metamorphosis, and their distributions (Fig. 156).
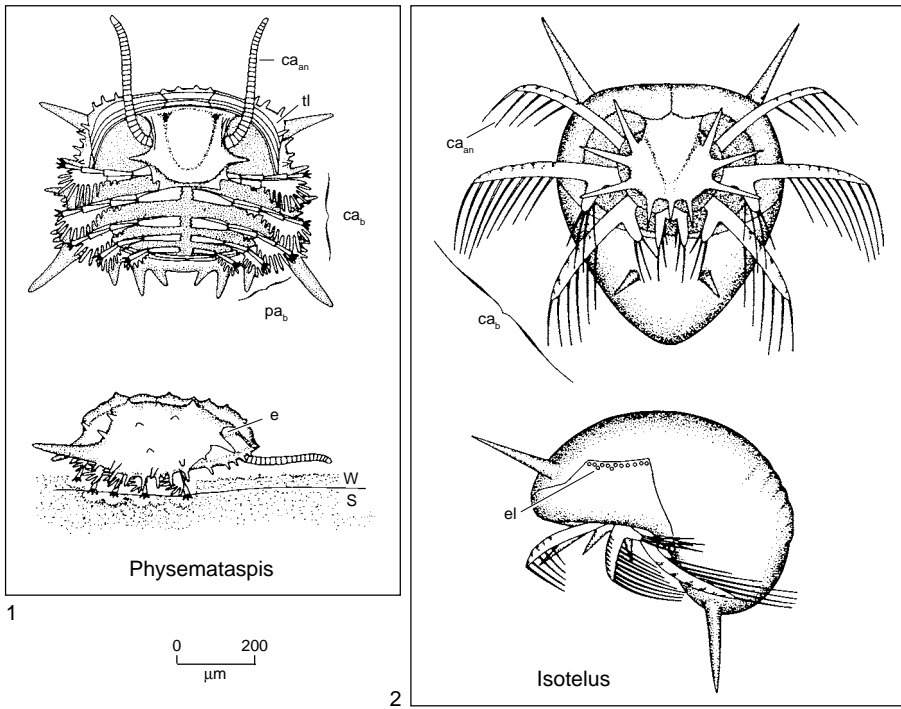
FIG. 155. Hypothetical appendages and life positions of an adult-like protaspis of encrinurid *Physemataspis* and a nonadult-like protaspis of asaphid *Isotelus*. Abbreviations: *ca,* cephalic appendage (*an,* antenna; *b,* biramous); *e,* eye; *el,* eye lenses; *pa,* pygidial appendages (*b,* biramous); *tl,* terrace ridges; *W/S,* water-sediment interface (adapted from Speyer & Chatterton, 1989).

LIFE-HISTORY STRATEGY I

In this strategy all protaspid growth stages were planktonic (or premetamorphic) in form, with the metamorphosis into benthic, heterotrophic forms at or after the end of the protaspid period. This pattern is one of the characteristic features of the Asaphida (FORTEY and CHATTERTON, 1988). CHATTERTON and SPEYER (1989) pointed out that almost all taxa with this life-history pattern became extinct during the Ordovician (including a number of taxa in the mass extinction near the end of the Ordovician). They also demonstrated that taxa with this life-history strategy were constrained geographically to lower paleolatitudes and suffered a minor extinction at about the time of onset of the Ordovician-Silurian glaciation. Examples of trilobites with this type of life-history strategy are *Isotelus* and *Remopleurides*. In *Isotelus* (Fig. 157), the metamor-

phosis from nonadult-like, planktonic stages to adult-like, benthic stages apparently took place at the transition between the protaspid and meraspid periods. In *Remopleurides*, this change occurs within the meraspid period in some, if not all, species (Fig. 158).

LIFE-HISTORY STRATEGY II

In this strategy the first calcified stage is planktonic or at least separated from later stages by a radical metamorphosis, and later stages are benthic. This pattern may have been acquired independently in several different Ordovician and younger clades. It is shared by such taxa as the Illaenina, the Lichidae, the Phacopida, and some ptychopariids. If this pattern were plesiomorphic or a synapomorphy of these groups, one might expect the smallest premetamorphosis larvae of these groups to be very similar. Since they are not and some of the taxa listed here prob-
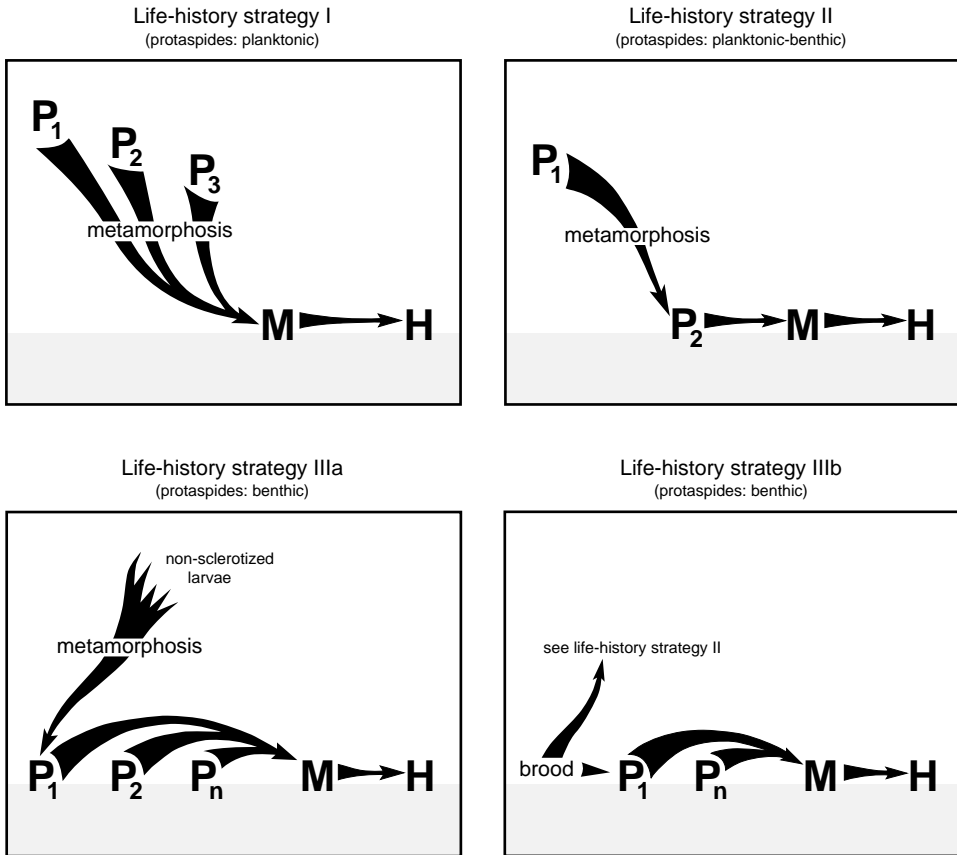
FIG. 156. Varied developmental patterns and life-history strategies indicated by trilobite ontogenies. *P* indicates a protaspid instar; *M* indicates meraspid instars (the meraspid period); and *H* indicates an indefinite number of holaspid instars (the holaspid period). The *subscripts* in the protaspid stages refer to the first, second, third, or nth sclerotized protaspid instar. The location of letters representing growth stages corresponds to presumed ecology, that is, whether they lived in the water column or on the sea floor (adapted from Speyer & Chatterton, 1990).

ably have sister groups that are excluded from this group, this life-history strategy probably evolved several times in different groups of trilobites. CHATTERTON and SPEYER (1989) showed that trilobites with this pattern were comparatively successful in surviving the end of the Ordovician mass extinction. Rare forms with this life-history pattern may have more than one premetamorphosis larva, as in *Flexicalymene* (see FIG. 178; CHATTERTON & others, 1990). It is possible that the phaselus belongs to some taxa with this strategy; FORTEY and MORRIS (1978) assigned the phaselus to *Cybelurus,* a form with this life-history strategy. *Failleana,*

an illaenid, provides an example of this life-history strategy (Fig. 159).

LIFE-HISTORY STRATEGY III

Here all calcified growth stages are benthic. Trilobites with this life-history strategy had a comparatively high rate of survivorship during the Ordovician extinctions and gave rise to many post-Ordovician trilobites (CHATTERTON & SPEYER, 1989). *Dimeropyge,* a bathyuroid with at least three adult-like protaspid instars, is an example of a trilobite with this life-history strategy (Fig. 160); *Scharyia* (see Fig. 180) is another (ŠNAJDR, 1981a). Earlier workers would have
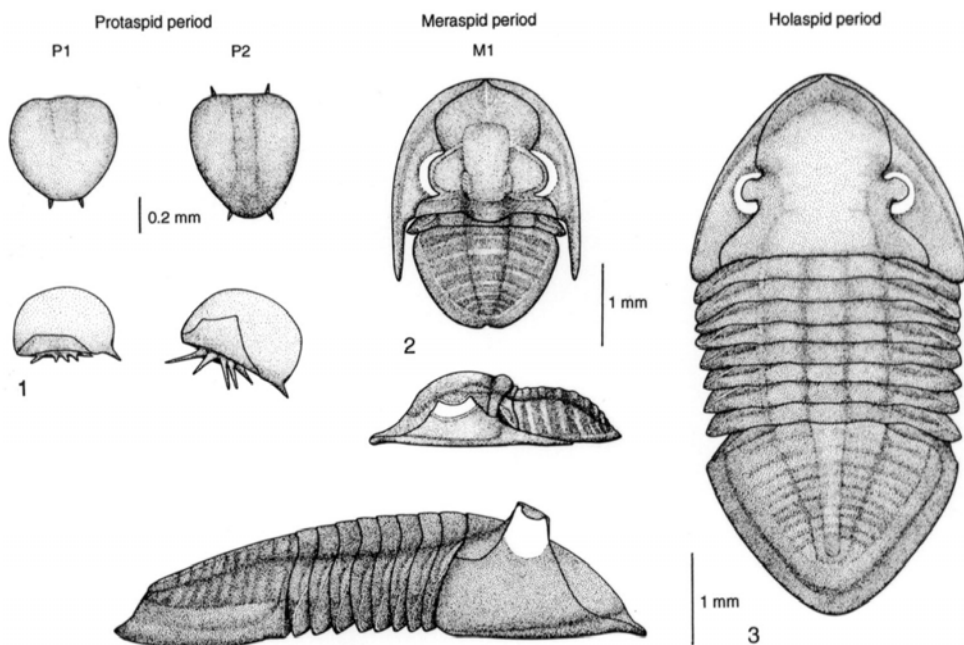
FIG. 157. Early growth stages in the life cycle of asaphid *Isotelus parvirugosus* CHATTERTON & LUDVIGSEN and a mature specimen of *Isotelus gigas* DEKAY. Drawings are of two nonadult-like protaspid instars (P1, P2), an instar representative of meraspid degree 1 (M1), and a mature holaspid. This genus appears to be a typical representative of life-history strategy I (see Fig. 156). All stages are shown in dorsal and lateral views (new).

called the smallest protaspis assigned to this growth series an anaprotaspis. Some might have argued that it was planktonic. We consider that the relatively two-dimensional form of this stage, when considered with the moderate-sized hypostome, which lacks strong marginal spines, and the moderate morphological change between this stage and the following growth stage (a large amount but less than in most planktonic to benthic metamorphoses), suggests that it was benthic rather than planktonic. Marginal spines, where they occur on the hypostomes of benthic larvae, are short and usually laterally or posteriorly directed rather than ventrodistally directed (the usual state in planktonic protaspides).

LIFE-HISTORY STRATEGY IV

Larvae are benthic or rarely planktonic; adults are pelagic. This life-history strategy is not as relevant to early ontogeny as the preceding strategies but strongly affects the survivorship of the group. No taxa showing this life-history pattern survived the late Ordovician mass extinction. For examples of this life-history strategy, see FORTEY (1985).

Some of the stages categorized above as benthic, particularly some of the larvae, for hydrodynamic reasons could have been part planktonic or nektonic and part benthic. We have assumed that those stages that could have operated efficiently on the sea floor did so, and those that could not, did not.

The four life-history strategies discussed above are broad and encompass distantly related taxa. They do, however, affect survivorship and dispersal of trilobite taxa (CHATTERTON & SPEYER, 1989) and are relevant in evolutionary, paleoecologic, and paleobiogeographic studies.

HETEROCHRONY

JAEKEL (1909) did not document in detail his suggestion that the Agnostida arose from
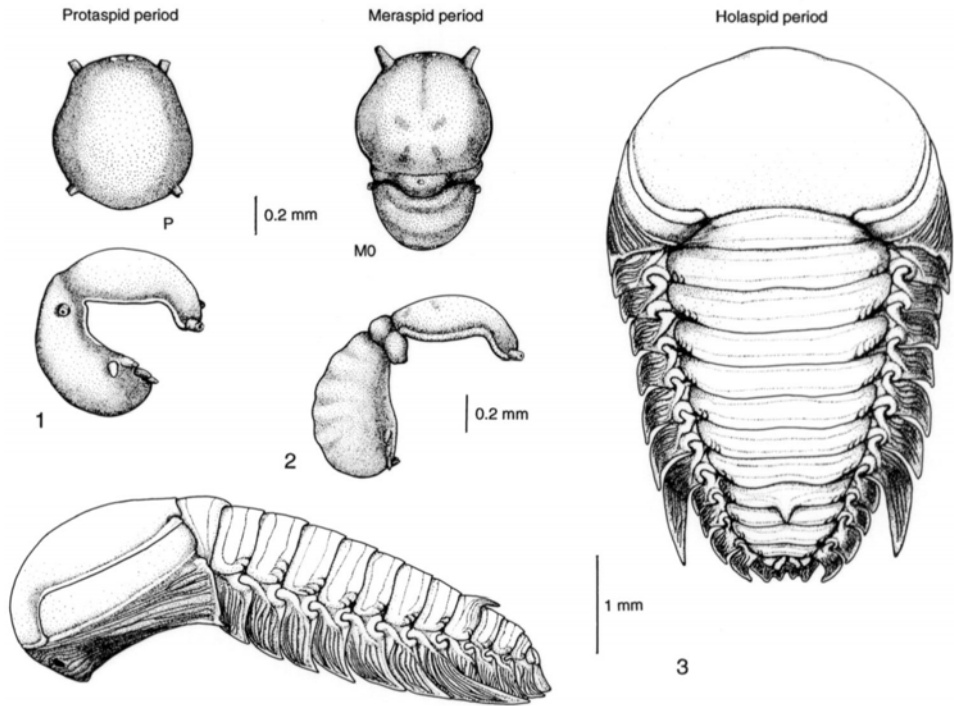
Fig. 158. The life cycle of the remopleuridid *Remopleurides eximius* Whittington. Drawings are of a late protaspis (*P*), a representative of meraspid degree 0 (M0), and a mature holaspid. This species appears to represent a variant of life-history strategy I (see Fig. 156), in which the metamorphosis from nonadult-like pelagic to adult-like benthic stages was retarded so that it took place during the meraspid period. All stages shown in both dorsal and lateral views (adapted from Whittington, 1959a).

polymerid trilobites through paedomorphosis. We presume that he was influenced by the small size of Agnostida, their small number of thoracic segments, their isopygous condition, and even, possibly, their blindness. Many of the distinctive features of Agnostida are not similar to characters known in small polymerid trilobites and cannot be interpreted as the result of paedomorphic evolution from any taxon with a well-known ontogeny. No proposed ancestor of the Agnostida has been widely accepted, and therefore any suggestions in regard to a heterochronic origin for this group must be regarded as speculative. STUBBLEFIELD (1936), HUPÉ (1954), JELL (1975a), and MÜLLER and WALOSSEK (1987) have commented on this possible mode of origin, the latter workers even suggesting that the slightly unusual form of the appendages of

Agnostus may be explained by their derivation from larval morphologies, which are frequently quite different from adult morphologies and extensively modified during ontogeny in the related Crustacea. We do not know of any examples of preserved, larval appendages of polymerid trilobites (those of Fig. 155 are purely speculative). Comparison with the ontogenies of polymerid trilobites suggests, from the radical nature of the changes and some of the morphological details, that heterochronic changes necessary to give rise to Agnostida would have to have occurred comparatively early in the ontogeny of the ancestral forms. These changes must have affected at least meraspid and probably protaspid stages of the ancestral forms. The small size and juvenile appearance of the Agnostida would imply that most of the changes were progenetic. The
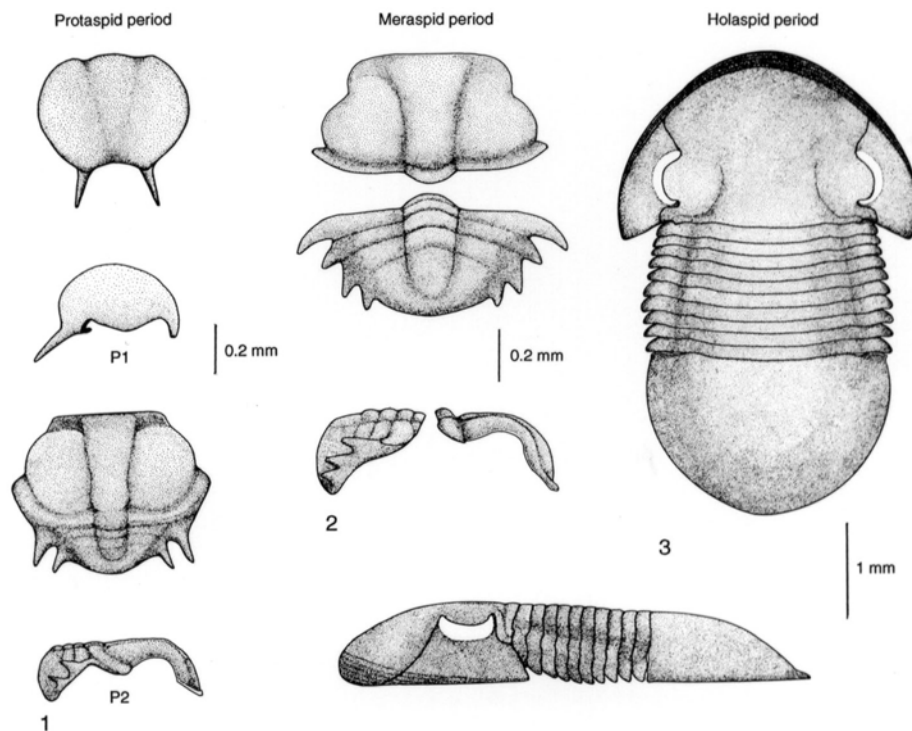
FIG. 159. The life cycle of the illaenid *Failleana calva* CHATTERTON & LUDVIGSEN. The life cycle of this species is representative of life-history strategy II (see Fig. 156). *P1* represents a nonadult-like, first protaspid instar; *P2* represents an adult-like, second protaspid instar. The meraspid period is represented by a cranidium and transitory pygidium belonging to early meraspid degree(s); and the holaspid period is represented by a reconstruction of a mature individual. All stages are shown in both dorsal and lateral views. The protaspid stages and meraspid degrees lack free cheeks, rostral plate, and hypostome (new).

Agnostida also have a number of autapomorphies that cannot be explained readily as the results of heterochronic evolution. After the separation of the Agnostida from other trilobites, considerable evolution took place within this group.

GOULD (1977) pointed out the prevalence of heterochronic evolution and suggested that there may be a relationship between heterochronic patterns of evolution and paleoecology, in particular the r and K life-history strategies of MACARTHUR and WILSON (1967).

It may be argued that the numerous evolutionary pathways available through using different heterochronic patterns (the six patterns shown by MCNAMARA, 1986b, fig. 1, plus an indefinite number of mosaic patterns

based on heterochrony taking place at the organ rather than the organism level) allow organisms to radiate rapidly when the opportunity presents itself. Such an opportunity may follow a mass extinction as niches become vacant.

Some workers (STUBBLEFIELD, 1936, 1959; STØRMER, 1942; HUPÉ, 1954; CLARKSON, 1971, 1975) suggested that heterochrony, in particular paedomorphosis, was the source of important evolutionary novelties that determined higher taxa within the Trilobita. WHITTINGTON (1957a) discussed the evidence for neoteny as an evolutionary process, particularly in regard to the origins of orders of trilobites, and was not convinced by the cases that had been made by earlier workers. He favored selection at the organ
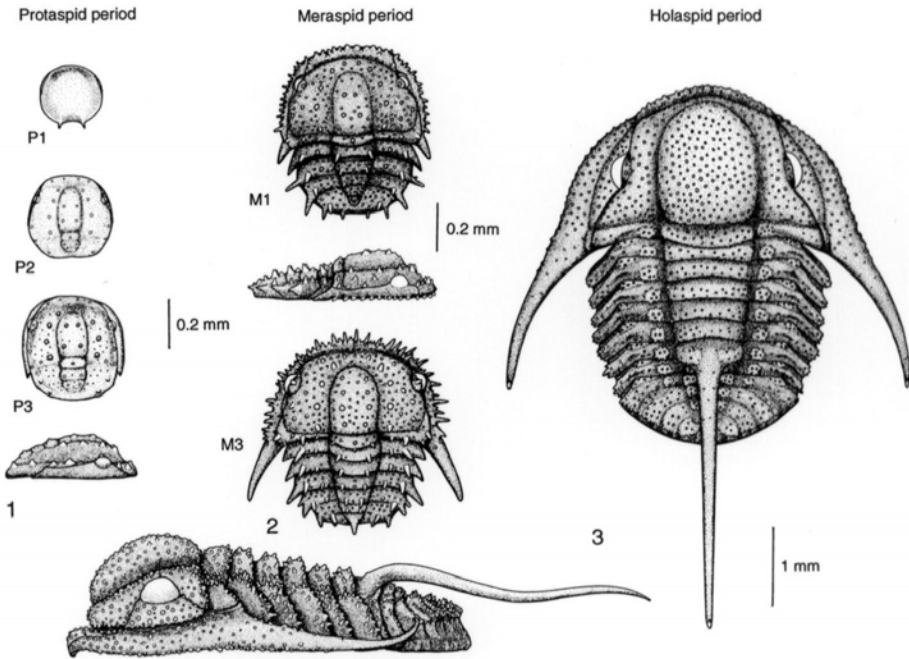
Fɪɢ. 160. The life cycle of the bathyuroid *Dimeropyge* n. sp. Drawings are of specimens from the Middle Ordovician Esbataottine Formation of northwestern Canada (see Fig. 182). The life cycle of this species is considered to represent life-history strategy III (see Fig. 156). All stages are considered to represent individuals that lived on the sea floor. *P1–P3* represent three protaspid instars; *M1* and *M3* represent meraspid degrees 1 and 3. Dorsal and lateral views are provided for the last protaspid instar (*P3*), a meraspid degree (*M1*), and a holaspid stage (new).

level in response to environmental pressures over any heterochronic process. Wʜɪᴛᴛɪɴɢᴛᴏɴ (1981, p. 593), while accepting some documented examples of paedomorphosis, was unconvinced that this form of evolution had been demonstrated for the "derivation in this way of a species ancestral to a new family or group" and did not believe that post-Cambrian proparian trilobites evolved from a single paedomorphic species. He also commented on the cryptogenetic origin of most trilobite higher taxa.

MᴄNᴀᴍᴀʀᴀ (1986a, p. 126) pointed out that most workers have concentrated on examples at the species level or on the origin of new genera (Rᴏʙɪsᴏɴ & Cᴀᴍᴘʙᴇʟʟ, 1974; Fᴏʀᴛᴇʏ, 1974b, 1975b; Jᴇʟʟ, 1975a; MᴄNᴀᴍᴀʀᴀ, 1978, 1981a, 1981b, 1983; Lᴜᴅᴠɪɢsᴇɴ, 1979b; Fᴏʀᴛᴇʏ & Rᴜsʜᴛᴏɴ, 1980; Wʜɪᴛᴛɪɴɢᴛᴏɴ, 1981; Cʜᴀᴛᴛᴇʀᴛᴏɴ &

Pᴇʀʀʏ, 1983; Rᴀᴍsᴋöʟᴅ, 1988; Eᴅɢᴇᴄᴏᴍʙᴇ & Cʜᴀᴛᴛᴇʀᴛᴏɴ, 1987).

MᴄNᴀᴍᴀʀᴀ (1978, 1981a, 1981b, 1983, 1986a) has described heterochronic patterns of Cambrian trilobites. He found that both peramorphosis and paedomorphosis are important in trilobite evolution. He discussed the role of paedomorphosis in developing major evolutionary novelties within the Trilobita and considered that perhaps the best example is the possible paedomorphic origin of the Corynexochida from the Ptychopariida, with meraspid stages of genera such as *Crassifimbra* (see Rᴏʙɪsᴏɴ, 1967) being very similar to adult corynexochids like *Bathyuriscus.* Most of the examples quoted by MᴄNᴀᴍᴀʀᴀ are based entirely on adult allometry, which is biased in regard to the amount of morphological change that takes place and the range of ecological factors

experienced by the animals. The most radical examples of heterochrony can be expected to involve morphological variation of larval as well as adult growth stages.

CLARKSON (1971, 1975) has argued that the origin of the schizochroal eye of the Phacopina and the usual forward position of the eye on the cephalon may have resulted from a paedomorphic, heterochronic pattern of evolution. He based this thesis on the facts that probable ancestral taxa have fewer lenses in their juvenile eyes and the eyes of phacopid larvae are located relatively farther forward than those of the adults. Thus cases have been made for the independent evolutionary origin of three trilobite orders using paedomorphic patterns: Agnostida, Corynexochida, and Phacopida.

MCNAMARA (1986a, p. 149) has also argued that a different pattern of heterochronic evolution may have played a part in the origin of some important post-Cambrian groups of trilobites. He noted the comparatively advanced morphological stage of the early growth stages of members of the Lichidae, Phacopida, and Illaenina. He suggested that this was an example of predisplacement, "one of the processes which result in peramorphosis" (ALBERCH & others, 1979). MCNAMARA also argued that most published examples of heterochronic evolution of post-Cambrian trilobites have been of peramorphosis, although undoubtedly paedomorphosis has occurred (e.g., LUDVIGSEN, 1979b; EDGECOMBE & CHATTERTON, 1987). In this context, MCNAMARA quoted GOULD (1977, p. 269): "evolution by acceleration must be an important path to the development of morphological complexity in specific features." MCNAMARA (1983) illustrated a number of small trilobites that he thought may have had a progenetic origin (Fig. 161). FORTEY argued that the origin of the Proetida could have been as a result of "adult morphology displaced back to protaspis stage" or, in other words, a form of predisplacement (1990a, fig. 16, p. 558–560).

MCNAMARA (1988, table 1) provided a list of published examples of heterochrony of trilobites. All of these are at generic or specific levels except for three: the origin of phacopids (CLARKSON, 1979a), the origin of the order Corynexochida (ROBISON, 1967), and the origin of the subfamily Calymeninae (SIVETER, 1980). Of the 36 examples that he listed, 21 are of paedomorphosis (12 Cambrian; 7 Ordovician; 2 Silurian), 13 are of peramorphosis (3 Cambrian; 8 Ordovician; 1 Silurian; and 1 Silurian-Devonian), and 2 are of mixed paedomorphosis and peramorphosis (both Silurian). Presumably, these examples provided the bulk of the data on which he based his generalization that paedomorphosis was more important among Cambrian trilobites and peramorphosis more important among post-Cambrian trilobites (MCNAMARA, 1986a). These 36 examples represent a very small proportion of the Trilobita, and MCNAMARA noted that some forms of heterochrony (e.g., progenesis) are more recognizable than others.

Recent work on ontogeny and heterochrony (CLARKSON, 1971, 1975) has shown that some patterns of heterochrony may affect primarily organs rather than whole organisms. An organism may evolve in a variety of heterochronic patterns at the same time, some of which may be paedomorphic and some peramorphic. This form of evolution, showing mixed heterochronic patterns (mosaic heterochrony of KOPASKA-MERKEL, 1987), apparently occurred in the origin of the *Encrinurus punctatus plexus* from an *Encrinuroides* ancestor (EDGECOMBE & CHATTERTON, 1987). EDGECOMBE and CHATTERTON (1987) also identified a mixture of paedomorphic and peramorphic patterns in a rapidly evolving lineage of *Kettneraspis* in Silurian strata of northwestern Canada. This lineage occurs in a sequence of strata (mainly limestones) laid down during a regression, from comparatively deep and stable, presumably K-selective environments to shallower, more unstable, r-selective environments. They argued that the combination of the
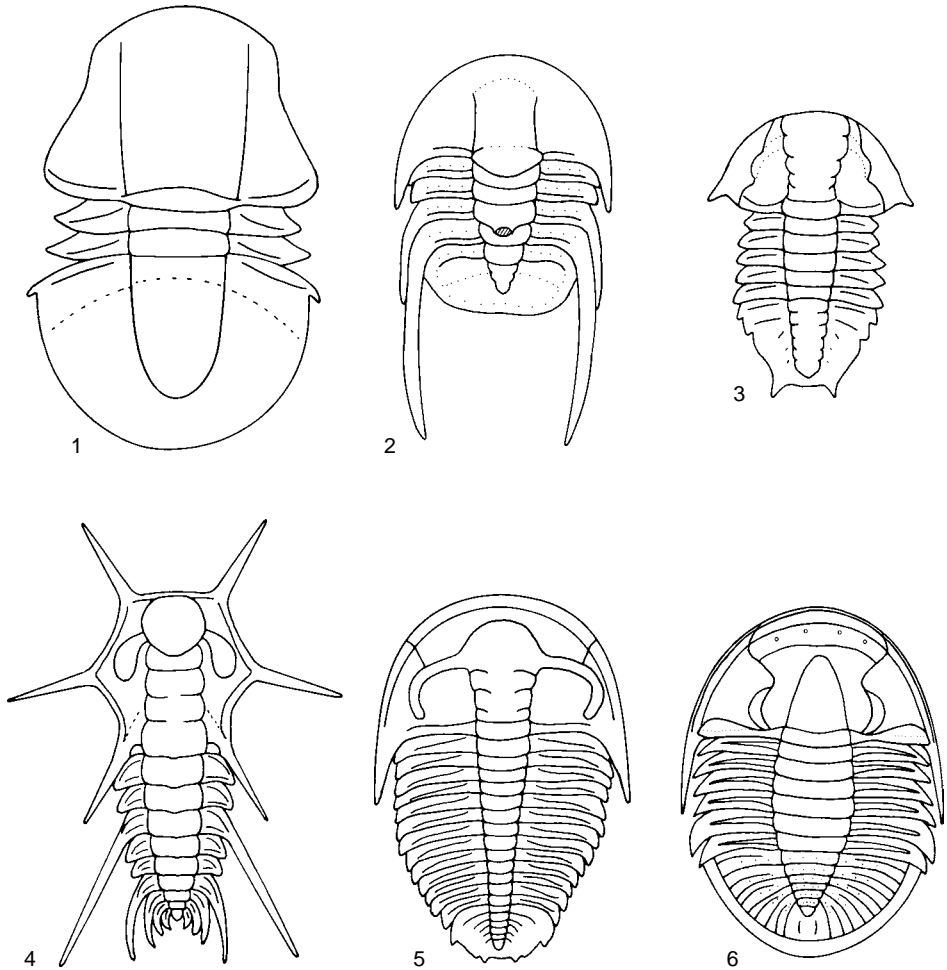
FIG. 161. Progenetic trilobites. *1, Thoracocare minuta* RESSER; *2, Acanthopleurella grindrodi* GROOM; *3, Vanuxemella nortia* WALCOTT; *4, Olenellus armatus* PEACH; *5, Galahetes fulcrosus* ÖPIK; *6, Scharyia redunzoi* PERRY & CHATTERTON (Chatterton & Speyer, 1990, fig. 4).

peramorphic acceleration and paedomorphic progenesis patterns is a consistent evolutionary response to this change in the ecology. MCKINNEY (1986) had earlier come to similar conclusions for Cenozoic echinoids. Some neontologists, however, consider the theory of r- and K-selection to be an overgeneralization: that all organisms show a mixture of such traits and that polarization of r- versus K-selection or even versus stress tolerance (VERMEIJ, 1978) is unnatural.

In order to examine heterochronic patterns in trilobites, it is necessary to select some benchmarks that may be used to determine relative rates of development and onset or timing of development of particular features. This may be accomplished by assuming that a feature increases in size at a regular rate in relation to time (such as the length of the glabella) and timing other events in relation to numerical increments in size of this feature. Alternatively, it may be done by contrasting the timing of the appearance of some morphological event in relation to that of some other morphological event considered to be a useful time marker. The number

of such time markers in the ontogeny of trilobites is large and includes several features: the timing of the first distinct appearance of axial furrows on the cranidium (or protocranidium), the appearance of a furrow marginal on the protocranidium (separating the protocranidium from the prototransitory pygidium), an anterior border, a preglabellar field, a distinct visual surface, a functioning hypostomal suture, a bulla, functioning connective sutures, the first segment on the protopygidium (or a particular number of segments), and the suture that causes separation of the cephalon from the transitory pygidium (protaspid-meraspid boundary). Other important heterochronic markers may include losses (such as loss of long marginal spines on the hypostome), movements of features (transfer of genal spine from the fixed cheek to the free cheek or the release of the last segment into the thorax at the transition from meraspis to holaspis), and even expansion of features (e.g., the bullae expanding to incorporate parts of more than one cranidial somite). Not all of these markers occur in all taxa. Which markers are the most suitable for the taxa being studied and which may be most convincingly argued must be chosen for each heterochronic study.

LUDVIGSEN (1979a) argued (Fig. 162) that *Pseudogygites* arose from *Isotelus* through paedomorphic (neotenic) evolution, since mature individuals of *Pseudogygites* are very similar to meraspid individuals of *Isotelus*. He pointed out that *Pseudogygites* is abundant in a very distinct, low-diversity facies (low-temperature, low-oxygen, dark shales). However, he considered that low temperature could not be the cause of this heterochronic pattern because *Pseudogygites* apparently originated on a warm, carbonate shelf and later became abundant in deeper, colder-water, terrigenous-mud environments. (It occurs first in low numbers in the upper parts of the Cobourg Formation.) LUDVIGSEN argued that neotenic, heterochronic evolution, perhaps as a K-strategy, preadapted *Pseudogygites* for the colder, deeper, more stable environments of the Whitby Forma-

tion, which was deposited later. He suggested that this situation may have occurred more than once, producing several species of *Pseudogygites* iteratively from *Isotelus*. If so, cladists would argue that *Pseudogygites* is polyphyletic and should be subsumed within *Isotelus*.

One of the better examples of heterochronic evolution among Cambrian trilobites is that of various species of *Xystridura* and the descendant genus *Galahetes* (Fig. 163; MCNAMARA, 1981a). Morphological details found in small cranidia of such stem-form Xystriduridae as *Xystridura templetonensis* and hypothesized to occur in *Xystridura carteri* occur in adult growth stages of the later species *Xystridura altera, Xystridura dunstani, Xystridura sandoverensis,* and *Galahetes fulcrosus;* these include retention of a preglabellar field, a wide fixed cheek and cranidium, and a smaller frontal glabellar lobe. MCNAMARA also considered whether ecological factors could explain the differences between the apparently progenetic pattern that produced *G. fulcrosus* and the neotenic pattern that produced *X. altera,* two species that occur in some cases on the same bedding planes. He argued that the former, progenetic species may have been r-selective and pelagic and that the latter species may have been K-selective and benthic. However, we believe that the adult morphology of both species is typical of benthic trilobites and consider it more likely that these two forms originated in different environments, which could have favored r- over K-selective taxa, and later occurred together as a result of migrations in response to environmental changes.

Most published examples of heterochronic evolution among trilobites are based on general inferences of ancestral-descendant relationships rather than detailed arguments in support of individual phyletic lineages and demonstrations of anagenetic evolution. Also, in a number of cases, the ontogenies are not known for either the hypothesized ancestral or the descendant species but have been inferred from the known ontogeny of a
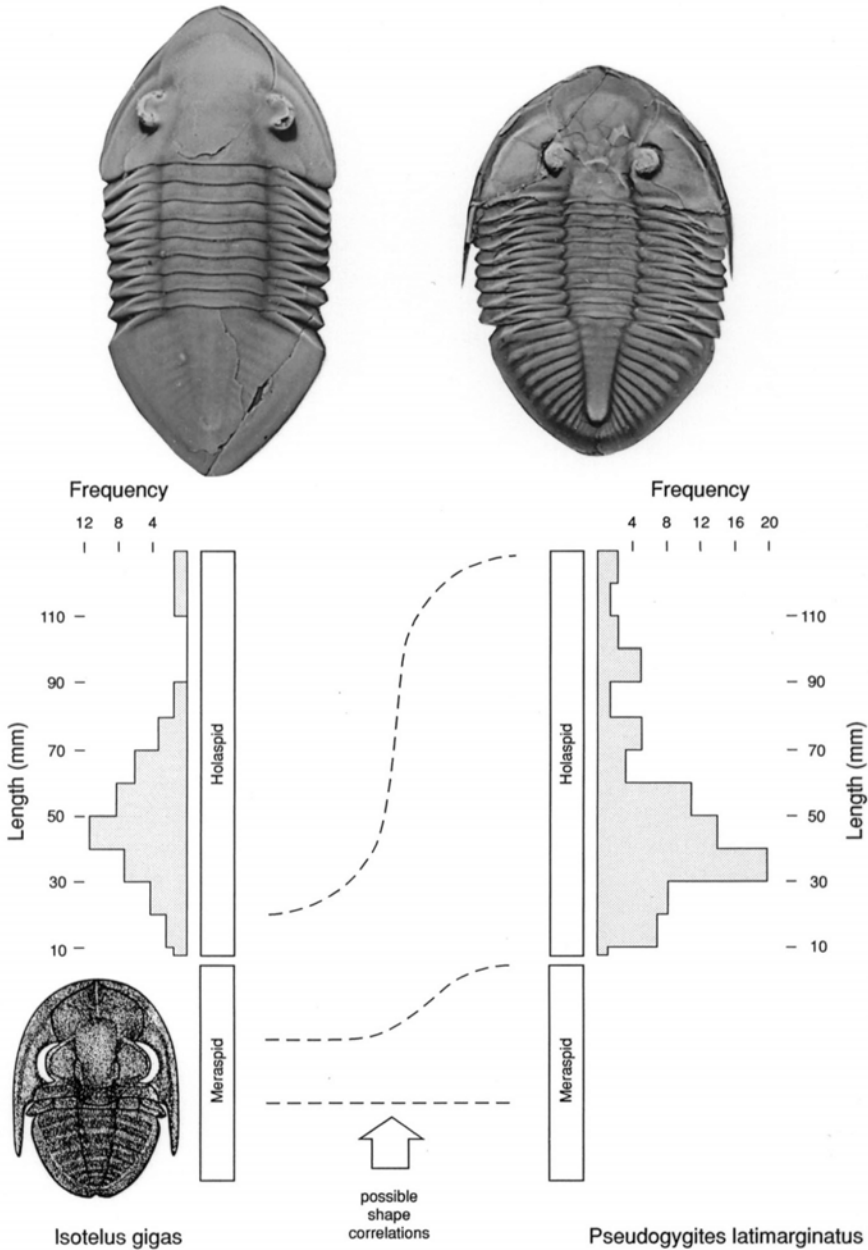
Fig. 162. Model of heterochronic (paedomorphosis, neoteny) derivation of *Pseudogygites* from *Isotelus* during the Ordovician, based on 46 specimens of *Isotelus gigas* from the Trenton Group of New York and 79 specimens of *Pseudogygites latimarginatus* from the Whitby Formation of Ontario. *Dashed lines* indicate tentative shape correlations. Drawing of *I. gigas* meraspid degree 1 based on specimen illustrated by Ludvigsen and silicified material of *Isotelus parvirugosus* Chatterton & Ludvigsen from the Esbataottine Formation, northwestern Canada (Chatterton & Speyer, 1990, fig. 7).
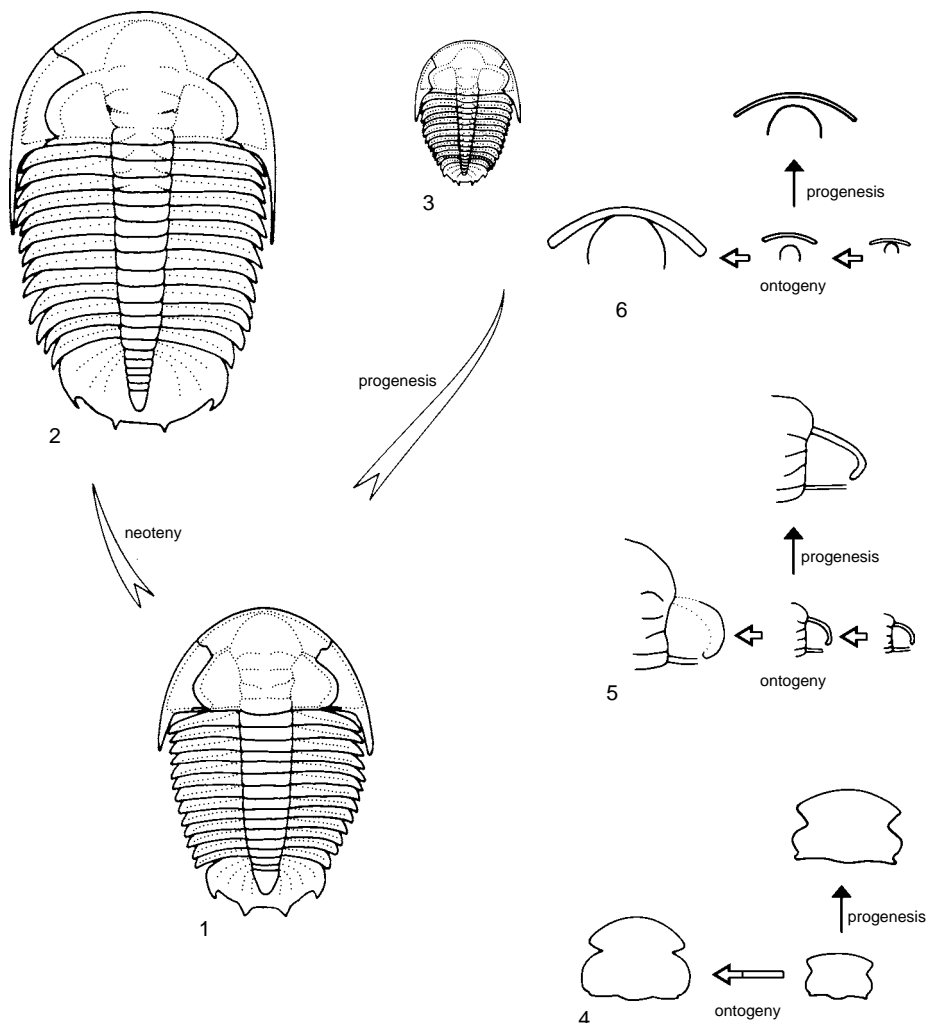
FIG. 163. Heterochronic patterns in Cambrian Redlichiina *Xystridura* and *Galahetes*. *1, X. templetonensis* (CHAPMAN); *2, X. altera* ÖPIK; *3, G. fulcrosus* ÖPIK. *4–6,* Horizontal row of drawings and *open arrows* show changes during ontogeny in cranidia of *X. templetonensis; vertical arrows* show characters present in the adult *G. fulcrosus* that occur in the ontogeny of *X. templetonensis; 4,* changes in the outlines of cranidia (note curvature of anterior margin); *5,* changes in width from axial furrow to back of eye as a percentage of cranidial length; *6,* changes in the length of the preglabellar field. [In one of MCNAMARA's original diagrams used for this figure (1981a, fig. 8), *X. carteri* ÖPIK is included as the stem-form species. However, since all his examples of ontogeny within *Xystridura* were based upon *X. templetonensis* and he noted (1981a, p. 216) that *X. templetonensis* is a stem-form species of *Xystridura,* we have chosen to use the latter species in this adaptation from McNamara (1981a).]

related species. (For an exception, see FORTEY & RUSHTON, 1980.) Ideally, ontogenies of both ancestral and descendant species should be known, and a considerable amount of data should be available supporting direct descent of one species from the other in the form of morphologically overlapping intermediate collections of fossils from appropriate stratigraphic levels and geographic locations. We can think of no published examples that fulfill all of these criteria. A number of sequences of silicified trilobites

have great potential as examples (Virginia, New York, the Mackenzie Mountains).

GROWTH FORMULAS AND POPULATION DYNAMICS

Several rules have been formulated for the amount of growth expected between adjacent instars of various types of arthropods. HARTNOLL (1982) discussed some of these and their application to crustaceans. One of these was Dyar's rule (DYAR, 1890): x/y = a constant, where x is a linear measurement for an instar and y is the same linear measurement for the previous instar; another was Brooks' rule, originally defined by FOWLER (1909) as $x - x/y$ = a constant but later redefined as the percentage by which the postmolt exceeds the premolt length (MAUCHLINE, 1976). HARTNOLL also discussed Przibram's rule (PRZIBRAM, 1929), where weight doubles between instars so that increase through Dyar's rule should be the cube root of 2, or 1.26.

Growth increments between molts in trilobites and their fit to these rules of growth have been discussed by PALMER (1957), HUNT (1967), CISNE (1973b), ROMANO (1976), KOPASKA-MERKEL (1981), BUSCH and SWARTZ (1985), BREZINSKI (1986a), SHELDON (1988), CHATTERTON and SPEYER (1990), and CHATTERTON and others (1990). In most examples, ontogenies have growth increments between instars that are in general agreement with these laws. However, the increments can be significantly above or below the expected values. In some, departure from these rules is associated with molts that involve radical metamorphoses. It is, however, difficult to quantify size differences between planktonic and benthic growth stages because the morphologies of the forms are so different, and volume may be more important than mere length and width. Rarely are the instars known with certainty for more than a small portion of the life cycle of the trilobite, although, as HUNT (1967) pointed out, distinct instars are usually identifiable with confidence for early growth stages.

Recent work on arthropods has demonstrated that correspondence with growth rules is far from general. Some workers have shown that the amount or type of food may affect the rate of growth, the number of instars, and thus the amount of growth between instars (e.g., BERNAYS, 1986; BERNAYS & HAMAI, 1987; LIPCIUS & HERRNKIND, 1982). The same was probably true for trilobites, and the growth increment between instars may provide evidence of genetic variation or indirect evidence of variation in environmental factors such as the availability of various types of food.

We agree with SHELDON (1988) that, while instars may often be recognized with confidence in bivariate plots (HUNT, 1967), they are usually more difficult or even impossible to identify on size-frequency histograms. An analysis of bivariate plots with distinct instars shows that the instars are usually more readily discriminated by size along one of the two axes.

Size-frequency diagrams of trilobites have sometimes been used to provide information of relevance to studies of population dynamics. These seldom involve bedding-plane assemblages and so usually represent a span of time rather than a moment frozen in time. SHELDON (1988), examining the size-frequency histograms of more than 5,000 trilobites from Ordovician shales in Wales, found that the histograms usually have normal to slightly negatively skewed distributions with very few small individuals preserved. He discussed the implications of their absence in light of the fact that the expected pattern is positive skewness. He argued that negative skewness may have resulted from high longevity and low recruitment to the fossil record of postlarval stages, with more adult than juvenile molts left behind by long-lived trilobites. A number of other factors, however, could cause negative skewness, including the poorer calcification of small sclerites (leading to preferential early taphonomic destruction), the tendency for shales to split at levels containing large but not small specimens (which does not occur with silicified

faunas, where the skewness appears to us to be typically positive), the possibility that small stages lived elsewhere and arrived in the area only as adults (perhaps most likely for species with planktonic larvae), and the washing away of small growth stages (which is unlikely in SHELDON's example). SPEYER and BRETT (1986) demonstrated that size variation across numerous facies was due to biological or ecological factors and possibly represented migratory patterns such as those demonstrated by annelids and many long-lived Crustacea. Thus population dynamics of trilobites are difficult to reconstruct from size-frequency histograms taken from bulk samples, and usually such diagrams provide data that are more likely to be of value to studies of paleoecology and taphonomy than taxonomy.

BIOGEOGRAPHY IN RELATION TO ONTOGENY

As a general rule, animals with long, pelagic growth stages will be more widely dispersed than those with purely benthic growth stages. THORSON (1936) commented that few organisms have planktotrophic larvae in high latitudes, but a high percentage of animals in equatorial latitudes have such larvae. Thus, the presence or absence of planktonic larvae in the life cycles of trilobites may be of use in determining their paleogeographic distributions. Those with planktonic larvae might be expected to be widespread in tropical or warm waters, and those with benthic growth stages may be expected to form a greater proportion of endemic faunas and faunas of high paleo-latitudes. A gradient of sorts occurs between the paleogeographic extremes, with the proportion of taxa with planktonic larvae increasing towards the equator.

CHATTERTON and SPEYER (1989, 1990) and SPEYER and CHATTERTON (1990) found that some trilobites with planktonic, nonadult-like larvae had very widespread paleogeographic distributions prior to the onset of the Ordovician-Silurian glaciation.

However, after the onset of that glaciation, with the introduction of a greater thermal gradient between high and low latitudes and the appearance of floating ice, the distribution of these trilobites was restricted to more equatorial latitudes. Thus the distribution of these taxa appears to have been controlled by the modes of life of their larval stages.

CHATTERTON and others (1990, p. 258) commented on the absence of known, nonadult-like protaspides among homalonotid trilobites, despite their presence in the closely related Calymenidae. They posited that the success of homalonotid trilobites in the "*Hirnantia* fauna," their survival of the Ordovician-Silurian mass extinction (CHATTERTON & SPEYER, 1989), and their later success in the cold, southern, Malvinokaffric faunas may be associated with their having had large embryos in a yolked egg and their having emerged from the egg to become large, benthic larvae.

FORTEY (1985) noted that some telephinids and cyclopygids with pelagic adults have wide geographic ranges, and these forms appear to have been more independent of facies changes than benthic trilobites found in the same collections. The cyclopygids probably also had planktonic larvae. Trilobites with mature stages that lived in deep, cold environments may also have dispersed widely (e.g., Agnostida) since the deep oceans may not have been barriers, except during periods when layering of the oceans took place, and deep water was anoxic (FORTEY, 1989).

CHATTERTON and SPEYER (1989) and SPEYER and CHATTERTON (1990) noted that trilobites with different life-history strategies were affected in different fashions at times of other extinctions in the Ordovician. Those with all pelagic larvae (strategy I) underwent a minor extinction at about the time of onset of the Ordovician-Silurian glaciation (see Fig. 164) and were virtually wiped out during the episode of mass extinction near the end of the Ordovician close to or at the level of maximum glaciation. Only one genus, *Raphiophorus,* containing very few species
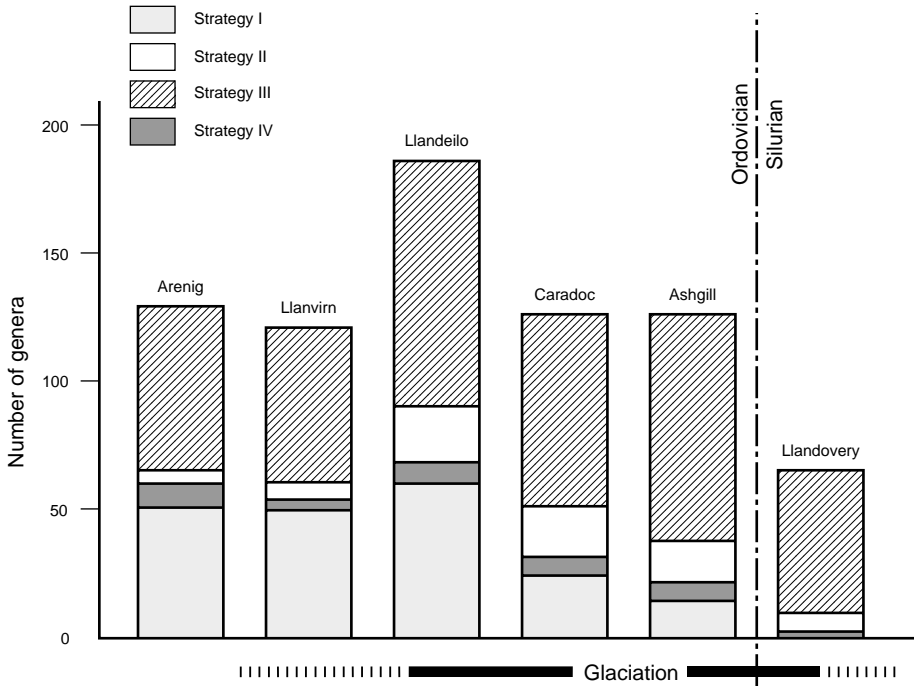
F<small>IG</small>. 164. Histogram of numbers of trilobite genera in Ordovician and Silurian stages. The legend refers to the life-history strategies shown in Figure 156; for strategy IV, see text. Note, in particular, the drop in diversity of trilobites with life-history strategy I between the Llandeilo and Caradoc at about the time of the start of the main part of the Ordovician-Silurian glaciation and the drops in diversity of all groups of trilobites but particularly those with life-history strategies I and IV, between the Ashgill and the Llandovery at about the time of maximum glaciation (Chatterton and Speyer, 1989, fig. 3).

survived. Trilobites with pelagic adults (strategy IV) were not obviously affected by the first of these episodes but did not survive the second. Trilobites that had a single, nonadult-like, planktonic stage with the rest of the life cycle being benthic (strategy II) were unaffected by the first episode and suffered to a lesser degree during the second. Trilobites with all known stages benthic (strategy III) were affected only slightly during the first episode and moderately during the second. C<small>HATTERTON</small> and S<small>PEYER</small> argued that these patterns could be explained best by environmental changes associated with the onset, advances, and retreats of the Ordovician-Silurian glaciation.

An important result of this pattern of extinctions was that almost all of the trilobite taxa that survived the Late Ordovician (Fig. 165) had life-history strategies II and III, and these two groups thus gave rise to almost all of the new taxa that radiated after that extinction. The only representative with life-history strategy I to survive, *Raphiophorus,* never radiated significantly and existed only in small numbers and with low diversity to near the end of the Silurian. The life history of that genus is not known in detail but is inferred from related raphiophorid trilobites such as *Lonchodomas* (see Fig. 174). When the autecology of this genus is better understood, we may understand why it alone managed to survive the Late Ordovician mass extinction but failed to radiate to occupy niches vacated by its relatives. Examination of life-history strategies at times of other extinctions (the Late Cambrian biomere boundaries and Late Devonian, in particu-

lar) may also throw new light on the causes of those extinctions.

ONTOGENY AND SYSTEMATICS

As a rule, monophyletic groups based on characteristics of adult growth stages have similar larvae and life-history strategies so that larval morphology appears to be a useful indicator of relationship. Despite the prevailing view that larvae may be expected to be simpler, more primitive, and more closely similar to one another than adults of the same trilobite taxa, many trilobite larvae have undergone radical evolution. Evolution apparent in larvae may not be reflected in the same manner or the same degree in more mature stages. The prevailing view, extending back to Von Baer and Haeckel (GOULD, 1977), is that changes in larval stages are necessarily added to and expanded upon in more mature stages so that they lead to even more extreme changes in mature stages. Changes in small stages, however, may not lead to equally large changes in more mature stages. Thus, there seems to be some decoupling between larval evolution and the evolution apparent in more mature stages. Some synapomorphies visible only in larval stages may be used to recognize and define large groups of trilobites (FORTEY & CHATTERTON, 1988). This may be particularly apparent when the early larvae are separated from later growth stages by a radical metamorphosis.

Work to date supports the contention that monophyletic groups of trilobites from the family at least to the subordinal level have similar larvae, which are distinct from those of other monophyletic clades (WHITTINGTON, 1956d, 1957b, 1959a, 1959b; FORTEY & OWENS, 1975; CHATTERTON, 1980; FORTEY & CHATTERTON, 1988; EDGECOMBE, SPEYER, & CHATTERTON, 1988; CHATTERTON & others, 1990). Some genera include species that have protaspides that are very similar to one another (e.g., *Scharyia,* see OWENS, 1974; ŠNAJDR, 1981a; see also Fig. 179); oth-
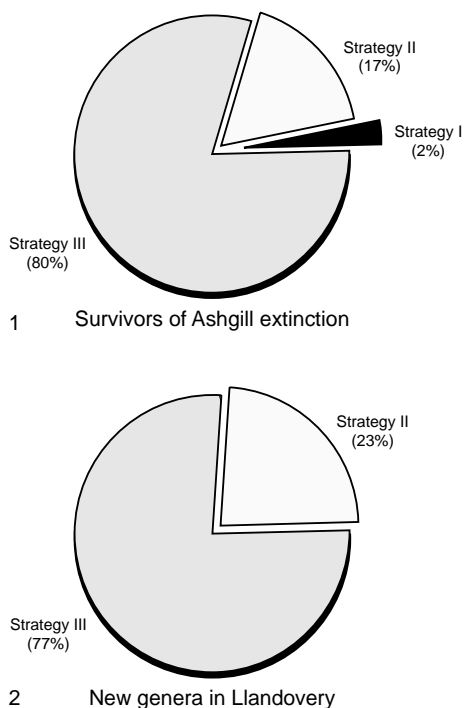
FIG. 165. Percentage of trilobite genera that survived the Ashgill extinction (*1*) and new genera that originated in the Llandovery (*2*) grouped into life-history strategy categories (for explanation of strategies, see Fig. 156 and text). Note the high proportion of forms that had benthic protaspides (strategy III).

ers show a greater degree of disparity in larval form (e.g., *Ceraurinella*); the protaspides illustrated in Figure 178 can be contrasted with those figured by CHATTERTON (1980).

Because radical metamorphoses occurred in the life cycles of a number of trilobites (SPEYER & CHATTERTON, 1989), a number of the nonadult-like protaspides remain unclassified with respect to growth series of individual taxa (Fig. 166). We know of a number of these early, probably planktonic, growth stages that have yet to be described because of problems with their taxonomic assignment. They can not be assigned to a species on the basis of similarity in morphology. One useful fact is that they are always earlier growth stages and therefore must, under most circumstances, be smaller than later,
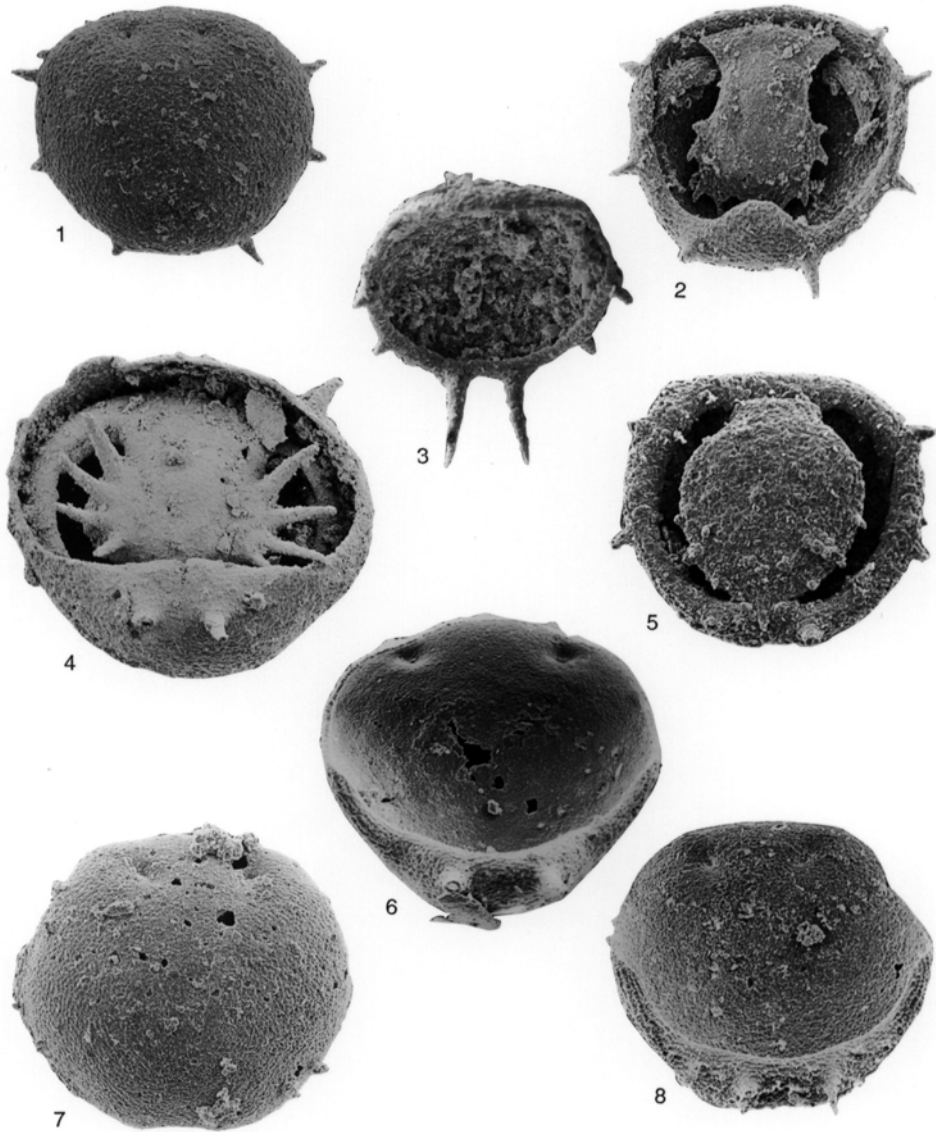
F<small>IG</small>. 166. Globular, nonadult-like protaspides, some of which are of uncertain attribution. *1–4,* From the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1, 2,* dorsal and ventral views of a protaspid, possibly of a premetamorphic growth stage of a lichid?; *1,* NYSM 16401, ×89; *2,* NYSM 16402, ×91; *3,* anteroventral view of very small protaspis of a cheirurid?, NYSM 16403, ×153; *4,* ventral view of nonadult-like protaspis of asaphid *Isotelus* sp., NYSM 16404, ×62 (new). *5,6,* From the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T); *5,* ventral view of nonadult-like early protaspis, possibly of an Illaenina, UA 8480, ×88; *6,* ventral view of protaspis of illaenid? trilobite, UA 8481, ×74 (new). *7,8,* Dorsal and ventral views of small protaspides of harpid? trilobite (*Dolichoharpes?*) from the Crown Point Formation, Middle Ordovician, New York (locality PB81); *7,* NYSM 16405, ×65; *8,* NYSM 16406, ×65 (new).

more adult-like stages in the same life cycle. The problem of correct association of these small, nonadult-like larval stages is exacerbated by the change in mode of life that apparently occurred at the same time as the radical metamorphosis. Thus, the small, nonadult-like stages did not necessarily live or die in the same place as later growth stages

of the same species. This renders correct assignment through repeated stratigraphic occurrence or matching abundance more difficult.

Ontogeny aids in the correct determination of homologies by allowing the tracing of the formation of structures. Phylogenetic studies depend on the homologies of the characters used in the analyses. It is often difficult to trace these characteristics back to a common ancestor. They can usually be considered to be homologous if they have a common embryological or early ontogenetic origin from the same part of the organism. The homologies of such structures as cranidial lobes of various taxa have been suggested by studying ontogenies (Lichidae by CHATTERTON, 1971, 1980; TRIPP & EVITT, 1981; *Cybeloides* by EVITT & TRIPP, 1977).

In this section, we define the more important larval characteristics evident at the ordinal level and also for some suborders and superfamilies.

ORDER AGNOSTIDA, SUBORDER AGNOSTINA

Meraspid to holaspid growth stages have been described by numerous authors, including BARRANDE (1852), PALMER (1955), ŠNAJDR (1958), ROBISON (1964), RUSHTON (1966, 1979), HUNT (1967), ÖPIK (1979), QIAN (1982), MÜLLER and WALOSSEK (1987), SHERGOLD (1991), and in this work (Fig. 167).

Protaspid stages assigned to *Pseudagnostus benxiensis* by QIAN (1982) come from a bed also containing *Parachangshania hsiaoshihensis*. The ontogeny of the latter was described by CHIEN (1958) from the same locality, the protaspis being different from that assigned to *P. benxiensis*. Both protaspides are very similar to those of polymerid trilobites, and X. ZHANG (1989, p. 13) expressed the opinion that they are "far more likely to be polymerid larvae." The smallest meraspides of Agnostina (including *Pseudagnostus benxiensis*) are all isopygous or almost isopygous. The largest protaspis illustrated by QIAN (1982) has a protopygidium that is considerably smaller than the cranidium,

requiring a radical metamorphosis between that stage and the earliest of *P. benxiensis*, should these two stages actually belong to the same taxon. Thus, if these protaspides belong to *Pseudagnostus*, they provide strong evidence of miomerid-polymerid affinity, which is also supported by the form of eodiscoid protaspides. If they do not, then they should be assigned to some polymerid that has yet to be described from this locality.

We find it difficult to understand why no protaspides of *Agnostus* have been discovered in the Swedish Orsten fauna if they existed (MÜLLER & WALOSSEK, 1987). This phosphatized fauna is so well preserved that the appendages are known for early meraspid stages of *A. pisiformis* (Fig. 82).

The reasons why no protaspides of Agnostina have so far been found have been discussed and center in part around the mode of life of the adult. A number of workers have argued in favor of a pelagic mode of life for Agnostina (ROBISON, 1972a; STITT, 1975; X. ZHANG, 1989), citing the small size of adults and their widespread distributions. Other workers consider Agnostina to have been benthic (FORTEY, 1975b; CHATTERTON & SPEYER, 1990), living in deep, cool, marginal environments where the levels of light (accounting for blindness) and oxygen (accounting for the paucity of other benthic organisms and high organic contents of the rocks) were often low. Both modes of life could account equally well for the widespread geographic distributions and deep-shelf, marginal or basinal distributions of Agnostina. Some workers have even suggested such alternative modes of life as parasitism (BERGSTRÖM, 1973a) and epifaunal attachment to algae (PEK, 1977). We favor the benthic mode of life for several reasons (see CHATTERTON & SPEYER, 1990). (1) Almost all pelagic arthropods have large eyes, whereas Agnostina were blind. (2) It is difficult to imagine an enrolled individual staying suspended in the water column. (3) The ventral side of the exoskeleton is virtually planar, implying that it was constrained in space, as is true of most benthic trilobites. (4) The exoskeleton of Agnostina, in
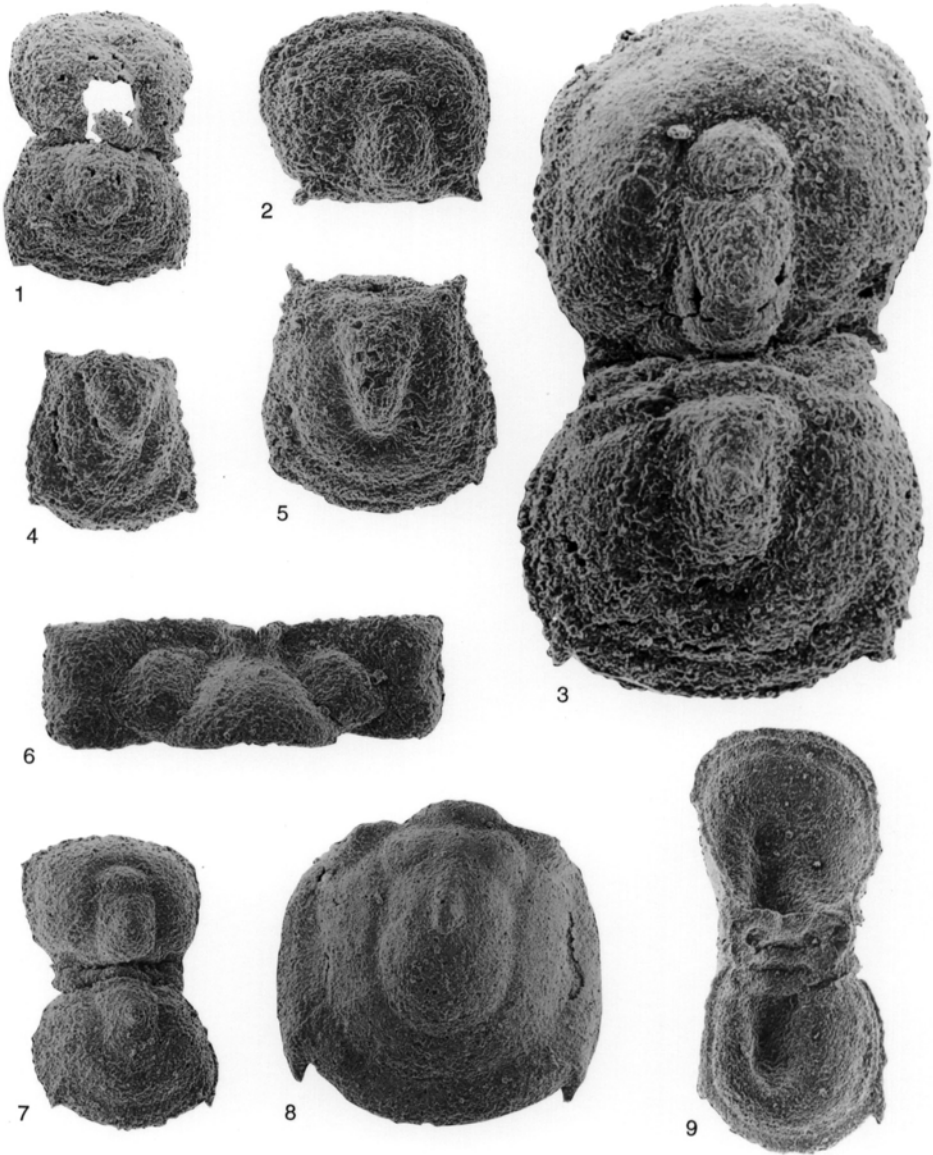
FIG. 167. Agnostina. Growth stages of *Geragnostus (Micragnostus) subobesus* (KOBAYASHI) from the Rabbitkettle Formation, Section K, Mackenzie Mountains, Upper Cambrian, northwestern Canada. For adult specimens from the same horizon, see LUDVIGSEN (1982, fig. 47a–p). *1,* Dorsal view of M0, UA 8424, ×48.5; *2,* dorsal view of cranidium of M0, UA 8425, ×49; *3,* dorsal view of M0 transitory pygidium, UA 8426, ×49; *4,* dorsal view of M0, complete enrolled specimen, UA 8427, ×49; *5,* dorsal view of complete M1, UA 8428, ×52.5; *6,* dorsal view of thoracic segment, UA 8429, ×32; *7,* dorsal view of M1, UA 8430, ×22.5; *8,* dorsal view of pygidium, UA 8431, ×16.5; *9,* ventral view of small holaspid, UA 8432, ×22.5 (new).

proportion to the size of the animal, shows few signs of weight reduction. We disagree with the view that the exoskeleton of Agnostina was thin. We have found that, in the Middle Ordovician Edinburg and Upper Cambrian Rabbitkettle formations, Agnos-

tina, although thin-shelled, are at least as thick-shelled as co-occurring, clearly benthic, usually olenid trilobites (see also data by Fortey and Wilmot, 1991). (5) The distribution data, with beds containing enormous numbers but a low diversity of Agnostina, matches the distributions of gregarious or low-diversity, benthic organisms much better than it does the stratigraphic distributions of pelagic organisms. Müller and Walossek (1987, p. 1) considered that *Agnostus pisiformis* inhabited a "flocculent zone at the bottom of the Alum Sea, where the animals swam or floated around." If Agnostina were benthic, it is feasible that they passed through the protaspid stages as uncalcified embryos or larvae. Such accelerated development is common in crustaceans of small size (e.g., ostracodes and copepods). X. Zhang (1989) presented the alternate hypothesis that the absence of a protaspis was the result of their inhabiting a different environment from the adults. If this were common in trilobites, associating larvae with more mature stages would be exceedingly difficult.

In attempting to assess whether Qian's (1982) assignments of protaspides to the agnostid *Pseudagnostus* are correct, it is useful to consider the following points. (1) Protaspides of Agnostina have not been described from extensive collections of silicified and phosphatized trilobites, including both Agnostina extending to M0 and many small polymerid protaspides. (2) The protaspides described by Qian (1982), at least in the shape of the simple glabella, are morphologically similar to small meraspides of Agnostina. (3) Marginal spines of the M0 transitory pygidium are not apparent, either through absence or lack of preservation on the protaspid protopygidia. (4) The disparity between the size ratio of the protopygidium to cranidium and the size ratio of the M0 transitory pygidium to cranidium is greater for *Pseudagnostus benxiensis* than for the eodiscoids *Neocobboldia chinlinica* and *Pagetia ocellata*. (5) The genal swellings, bacculae, and more anterolateral lobes apparent in the eodiscoid protaspides are not apparent on the protaspides assigned to the Agnostina. Because of the comparatively poor state of preservation of the protaspides described by Qian (1982) and their broad morphological similarity to meraspid cranidia of Agnostina from the same locality, we are reluctant to state categorically that they are not Agnostina. However, their greater similarity in gross morphology to some polymerid protaspides, rather than to those of eodiscoids, and the comparatively radical metamorphosis required to change these protaspides into meraspides of Agnostina leads us to favor the hypothesis that these specimens are polymerid protaspides.

ORDER AGNOSTIDA, SUBORDER EODISCINA

Protaspides have been assigned to eodiscoid trilobites by Hu (1971), X. Zhang (1989), Shergold (1991), and X. Zhang and Clarkson (1993). Jell (1975a) and X. Zhang (1989) suggested that the protaspis assigned to *Pagetia clytia* by Hu (1971) may belong to a polymerid trilobite. However, as discussed below, we consider that this specimen is very similar to those assigned to the eodiscoids *Neocobboldia* (X. Zhang, 1989) and *Pagetia* (Shergold, 1991). There is little doubt that the latter forms are correctly assigned because of the number of specimens available, the size progression, and the clear similarity between protaspid and meraspid stages demonstrated by X. Zhang (1989) and Shergold (1991). We note here that the forms called anaprotaspides by X. Zhang would be termed metaprotaspides by most workers (see Hu, 1971, who called the similar protaspis of *Pagetia* a metaprotaspis), and the forms referred to as metaprotaspides by X. Zhang are meraspides.

Characteristics of eodiscoid protaspides (Fig. 168.1; and X. Zhang & Clarkson, 1993, fig. 3, 7) include: (1) a distinct axis that extends backward almost to the posterior margin and forward to just behind a very short (sag.) anterior border and that has a distinct occipital ring and at least two poorly
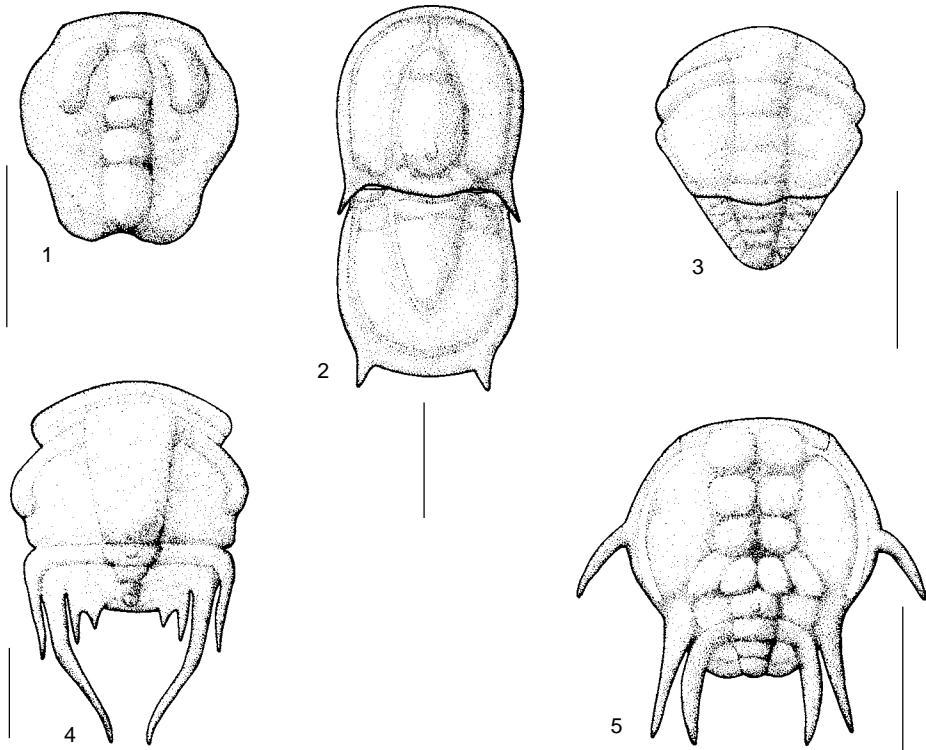
FIG. 168. Protaspides and meraspides of various Cambrian trilobite taxa. Scale bars are 0.5 mm long. *1,* Dorsal view of protaspis of *Neocobboldia* (Agnostida, Eodiscina) (adapted from X. Zhang, 1989); *2,* dorsal view of meraspid degree 0 of *Pseudagnostus benxiensis* QIAN (Agnostida, Agnostina) (adapted from Qian, 1982); *3,* dorsal view of meraspid degree 0 of *Balcoracania flindersi* POCOCK (Redlichiina, Emuelloidea) from the Lower Cambrian of South Australia (Pocock, 1970); *4,* dorsal view of a protaspis of *Xystridura* sp. (Redlichiina, Paradoxidoidea) (adapted from Öpik, 1975a); *5,* dorsal view of a protaspis of *Paradoxides pinus*? HOLM (Redlichiina, Paradoxidoidea) (Whittington, 1957b, fig. 5a).

defined transglabellar furrows; (2) two distinct lobes on the fixigena, one subcircular a short distance anterolateral to the occipital ring (baccula?) and the other much larger (elongate-ovoid in outline and almost bicomposite), located farther anterolaterally and having an anteromedially directed axis; (3) a proparian facial suture; (4) a comparatively large protopygidium that comprises about one-third of the area of the cranidium; and (5) a protopygidium that appears to be indented posteromedially in dorsal view. The specimens of *Neocobboldia* illustrated by X. ZHANG (1989) also have a sculpture of fine ridges and grooves and some tubercles, particularly posterolaterally, somewhat similar to that of asaphoid protaspides illustrated by

SPEYER and CHATTERTON (1989). The protopygidium is turned down and slightly forward posteromedially. The doublure is incurved rather than inturned. The overall form of the eodiscoid larvae is adult-like and benthic in the terms of SPEYER and CHATTERTON (1989), and we also regard the adults as having a benthic morphology. The progressive loss of the eyes in eodiscoids appears to be an example of convergent evolution with the Agnostina. This is not surprising when the functional significance of the similarity in size and overall morphology of the two groups is considered.

X. ZHANG (1989) recognized 13 instars of *Neocobboldia.* This species apparently underwent ecdysis more than once within some

meraspid degrees (perhaps three times as M0, termed metaprotaspides Mp0–Mp2 by X. Zhang). The number of ecdyses suggested by X. Zhang was based on the assumption that the linear dimensions of successive instars increase at a constant geometric rate for each species. While exceptions to this rule occur, particularly in association with radical metamorphoses, it applies in general among trilobites and among other arthropods (see earlier discussion of growth). Hunt (1967) certainly demonstrated that the nine instars of *Trinodus elspethi* increased in size by a nearly constant geometric ratio (1.21 to 1.25). The ratio used by X. Zhang (1.20) was close to that determined by Hunt. X. Zhang, however, was unable to distinguish instars as distinct size clusters. Both workers demonstrated that more than one instar may occur within the same meraspid degree in the Agnostida. The comparatively small number of instars, due to the early onset of maturity, apparently was a cause of the small size and low number of thoracic segments in the Agnostida.

ORDER REDLICHIIDA

Small growth stages of Redlichiida (Fig. 168.3–5, 169) usually have large eyes with well-developed ocular lobes that curve forward and inward to be adjacent to the glabella in the region of the frontal glabellar lobe, if distinguishable as a separate lobe. There is a short, complete anterior border and usually a very short or indistinct preglabellar field that lengthens in later meraspid stages. The rostral plate is wide (tr.), short (sag.), and curved to accommodate the curved anterior outline of the cephalon. Transverse segmentation of the glabella and even the fixed cheeks may be well developed in some taxa, which were regarded as primitive by Weller (1969).

Superfamily Redlichioidea

Protaspides have been described by Lu (1940), Kautsky (1945), Kobayashi and Kato (1951), W. Zhang, Lu, and others (1980), and Pillola (1991). *Strenuella* is

Fig. 169. Redlichiida, Olenellina. Small meraspid cranidia of *Olenellus clarki* (Resser) from the Combined Metals Bed of the Pioche Shale, Lower Cambrian, Lincoln County, Nevada (see Palmer, 1957); *1,* ventral view of BMNH It 21252, ×46; *2,* dorsal view of BMNH It 21253, ×45 (new; specimens courtesy of H. B. Whittington and A. R. Palmer).

usually classified in the Ellipsocephalidae, but Fortey (1990a, p. 549, 563) suggested that some ellipsocephalids should be included in the Ptychopariina. These are small and ovoid and are preserved in shales; little is known of their ventral morphology. The apparent lack of intergenal spines on most specimens may be a function of this mode of preservation, or it may have been their nature in life. Drawings by W. Zhang, Lu, and others (1980) do not show any intergenal spines, but such intergenal spines are apparently present in a meraspid degree 3 of *Redlichia chinensis* (see Kobayashi & Kato, 1951, fig. 2). Some of the protaspides of that

species illustrated by those authors have marginal spines, the anteriormost of which may be intergenal spines; and one specimen apparently has genal spines (KOBAYASHI & KATO, 1951, pl. 4, fig. 6). Some of these specimens were reassigned to *R. (Pteroredlichia) murakamii* by W. ZHANG, LU, and others (1980, pl. 26). KOBAYASHI and KATO (1951, pl. 4, fig. 1, 2, 11) included sagittal glabellar furrows in their drawings of some of the redlichioid protaspides. These were not, however, apparent in any of the drawings of redlichiid protaspides by W. ZHANG, LU, and others, despite the fact that one of the specimens upon which these furrows are based is reproduced in both works several times (KOBAYASHI & KATO, 1951, pl. 1, fig. 1, pl. 2, fig. 1, pl. 4, fig. 2; W. ZHANG, LU, & others, 1980, fig. 61.1, pl. 26, fig. 1). All workers appear to agree that transglabellar furrows are well developed in these protaspides.

Superfamily Paradoxidoidea

Paradoxidid protaspides (Fig. 168.4,5) have been described by BARRANDE (1852), RAYMOND (1914a), ŠUF (1926), WESTERGÅRD (1936), RŮŽIČKA (1943), WHITTINGTON (1957b), and ŠNAJDR (1958); and meraspides have been described by most of these workers and ŠNAJDR (1990). Most of the paradoxidid protaspides can be assigned to species of *Paradoxides* and others to *Hydrocephalus.*

Xystridurid protaspides (Fig. 168.4) have been described by ÖPIK (1975a); and meraspides were illustrated earlier by WHITEHOUSE (1939) and later by MCNAMARA (1981a, 1986a). Several features are shared with paradoxidid protaspides. These include a forwardly expanding glabella; long, sharply pointed intergenal spines; comparatively large and long ocular lobes that are adjacent to the anterior portion of the glabella anteriorly and separated from the glabella by a comparatively broad (tr.) fixigena posteriorly; and a complete, short anterior border. The genal spines are apparently located at the genal angle on the free cheeks of both groups. Some paradoxidid protaspides have

more expanded glabellas that are often subdivided by sagittal and transverse glabellar furrows to produce as many as eight separate glabellar lobes. These furrows are often reduced in number, with only a few of the lobes distinguishable. Early meraspid cranidia of these two groups are even more similar, except that S1 and S2 are usually complete medially in paradoxidids but not in *Xystridura.* Intergenal spines disappear from both groups at a stage early in the meraspid period. Preglabellar fields are very short to insignificant in protaspides and early meraspides but lengthen during the meraspid period to become well developed in both families. Distinct occipital rings are visible in all protaspid and meraspid cephala, and occipital nodes are usually present on meraspid cranidia and in some protaspid cranidia. Protopygidia and transitory pygidia are not particularly well known, but marginal spines are present. The axis is well developed, macropleural spines can be recognized on more anterior thoracic segments early in the ontogeny, and pleural furrows are distinct on more anterior segments.

The early growth stages of paradoxidids and xystridurids are similar enough to each other to justify their inclusion in the same superfamily and similar enough to those of the redlichioids to be included in the same order.

Superfamily Emuelloidea

POCOCK (1970) described the only known ontogenetic series of this group. Its members have dorsal facial sutures and a protaspis but like Olenellina, which lack these features, have a prothorax and opisthothorax and transverse furrows on the fixed cheeks of small meraspid cranidia.

The protaspis of *Balcoracania flindersi* (POCOCK, 1970, fig. 8) has a glabella and fixed cheeks with transverse furrows (SO, S1, S2, S3 on the glabella), a distinctly expanded frontal lobe that reaches the anterior margin, and a protopygidium that has an undifferentiated axis and is considerably shorter than the cranidium. His photographs and

drawings of early meraspid degrees are considerably more instructive (see Fig. 168.3). These have what can be interpreted as proparian facial sutures; medium-sized eyes near the midlength of the cranidium; distinct eye ridges running into the posterior half of the frontal lobe; transverse glabellar furrows (SO, S1, S2, S3 and S4); subtransverse fixigenal furrows that run outward and slightly backward; posterior border furrows on the cranidium that turn forward distally; genal spines on the free cheeks but no intergenal spines; and interpleural, axial, and ring furrows on the transitory pygidium. A short anterior border develops and increases slightly in length during the meraspid period. A sagittal furrow is not distinct but could be present in the frontal lobe of early meraspid cranidia. One of POCOCK's photographs (1970, pl. 110, fig. 2) could be interpreted as showing a very faint sagittal furrow, but no furrow was shown in his reconstruction of early meraspid cranidia. In his description of the earliest meraspid cranidia, he did mention (1970, p. 541) that the "frontal glabellar lobe is thus expanded to the anterior (although partially subdivided)." It is not clear whether this partial subdivision is longitudinal or transverse, although he noted earlier in his description that the frontal lobe is partially subdivided by an indistinct furrow aligned with the anterior edge of the eye ridge. The absence of an anterior border in the early cranidia of this superfamily, if real, is also unusual among primitive Lower Cambrian trilobites. The absence, however, could be only apparent and a function of the quality of preservation of POCOCK's material. Only one poorly preserved protaspis is illustrated in that work. A reexamination of POCOCK's material or collection of new, better-preserved specimens might resolve these problems.

Suborder Olenellina

Small growth stages of a number of Olenellina have been described, but none is an undoubted protaspid, although some small meraspid cranidia have been referred to as protaspides (e.g., WALCOTT, 1910; C. POULSEN, 1932; STØRMER, 1942; LOCHMAN, 1956; V. POULSEN, 1974). Workers who have described small meraspid stages of Olenellina include FORD (1877, 1881), WALCOTT (1886, 1910), KIAER (1917), C. POULSEN (1932), STØRMER (1942), RICCIO (1952), LOCHMAN (1952, 1956), WHITTINGTON (1957a, 1959b), PALMER (1957), HU (1971, 1985b), FRITZ (1972), and in this publication (Fig. 169). PALMER (1957, p. 106–107, fig. 1) discussed and illustrated a silicified, ontogenetic series of *Olenellus gilberti* and *Olenellus clarki* (Fig. 169). Despite the discovery of very small meraspid cranidia, he found no protaspides. The smallest meraspid cranidia are comparable morphologically to the specimens that have been called protaspides by earlier workers. Thus, there is reason to believe that growth stages equivalent to the protaspides of other trilobites may have been passed through as embryonic stages. Olenellina share with the Agnostina the lack of known protaspid stages, and they compete for a position as the sister group of all other trilobites (FORTEY & WHITTINGTON, 1989; FORTEY, 1990a; RAMSKÖLD & EDGECOMBE, 1991). An alternative hypothesis is that the protaspis is an acquired synapomorphy of advanced trilobites. If so, the absence of a protaspis in Olenellina and Agnostina is the result of these taxa having diverged from the rest of the trilobites before this feature was acquired.

Distinctive morphological features of early meraspid cephala of Olenellina include the following: (1) well-developed intergenal spines, which usually disappear in later stages; (2) an anterior border and a preglabellar field; (3) large ocular lobes that are greater than one-third the sagittal length of cranidium; (4) a distinct, often narrow (tr.), frontal lobe opposite, adjacent to, and sometimes continuous with the anterior parts of the ocular lobes; (5) small, marginal genal and precranidial spines; (6) three glabellar lobes between distinct frontal glabellar and occipital lobes; (7) a small occipital node; (8) interocular areas that may have

posterolaterally directed furrows that are often convex anterolaterally; and (9) hypostomes with numerous (usually 13) marginal spines, wide, transversely pointed anterior wings, distinct posteromedially directed middle furrows, and shallow posterior border furrows. The early thoracic segments are much narrower than the cephalon (see PALMER, 1957, pl. 19, fig. 3, 12), and macropleural spines are distinct in these early stages.

PALMER (1957, p. 126) discussed the sutures of Olenellina and commented that the "only suture whose presence is recognized by all workers with olenellid trilobites is the marginal or perrostral suture that separates the rostrum from the doublure." He also pointed out that the position of this suture does not appear to change during ontogeny (contra STØRMER, 1942). The anterior and posterior ocular lines (Fig. 16) observed in holaspid Olenellina were discussed in an earlier section on the patterns of facial sutures (p. 25).

ORDER CORYNEXOCHIDA, SUBORDER CORYNEXOCHINA

Protaspides of Corynexochina have been described by the authors listed below (see also Fig. 170.10–12).

Albertella	HU, 1985a
Bathyuriscus	ROBISON, 1967; ?FORTEY & CHATTERTON, 1988
Corynexochides	RASETTI, 1967
Fieldaspis	HU, 1985a
Fuchoia	ÖPIK, 1982; LU & QIAN, 1983
Glossopleura	HU, 1985b
Ptarmigania	HU, 1971

Protaspides of *Corynexochides* and *Bathyuriscus* are similar to those of other Corynexochina. This similarity of form supports the monophyly of the group that includes these two genera. ROBISON (1967) argued for a heterochronic origin of this order through paedomorphosis from the Ptychopariida. One of the important synapomorphies of corynexochines, the fused hypostomal suture, could be regarded as paedomorphic since this feature is often fused in early growth stages and functional in

later growth stages of other groups of trilobites. This suture remains fused throughout the life cycle of Corynexochina. We note, however, that in some taxa the hypostomal suture may be fused secondarily in later growth stages and free in early growth stages (e.g., the cheirurid *Hyrokybe,* see CHATTERTON & PERRY, 1984). The strong similarity between Corynexochina and Ptychopariina at all growth stages certainly supports common ancestry of these two taxa.

Distinctive features of protaspides of Corynexochina appear to include: (1) a widely (tr.) anteriorly expanded frontal lobe on the glabella; (2) a glabella that is very narrow, reaches the anterior margin, and is depressed slightly below the level of the cheeks immediately behind the anterior lobe (L3); (3) a pair of pits that deepens the axial furrows adjacent to the frontal lobes of the glabella, possibly for attachment of the rostral-hypostomal plate; (4) distinct anterolateral palpebral lobes that are almost continuous with the anterolateral extremities of the frontal glabellar lobe; (5) transglabellar furrows that are very shallow to indistinct; (6) a proparian facial suture; (7) a protopygidium that is downturned to even slightly curved anteroventrally, with short marginal spines; (8) small anterior, middle, and posterior fixigenal spines; (9) a rostral plate that is fused to the hypostome in all growth stages; and (10) a hypostome that has marginal spines in small protaspides, with the anteriormost pair being longer, posterolaterally directed, and quite close to the back of the hypostome.

At least two and probably more protaspid instars occur in the life cycle of Corynexochina. ROBISON (1967, fig. 2) showed that there is a considerable range in the size and morphology of protaspides of *Bathyuriscus fimbriatus*. A distinct increase in width occurred with the acquisition of a protopygidium. He suggested that at least four instars occurred within the protaspid period but was unable to distinguish biometrically or morphologically separate groups for the smallest instars. The two largest protaspid instars, which have protopygidia, are morphologi-
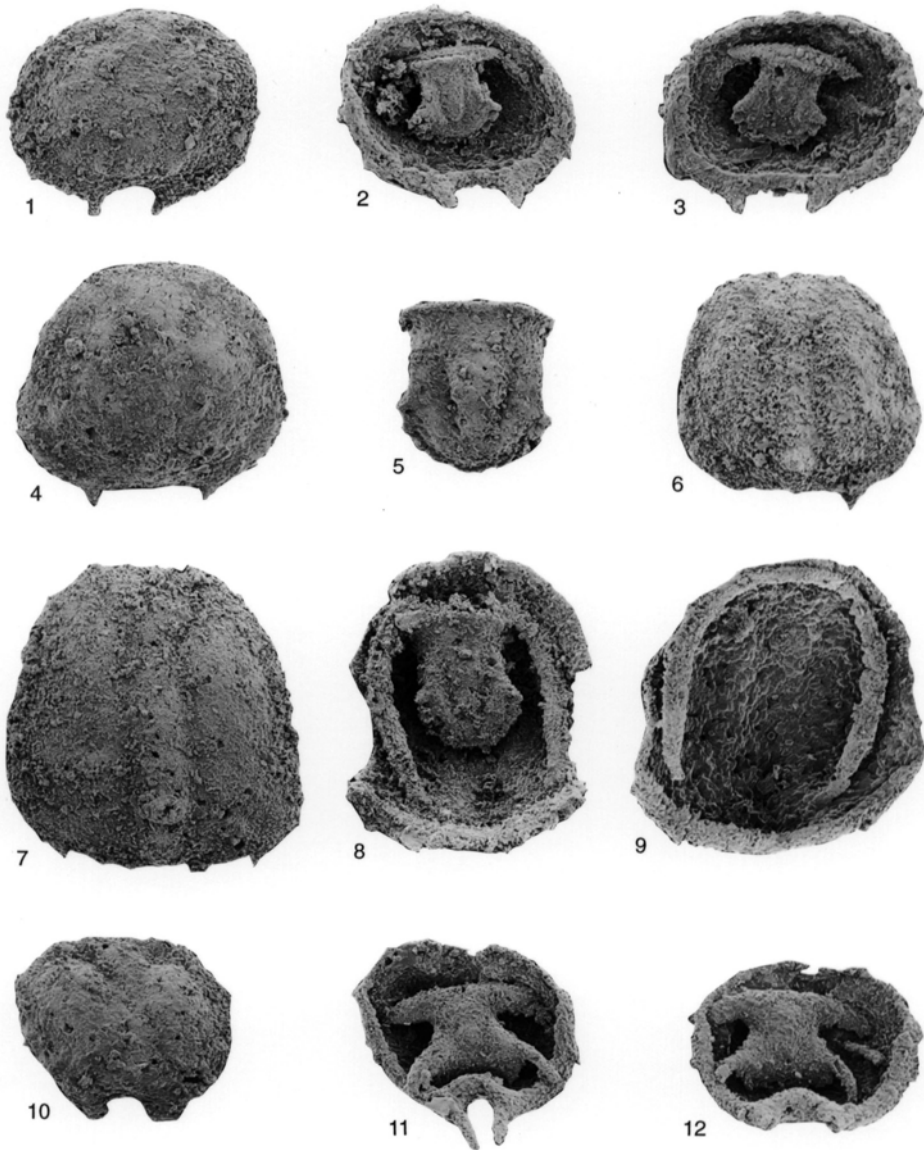
Fig. 170. Ptychopariina and Corynexochida from the Pika? Formation, Middle Cambrian, near Columbia Ice Fields, western Canada. *1–9,* Ptychoparioidea, *Spencella?* sp.; *1,* dorsal view of small protaspis, UA 8433, ×62.5 (new); *2,3,* ventral views of small protaspides (rostral plate and hypostome are attached in each case), UA 7751, 7752, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 9,10); *4,* dorsal view of second protaspid stage, UA 8434, ×62.5 (new); *5,* ventral view of small hypostome, UA 7757, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 19); *6,* dorsal view of second protaspid stage, UA 7754, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 13); *7,* dorsal view of largest protaspid stage, UA 7753, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 16); *8,* ventral view of broken largest protaspid stage (free cheeks and hypostome are attached), UA 7756, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 18); *9,* ventral view of largest protaspid stage (free cheeks and rostral plate are attached), UA 7755, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 17). *10–12,* Corynexochina, *Bathyuriscus* sp.; *10,* dorsal view of small protaspis, UA 8435, ×62.5 (new); *11,* ventral view of small protaspis (fused hypostome and rostral plate are attached to ventral surface, out of place), UA 7760, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 12); *12,* ventral view of small protaspis (note out-of-place attached fused hypostome and rostral plate), UA 8436, ×62.5 (new). [In Fortey & Chatterton (1988, pl. 17), the taxonomic names were inadvertently reversed in the plate explanation.]

cally and biometrically distinct and can be clearly distinguished from earlier growth stages.

ORDER CORYNEXOCHIDA, SUBORDER ILLAENINA

Protaspides have been described by the following authors (see also Fig. 171).

Breviscutellum	FEIST, 1970
Dentaloscutellum	CHATTERTON, 1971
Failleana	CHATTERTON, 1980; LUDVIGSEN & CHATTERTON, 1980
Illaenus	HU, 1976
Kosovopeltis	KÁCHA & ŠARÍČ, 1991
Nanillaenus	CHATTERTON, 1980
Raymondaspis	HU, 1974a
Scutellum	CHATTERTON, 1971

HU and CHATTERTON included protaspides separated by a distinct metamorphosis within the ontogeny of taxa within this suborder. We now believe this to be the rule rather than the exception for species in this suborder. That is, illaenids characteristically display a Type II life-history strategy. There is, however, some doubt as to which of the small, bulbous protaspides found associated with these trilobites actually belong in the growth series as premetamorphic growth stages.

There is little doubt as to the form of later, more adult-like protaspides of this group. They are very similar to meraspides and holaspides, and distinctly different forms can be recognized for styginids and illaenids. Adult-like styginid protaspides are comparatively large (about 1 mm long) and have a distinct cranidium and protopygidium. The glabella expands forward and may reach the anterior margin; an occipital spine or node is usually present; a pattern of paired tubercles or spines may be apparent on the glabella and fixed cheeks that is similar to those of some odontopleurids, lichids, and proetids; the facial suture is opisthoparian; the connective sutures are paired and functional; a posterior border on the cranidium is usually transversely directed but may turn forward distally; the palpebral lobes are large and near the midlength of the cranidium; the protopygidium is subdivided by shallow to indistinct pleural furrows into several seg-ments that terminate distally in tubular, pointed spines and has a distinctively shaped, slightly posterodorsally swollen and downturned posteromedian portion; the doublure is narrow and tightly incurved with a small number of terrace ridges and is usually slightly pinched posteromedially; the hypostome is subrectangular with the marginal spines short and bluntly tipped so that they appear more like a posterolateral border that is subdivided by four slits (Fig. 152.9–10). In this character, they are quite similar to the Lichida.

Illaenid adult-like protaspides differ from styginid adult-like protaspides in that the posterior border of the cranidium is usually turned backward distally; the posteromedian portion of the protopygidium is shaped differently with a strong median indentation and without posterodorsal inflation and downturning; and the marginal spines are more flattened in section and triangular (less tubular) in plan view. CHATTERTON (1980, pl. 3, fig. 17) illustrated a protaspid free cheek of *Nanillaenus* that has a distinct genal spine. Protaspid free cheeks are not known with certainty for any Illaenina, but we consider that they are probably similar in form (perhaps with more tubular genal spines, as shown by CHATTERTON, 1971, fig. 4a,b).

There is a greater problem as to the form of the earlier, premetamorphic larvae. HU (1976, pl. 28) assigned protaspides to *Illaenus valvulus* that we would assign to three different taxa, and only the most mature of these would we assign to that species. CHATTERTON (1980) assigned two very different protaspides to the illaenid *Failleana calva*.

Meraspides of Illaenina have been described by several workers, in addition to those listed above, including ŠNAJDR (1960) and WHITTINGTON and CAMPBELL (1967).

ORDER CORYNEXOCHIDA, SUBORDER LEIOSTEGIINA

HU (1970, 1971) described two protaspides of Leiostegiina: *Komaspidella* (Leiostegiidae) and *Missisquoia* (Missisquoiidae). More recently, several workers have assigned
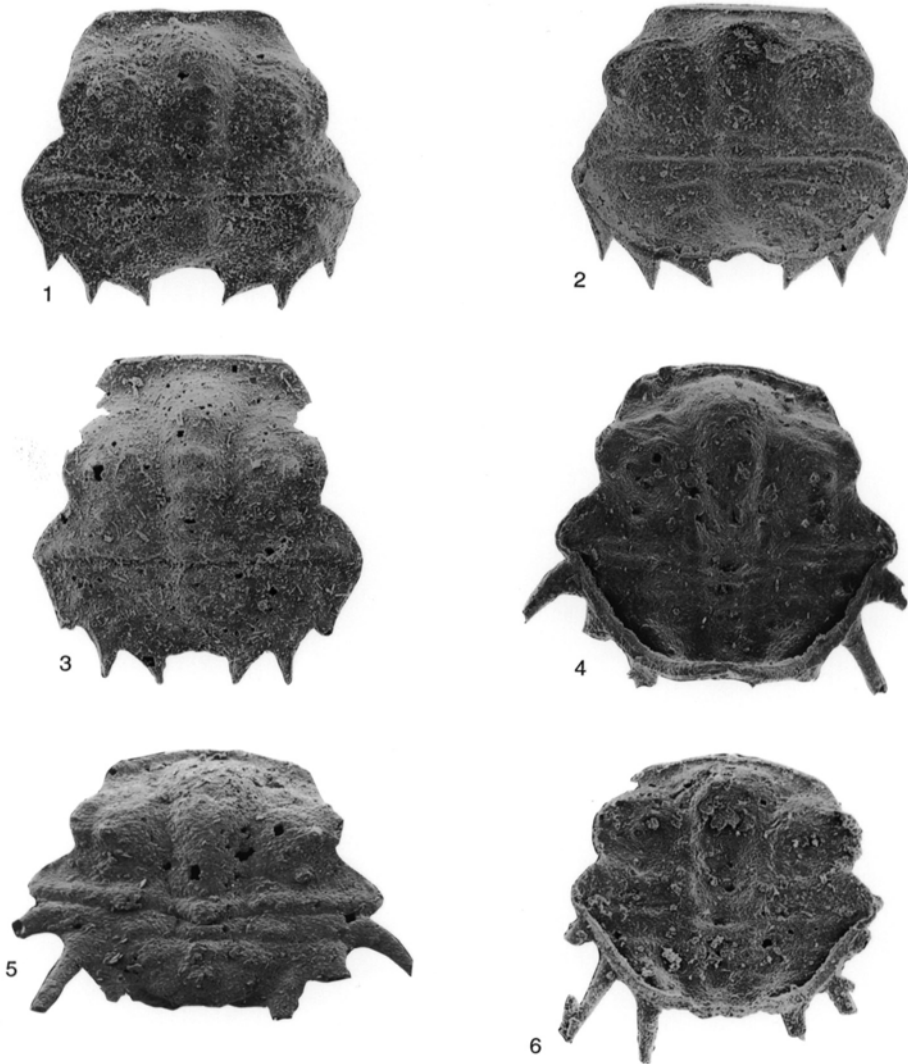
Fig. 171. Corynexochida, Illaenina. *1,2,* Dorsal and ventral views of an illaenid protaspis from the Crown Point Formation, Middle Ordovician, New York (locality PB 81), NYSM 16326, ×42.25; *3,* dorsal view of protaspis of *Bumastoides lenzi* CHATTERTON & PERRY from the lower Esbataottine Formation, northwestern Canada (locality P 17.2), UA 8437, ×50; *4–6,* Styginidae (*Kosovopeltis*? spp.) from the Wenlock Delorme Formation, northwestern Canada (locality AV4 126T); *4,5,* ventral and dorsal views of UA 8438, ×49; *6,* ventral view of UA 8439, ×49 (new).

Missisquoia to the Leiostegioidea, including SHERGOLD (1975), LUDVIGSEN (1982), and WESTROP (1986b). The protaspides of *Komaspidella* and *Missisquoia* are not very similar to one another. They are more similar to generalized protaspides of Ptychopariina than to those of Corynexochida, leading one to question why the Leiostegiina is included in the Corynexochida and not

the Ptychopariida. Certainly, the hypostome of neither of these taxa is fused to the rostral plate, one of the distinguishing features of corynexochids.

ORDER PTYCHOPARIIDA, SUBORDER PTYCHOPARIINA

The disparity between some of the protaspides included in this order reflects the

distant relationships among some of the taxa. Thus, the protaspides are dealt with here at the superfamily level so that larval characters of very different trilobites are not confused. The ontogenies of many ptychopariids include at least three or four different protaspid instars, and few of these are very well preserved or have been illustrated with scanning electron micrographs.

Superfamily Ptychoparioidea

Protaspides referred to genera and families mainly within the Ptychoparioidea have been described and are listed below (see also under Classification Uncertain below). [Phylacteridae LUDVIGSEN & WESTROP (in LUDVIGSEN, WESTROP, & KINDLE, 1989) is a senior synonym of Cliffiidae HOHENSEE (in HOHENSEE & STITT, 1989) by a few weeks.]

Cedariidae
   Cedaria   HU, 1971; HU & LI, 1971
   Cedarina   HU, 1971; HU & LI, 1971
   Paracedaria HU, 1971; HU & LI, 1971
Coosellidae
   Coosella   HU, 1968, 1978
   Nixonella   HU, 1972
Crepicephalidae
   Crepicephalus HU, 1971
   Syspacheilus HU, 1972
Elviniidae
   Elvinia   HU, 1979
   Irvingella   HU, 1979
Kingstoniidae (including the Shumardiidae)
   Kingstonia HU, 1968, 1986
   Shumardia STUBBLEFIELD, 1926
Lonchocephalidae
   Glaphyraspis PALMER, 1962b; HU & TAN, 1971
   Welleraspis RASETTI, 1954; HU, 1964b, 1968, 1969, 1978; HU & TAN, 1971
Norwoodiidae
   Hardyoides PALMER, 1962b
   Holcacephalus HU, 1978; HU & LI, 1971
   Norwoodella HU, 1963
Phylacteridae
   Aphelotaxon HU, 1980
   Cliffia   HU, 1979
Plethopeltidae
   Arapahoia   HU, 1986
Ptychopariidae
   Amecephalus HU, 1985b
   Chancia   HU, 1985b
   Crassifimbra PALMER, 1958
   Dunderbergia HU, 1971
   Ehmaniella HU, 1984, 1986; KOPASKA-MERKEL, 1981

   Kochina   HU, 1985b
   "Liostracus" BRÖGGER, 1875; MATTHEW, 1888, 1889 (reillustrated as *Ptychoparia*)
   Pachyaspis HU, 1986
   Piazella   HU, 1985b
Solenopleuridae
   Sao   BARRANDE, 1852; WHITTINGTON, 1957a; ŠNAJDR, 1990

FORTEY and RUSHTON (1980) illustrated meraspides for *Acanthopleurella* from degree 0 up, and FORTEY and OWENS (1991) illustrated those of *Shumardia*.

ÖPIK (1970a) described some meraspides of nepiid trilobites and described the origin of typically nepeiid characters during the meraspid period. Small meraspides of this group are for the most part similar to equivalent growth stages of other ptychoparoids.

Very small ptychoparioid protaspides (Fig. 170.1–3) are shaped like an inverted saucer, with weak axial furrows. A few taxa have a sagittal furrow, particularly behind the frontal lobe and dividing L2 and L3. The frontal lobe reaches the anterior margin; the posterior margin may be convex or slightly concave; the protopygidium is usually difficult or impossible to distinguish; transverse glabellar furrows are usually indistinct, except in those taxa with a sagittal furrow, forming two pairs of glabellar lobes behind the frontal lobe; a weak, bicrescentic posterior border may be present; a palpebral lobe or ridge runs for a short distance along the anterior margin from the anterior half of the frontal glabellar lobe; the fossula may be present at the junction between the posterior edge of the palpebral ridge and the glabella; and three pairs of small marginal spines are apparent in a few taxa (e.g., *Dunderbergia*, *Pachyaspis*, *Piazella*).

Later ptychoparioid protaspides (Fig. 170.4–9) lack a sagittal furrow and usually have very short, shallow, or indistinct glabellar furrows outlining an occipital lobe (LO) and four preoccipital lobes (L1, L2, L3, and the frontal lobe). The eye ridge is slightly behind the anterior margin; a posterior border of the cranidium turns forward distally and a protopygidium becomes distinguishable;

the glabella is usually semicylindrical with a slightly wider, rounded frontal lobe; one or more segments on the protopygidium may be delineated by interpleural furrows; pleural furrows are apparent in late larval stages of very few taxa; and marginal spines are usually blunt or absent, and restricted to the genal angles and protopygidial segments. Larval hypostomes, where known, are attached to the doublure (HU, 1971; FORTEY & CHATTERTON, 1988) and have spinose margins, which may be blunted in later protaspides. Because in adult ptychoparioids the hypostome was natant, it must have become detached from the doublure during later ontogeny. Details of the sculpture are poorly known, but granules and small, paired tubercles are present on the glabella and genae of some taxa. The glabellas of ptychoparioid protaspides do not have the degree of narrowing and depression in height just behind the frontal lobe that is characteristic of the glabella in protaspides of Corynexochina.

Similarities between some ptychoparioid protaspides with both adult-like and nonadult-like forms and those of other, later orders, Phacopida in particular, suggest that the paraphyletic Ptychopariida includes the ancestors of several other orders.

Superfamily Ellipsocephaloidea

Protaspides of the Ellipsocephalidae were described by KAUTSKY (1945, *Strenuella*). The form of the protaspis of this genus is in some ways as similar to those of Redlichiina as it is to some ptychoparioids. For instance, the sagittal subdivision of the frontal lobe of the glabella is found in the Redlichiina but absent in most ptychoparioids (with the exception of some Olenina; see below). The similarity between some of the small meraspid cranidia illustrated by KAUTSKY (pl. 16, fig. 4–5, 9) and those of a meraspid cranidium assigned to *Paradoxides* by RAYMOND (1914a) is striking. Differences, however, include an absence of glabellar furrows (except for an occipital furrow) behind the furrow that delineates the frontal lobe in *Strenuella.* Other close similarities of the protaspides of *Strenuella* are mainly with those of the Olenina.

ORDER PTYCHOPARIIDA, SUBORDER OLENINA

Protaspides of Olenina were described by the authors listed below (see also Fig. 172).

Acerocare	HU, 1971
Hedinaspis	TAYLOR, 1976
(Papyriaspididae)	
Highgatella	HU, 1971
Leptoplastus	WHITWORTH, 1970
Olenus	STRAND, 1927; HU, 1971;
	CLARKSON & TAYLOR, 1995
Parabolinella	LUDVIGSEN, 1982
Peltura	C. POULSEN, 1923; WHITTINGTON, 1958; HU, 1964a
Triarthrus	FORTEY, 1974b
(=*Bienvillia*)	

BEECHER (1893b) described a protaspis of *Triarthrus,* which is not very similar to the specimen described by FORTEY (1974b) of the same genus and is much more similar to those normally assigned to the Proetida (WHITTINGTON, 1957b and CHATTERTON, 1980, but not CISNE, 1973b). EDGECOMBE (personal communication, 1991) has found proetid meraspid cranidia associated with these protaspides that overlap in size with the smallest definite meraspides of *Triarthrus* so that BEECHER's specimen is almost certainly a proetid and not *Triarthrus.* WALCOTT (1879), WHITTINGTON (1957b), and CISNE (1973b) described a series of meraspid degrees of *Triarthrus* from New York. RAW (1925) described in detail meraspid to holaspid ontogeny for *Leptoplastus.* FORTEY (1974b) and WHITTINGTON (1965) also described meraspid stages of olenid trilobites.

Features shared by protaspides assigned to the Olenina include (1) well-developed, transverse glabellar furrows; (2) a transverse anterior margin without an anterior border or preglabellar field medially; (3) broad fixigenae; (4) a well-developed posterior border furrow on the cranidium that turns forward distally to delineate a lateral border extending into a sutural ridge anteriorly; (5) a weak eye ridge extending outward from
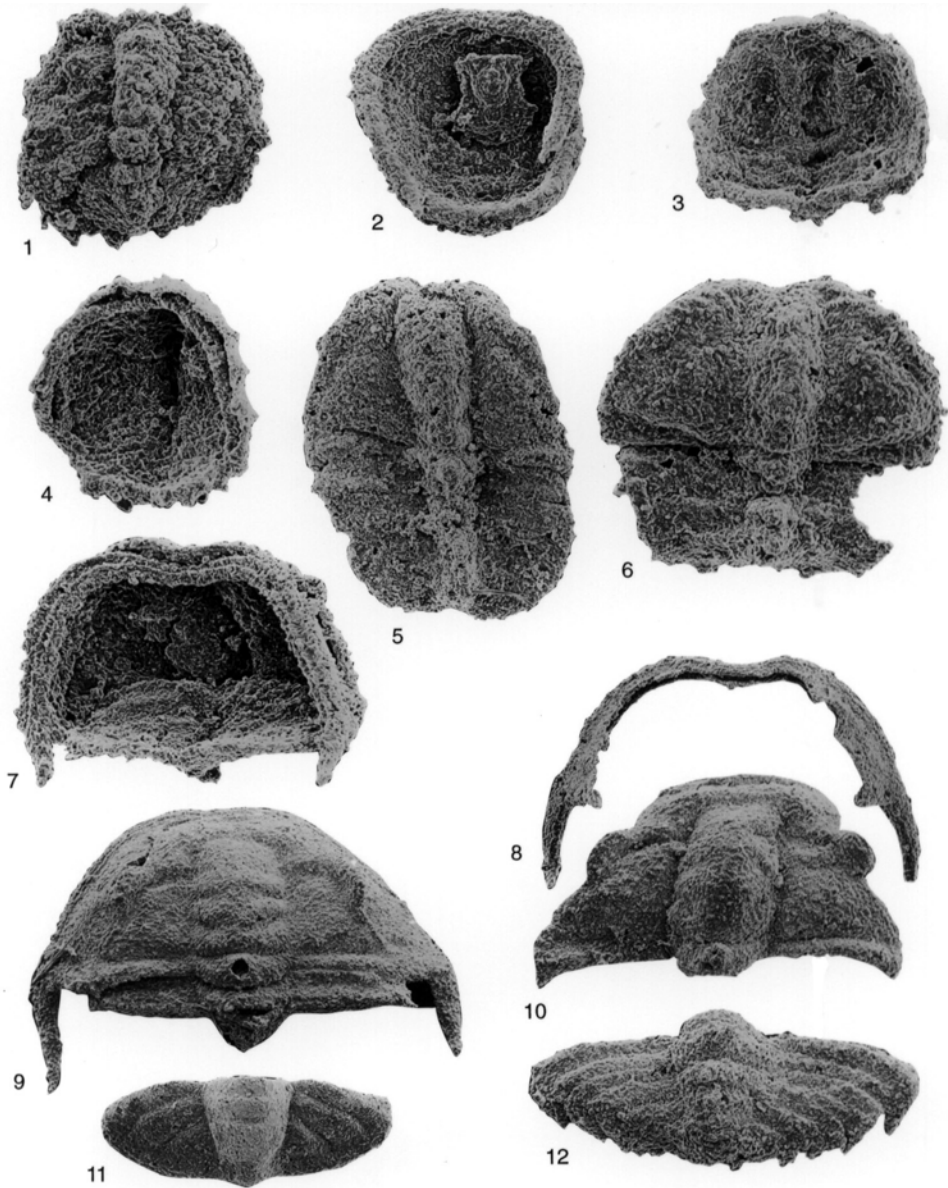
FIG. 172. Ptychopariida, Olenina. *Parabolinella panosa* LUDVIGSEN from the Rabbitkettle Formation, Lower Ordovician, northwestern Canada (locality KK113). We consider specimens assigned by LUDVIGSEN to *P.* cf. *P. prolata* ROBISON & PANTOJA-ALOR to be synonymous with *P. panosa*. *1,* Dorsal view of protaspis, UA 8440, ×65; *2,* ventral view of protaspis; note attached yoked free cheeks and hypostome, UA 8441, ×61; *3,* ventral view of protaspis, UA 8442, ×60; *4,* ventral view of protaspis; note attached but out-of-place yoked free cheeks, UA 8443, ×63; *5,* dorsal view of meraspid degree 1 with free cheeks missing, UA 8444, ×44; *6,* dorsal view of outstretched meraspid degree 0 with free cheeks missing, UA 8445, ×63; *7,* ventral view of meraspid degree 0? with free cheeks present but slightly out of place, UA 8446, ×62.5; *8,* dorsal view of yoked free cheeks, transitory pygidium and free cheeks attached but out of life position, UA 8447, ×32.5; *9,* dorsal view of small cephalon and attached thoracic segments, UA 8448, ×26.25; *10,* dorsal view of small cranidium, UA 8449, ×27.5; *11,* dorsal view of small pygidium, UA 8482, ×16; *12,* dorsal view of transitory pygidium, UA 8450, ×43 (new; specimens courtesy of R. Ludvigsen).

near the front of the frontal lobe; and (6) an initial, proparian facial suture.

Features that vary among the olenid protaspides include a sagittal glabellar furrow, which is present in L2 and L3 of the smallest protaspides of *Olenus* and *Acerocare* (Hu, 1971). A sagittal glabellar furrow occurs in the anterior part of the frontal lobe of some olenid early growth stages (*Olenus* in Strand, 1927; *Balnibarbi, Cloacaspis,* and *Hypermecaspis* in Fortey, 1974b) and may persist into more mature stages of some olenids (*Cloacaspis, Hypermecaspis,* and *Plicatolina* in Fortey, 1974b). Late protaspides or early meraspides may show pitting in the genae. Examples include protaspides of *Bienvillia* (Fortey, 1974b, personal communication, 1986); *Acerocare* (Hu, 1971); meraspides of *Peltura* (C. Poulsen, 1923; Whittington, 1958); and *Olenus* (Strand, 1927; Hu, 1971). The glabella may be barrel shaped, with the frontal lobe narrower than L3 (*Peltura, Leptoplastus, Acerocare*), or may expand very slightly forward and have a frontal lobe wider than L3 (*Olenus, Bienvillia*?). The facial suture usually changes from proparian to opisthoparian well into the meraspid period. The anterior border and preglabellar field that are so distinctive of mature olenid trilobites develop comparatively late in the ontogeny and appear only in the meraspid period. Genal spines are present at the posterolateral corners of the fixigenae in protaspid and early meraspid stages, and the genal spines were presumably transferred to the librigenae some time during the meraspid period, when the suture became opisthoparian.

The smallest stages of *Parabolinella* found with librigenae attached are protaspides (see Fig. 172). These specimens, which are not very well preserved, have cheeks already fused to one another. Their preservation is such that it is not clear whether the free cheeks have genal spines until the meraspid period. There is no doubt, however, that early meraspid cranidia (degree 0) of *Parabolinella* are opisthoparian and no longer have fixigenal spines.

Fortey (1974b, p. 40) discussed the usefulness of examining morphological similarity between early meraspid cranidia within the Olenidae. He was impressed by the differences shown within the family and concluded that "ontogenies are useful only in confirming relationships between closely related genera, for example within a single subfamily."

ORDER ASAPHIDA

Fortey and Chatterton (1988) described larval and adult stages of this group and noted that one of the more important synapomorphies is the presence of a median connective suture. Most taxa within this order also share a planktonic, nonadult-like protaspis (Fig. 148, 155); this type of protaspis was termed **asaphoid** by Fortey and Chatterton (1988, p. 178, fig. 9.1, 11.1–11, and 14). More primitive members of this order (Anomocaroidea) lack the asaphoid protaspides and have larvae that are very similar to those of the Ptychopariida.

Superfamily Anomocaroidea

The authors listed below have described protaspides of species of genera in the superfamily Anomocaroidea.

Aphelaspis	Palmer, 1962b; Hu, 1969, 1983; Hu & Tan, 1971
Dytremacephalus	Hu, 1971
Glyphaspis	Hu, 1971
Glyphopeltis	Hu, 1986
Housia	Hu, 1970
Parabolinoides	Hu, 1969, 1970, 1981
Taenicephalus	Hu, 1981

Anomocaroid protaspides are so similar to those of ptychoparioids that the rather general description of ptychoparioid protaspides provided above would serve equally well here. They are certainly more similar to ptychoparioid protaspides than they are to asaphoid protaspides, although shared characters are evidently primitive. The morphology suggests to us that the Anomocaroidea are more closely related to Ptychopariida than to Corynexochida, Redlichiida, or Agnostida. Classification of anomocaroids in

the Asaphida is based largely upon sharing a median connective suture. One interesting possible synapomorphy between anomocaroids and other Asaphida, however, is the discovery of a rostellum in some protaspides of *Lonchodomas* (see below). This feature was first described for the anomocaroid *Auritama* and the asaphid *Griphasaphus* by ÖPIK (1967, p. 60).

Connective sutures have been described for the early growth stages of few anomocaroids. PALMER (1962b, fig. 2.6) showed paired connective sutures in a small protaspis assigned to the pterocephaliid *Aphelaspis*. HU (1969, fig. 3.j) illustrated a hypostome and rostral plate that suggest a similar connective suture for an early growth stage of the same genus. This pattern is different from that found in asaphoid protaspides. However, FORTEY and CHATTERTON (1988) noted that the width of the rostral plate in relation to the hypostome may vary ontogenetically and phylogenetically. Recent work (CHATTERTON & others, 1994) on the raphiophorid *Lonchodomas* suggests that the asaphoid median connective suture may have originated through narrowing of the rostral plate and its reduction into a small triangular plate separating only the anterior parts of the free cheeks in some early growth stages (the rostellum of ÖPIK, 1967). In the trinucleoids, this small plate apparently became fused into the yoked cheeks, but in the later Asaphida it may have been further reduced in size finally to disappear and leave only a median connective suture.

Superfamilies with asaphoid protaspides?

Asaphoid protaspides have been described by the following authors (see also Fig. 144.3, 145.5, 146.3, 150.3–6, 151.1–5, 152.12, 173–174). HU's (1975a) taxonomic assignment of certain sclerites seems problematical.

Ampyx	WHITTINGTON, 1959a
Ampyxoides	FORTEY & CHATTERTON, 1988
Cryptolithus	WHITTINGTON, 1959a; FORTEY & CHATTERTON, 1988; CHATTERTON & others, 1994
Globampyx	FORTEY & CHATTERTON, 1988
Isotelus	EVITT, 1961; HU, 1975a; CHATTERTON, 1980; TRIPP & EVITT, 1986; SPEYER & CHATTERTON, 1989
Lonchodomas	SHAW, 1968; SPEYER & CHATTERTON, 1989; CHATTERTON & others, 1994
Menoparia	ROSS, 1951a
Remopleurides	WHITTINGTON, 1959a; HU, 1975a; CHATTERTON, 1980; FORTEY & CHATTERTON, 1988; SPEYER & CHATTERTON, 1989
Tretaspis	WHITTINGTON, 1959a; HU, 1975a
asaphid protaspis	WHITTINGTON, 1965
possible Asaphidae	DEMETER, 1973
nileid	FORTEY & CHATTERTON, 1988

These planktonic, asaphoid protaspides are spherical to ovoid, with up to three main pairs of submarginal spines. The doublure is curved inward in a continuous fashion with the dorsal exoskeleton or is very narrow and inturned. The hypostome is large and has up to nine marginal spines that are usually long and sharply conical. The connective suture is fused or median, and the rostral plate is either absent or a small anterior rostellum is present. There is no obvious preglabellar field or anterior border medially.

FORTEY and CHATTERTON (1988) included the Trinucleoidea in the Asaphida on the basis of both larval and adult characters. A metamorphosis took place between these planktonic juvenile stages and more mature, usually benthic, stages (see Fig. 154, 173, 174). This metamorphosis typically took place between the protaspid and meraspid periods. In some remopleuridids, however, it took place later during the meraspid period (Fig. 158). FORTEY (1985) suggested that adults of some remopleuridids may have been pelagic. The metamorphosis might have been delayed or not have been as extreme in taxa with pelagic adults. Meraspides of trinucleoids were described by RUSHTON and HUGHES (1981).

HU (1975a) clearly disagreed with WHITTINGTON (1959a) in the assignment of protaspides and early meraspides of *Remo-*
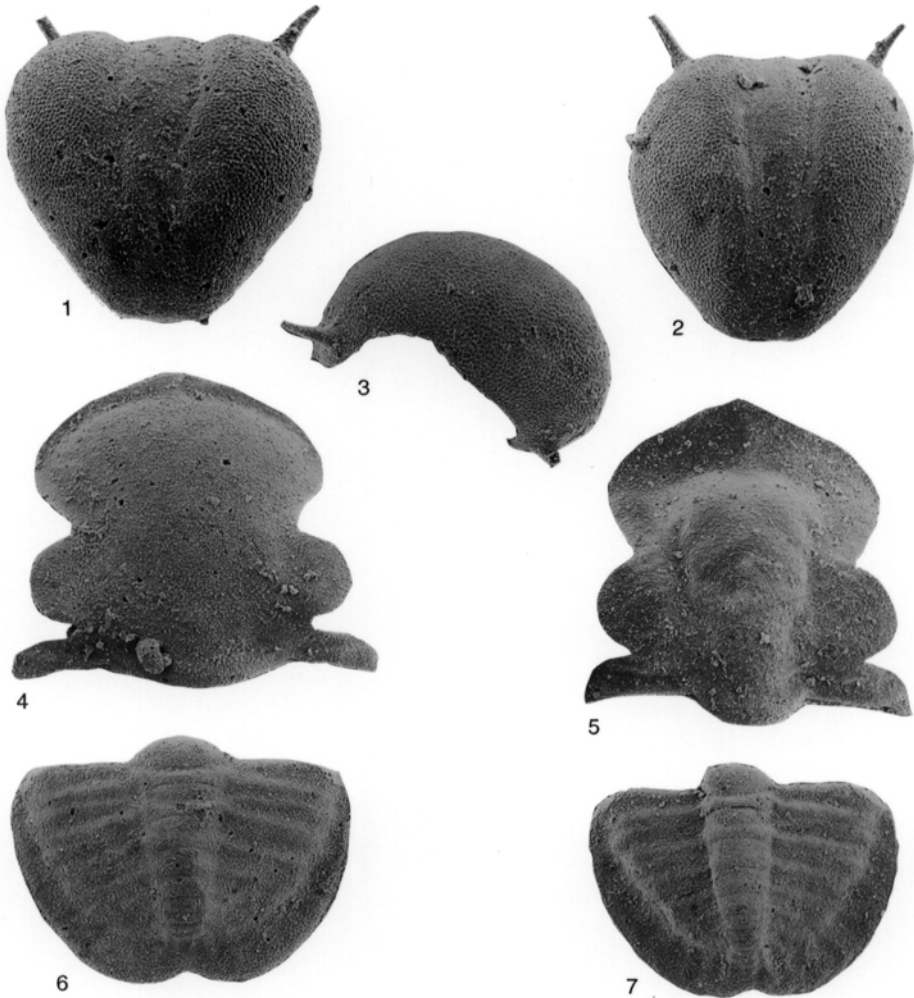
FIG. 173. Asaphida, Asaphidae. All specimens of *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York (locality PB 81). *1–3,* Dorsal and lateral views of large protaspid stage, NYSM 16327–16329, ×45; *4,* cranidium, NYSM 16330, ×19; *5,* dorsal view of small cranidium, NYSM 16331, ×31.25; *6,7,* dorsal views of transitory pygidia; *6,* NYSM 16332, ×31.25; *7,* NYSM 16333, ×32 (new).

pleurides and *Isotelus*. Later workers, however, have supported WHITTINGTON's earlier work rather than HU's assignment of the protaspides to *Isotelus* (HU appears to have included protaspides of *Tretaspis* and protaspides and meraspides of *Remopleurides* in this genus). CHATTERTON (1980), however, assigned protaspides very similar to some of those assigned by HU (1975a, pl. 2, fig. 3–4, 6–7, 12–13) to *Remopleurides caelatus* to *Remopleurides pattersoni.*

Meraspides of Asaphida have been illustrated by the following workers.

Illaenopsis	FORTEY & OWENS, 1987
Isotelus	CHATTERTON, 1980; LUDVIGSEN, 1979a
Nobiliasaphus	KŘÍŽ & PEK, 1974
Parabarrandia	ŠNAJDR, 1975, 1990
Pseudogygites	LUDVIGSEN, 1979a
nileid meraspides	FORTEY & CHATTERTON, 1988

Nileid meraspides are unusually large, following large protaspid stages (FORTEY &
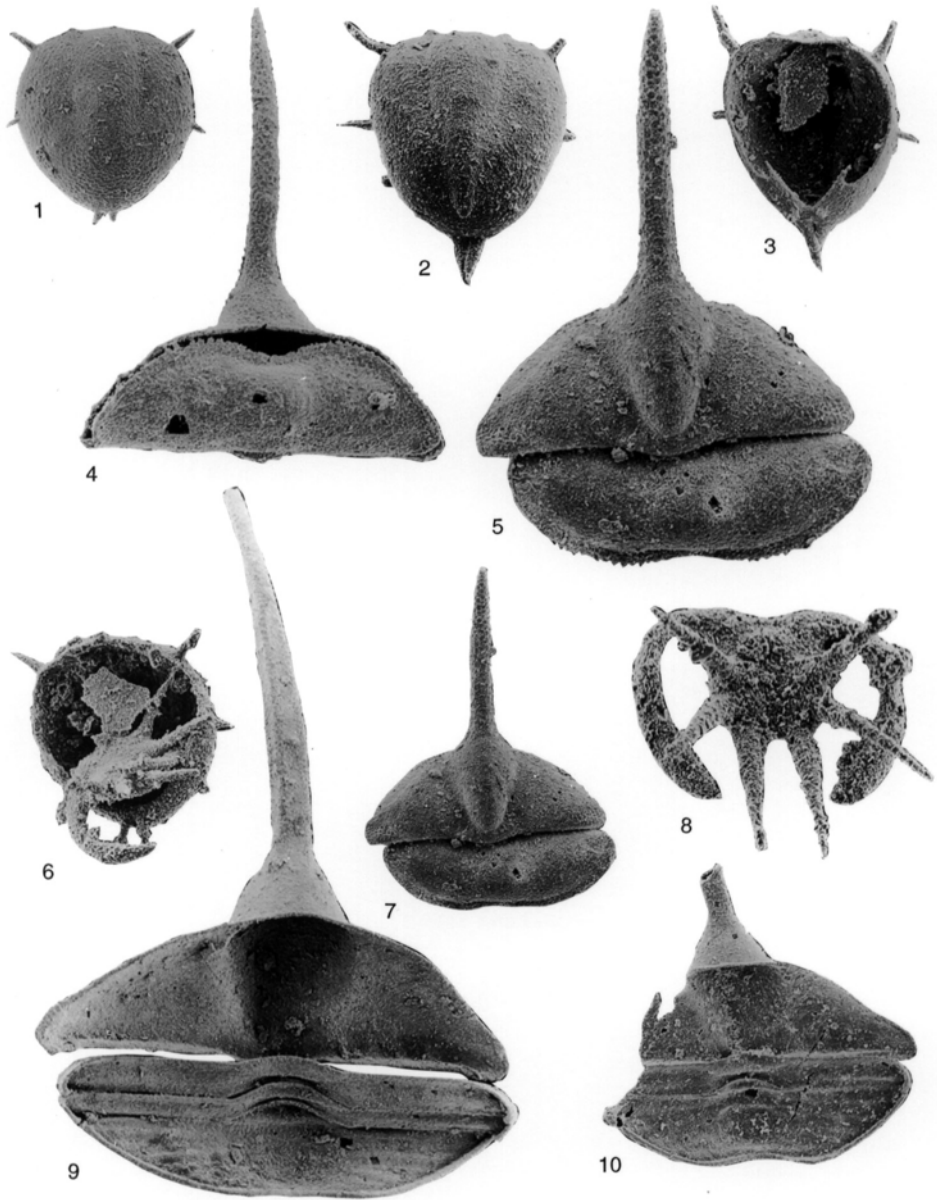
FIG. 174. Asaphida, Raphiophoridae. All specimens are of *Lonchodomas* spp. from the Crown Point Formation, Middle Ordovician, New York (locality PB 81). *1,* Dorsal view of protaspis type P1, NYSM 16334, ×62.5; *2,* dorsal view of protaspis type P2, NYSM 16335, ×62.5; *3,* ventral view of protaspis type P2, NYSM 16020, ×62.5; *4,* external view of enrolled meraspid degree 0, NYSM 16336, ×58; *5,7,* dorsal view of meraspid degree 0, NYSM 16337; *5,* ×58, *7,* ×38; *6,* ventral view of small protaspid stage; note attached, out-of-place fused cheeks and hypostome, NYSM 16338, ×62.5; *8,* ventral view of fused free cheeks and hypostome of small protaspid stage, NYSM 16339, ×90; *9,* ventral view of meraspid degree 2, NYSM 16340, ×39; *10,* ventral view of meraspid degree 1, USNM 16341, ×40 (new).

CHATTERTON, 1988), compared to those of most other trilobites. Meraspides of *Para-*

bandia illustrated by ŠNAJDR (1975, 1990) are very large (M1 = 7.5 mm for *P. crassa*),

and the meraspid pygidium of *Illaenopsis* (FORTEY & OWENS, 1987, fig. 69) is the largest transitory pygidium known (approximately 18 mm wide). This may have resulted from a heterochronic pattern involved in the evolution of the Nileidae (perhaps post-displacement). A M0 meraspid, 3.8 mm long, that was illustrated by ŠNAJDR (1990, p. 45) and assigned to *Zbirovia arata* is more similar to nileid meraspides than it is to illaenid meraspides.

ORDER PHACOPIDA

WHITTINGTON (1954c) first suggested the grouping together of a number of higher taxa now included in the Phacopida on the basis of their larval characters. This suggestion was followed by HARRINGTON, MOORE, and STUBBLEFIELD (1959). CHATTERTON and others (1990), using cladistic methodology and morphological data from protaspides, found evidence for monophyly of the Calymenoidea and the Phacopina.

Suborder Phacopina

Protaspides of Phacopina have been described by the authors listed below (see also Fig. 175).

Calyptaulax annulata	SHAW, 1968; SPEYER & CHATTERTON, 1989
Calyptaulax callirachis	CHATTERTON, 1980
Calyptaulax strasburgensis	HU, 1971
Dalmanites puticulifrons	WHITTINGTON & CAMPBELL, 1967
Dalmanitina	ŠNAJDR, 1990
Dalmanitina olini	TEMPLE, 1952
Dalmanitina socialis	BARRANDE, 1852; WHITTINGTON, 1956a

CHATTERTON (1971) assigned a nonadult-like protaspid to *Phacops*. We now believe that this larva should, perhaps, be assigned to the suborder Illuaenina.

Meraspid to holaspid Phacopina were described by the following authors.

Acernaspis	RAMSKÖLD, 1988
Dalmanitina	ŠNAJDR, 1990
Dalmanitina nanchangensis	LU & WU, 1983
Phacops	JAHNKE, 1969; CHATTERTON, 1971; H. ALBERTI, 1972

Trimerocephalus OSMÓLSKA, 1963

Distinctive characters of protaspides of Phacopina include (1) the highly arched (tr.) form of smaller protaspides; (2) proparian sutures; (3) eye lobes that are far forward; (4) a glabella that widens anteriorly; (5) up to four transglabellar furrows, including occipital ones; (6) fixigenae that may be pitted; (7) a short anterior border that is present medially; (8) marginal spines that are present on genae and that may splay out laterally in a radial arrangement; (9) an occipital node; (10) paired spines that are present on the anterior border and may also occur on glabella and genae; (11) a distinct, posterior marginal cephalic furrow and posterior cephalic border that are present in larger protaspides; (12) sharp, tubular marginal spines in the protopygidium; (13) paired spines that may be visible on axial rings of protopygidium; and (14) an incurled, narrow doublure that may have fine terrace ridges. Marginal spines on the cephalon may be restricted to a small pair of anterior fixigenal spines (next to the eye lobes) and a large pair of posterior fixigenal spines.

Suborder Cheirurina

Protaspides of Cheirurina have been described by the following workers (see also Fig. 176–178).

Acanthoparypha	WHITTINGTON & EVITT, 1954; WHITTINGTON, 1959b; HU, 1974b (*non Ceraurinella*); CHATTERTON, 1980
Balizoma	EDGECOMBE, SPEYER, & CHATTERTON, 1988
Ceraurinella	CHATTERTON, 1980
Cromus	EDGECOMBE & CHATTERTON, 1992
Cybeloides	EVITT & TRIPP, 1977; CHATTERTON, 1980; FORTEY & CHATTERTON, 1988
Cybelurus	FORTEY & MORRIS, 1978
Deiphon	CHATTERTON & PERRY, 1984
Encrinuroides	HU, 1975b (assigned to *"Otarion trilobus"*); EVITT & TRIPP, 1977; CHATTERTON, 1980; EDGECOMBE, SPEYER, & CHATTERTON, 1988
Hadromeros	CHATTERTON & PERRY, 1984
Heliomeroides	CHATTERTON, 1980
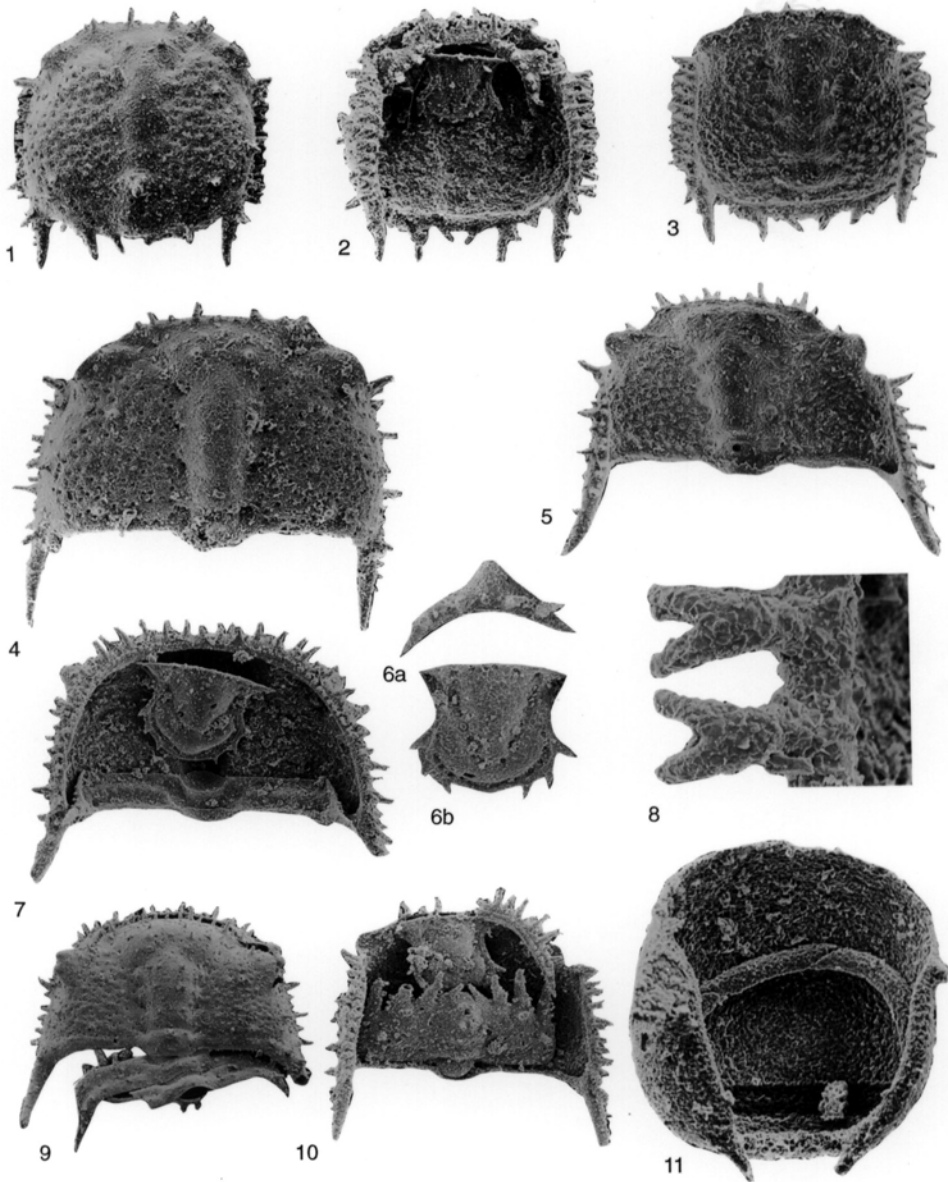
Fig. 175. Phacopida, Pterygometopidae. All specimens are of *Calyptaulax annulata* (Raymond) from the Crown Point Formation, Middle Ordovician, New York (locality PB 81); *1–3,* examples of large protaspid; *1,* dorsal view, NYSM 16342, ×62.5; *2,* ventral view; note attached free cheeks, hypostome, and rostral plate, USNM 16343, ×62.5; *3,* ventral view, example lacking free cheeks, rostral plate, and hypostome, NYSM 16344, ×65; *4,* dorsal view of small meraspid cranidium, NYSM 16345, ×67.5; *5,* ventral view of small cranidium, NYSM 16346, ×48; *6,* lateral view of free cheek (*6a*) and ventral view of hypostome (*6b*) of same larger protaspis, NYSM 16347, ×103; *7,* ventral view of cephalon with attached hypostome and thoracic segment, NYSM 16348, ×46; *8,* detail of ventral cephalic margin of larger protaspis, NYSM 16349, ×500; *9,* dorsal view of enrolled meraspid, degree uncertain, NYSM 16350, ×31; *10,* ventral view of enrolled meraspid degree 0, NYSM 16351, ×49; *11,* ventral view of smaller protaspid stage; note free cheeks and rostral plate attached to ventral surface, NYSM 16352, ×125 (new).
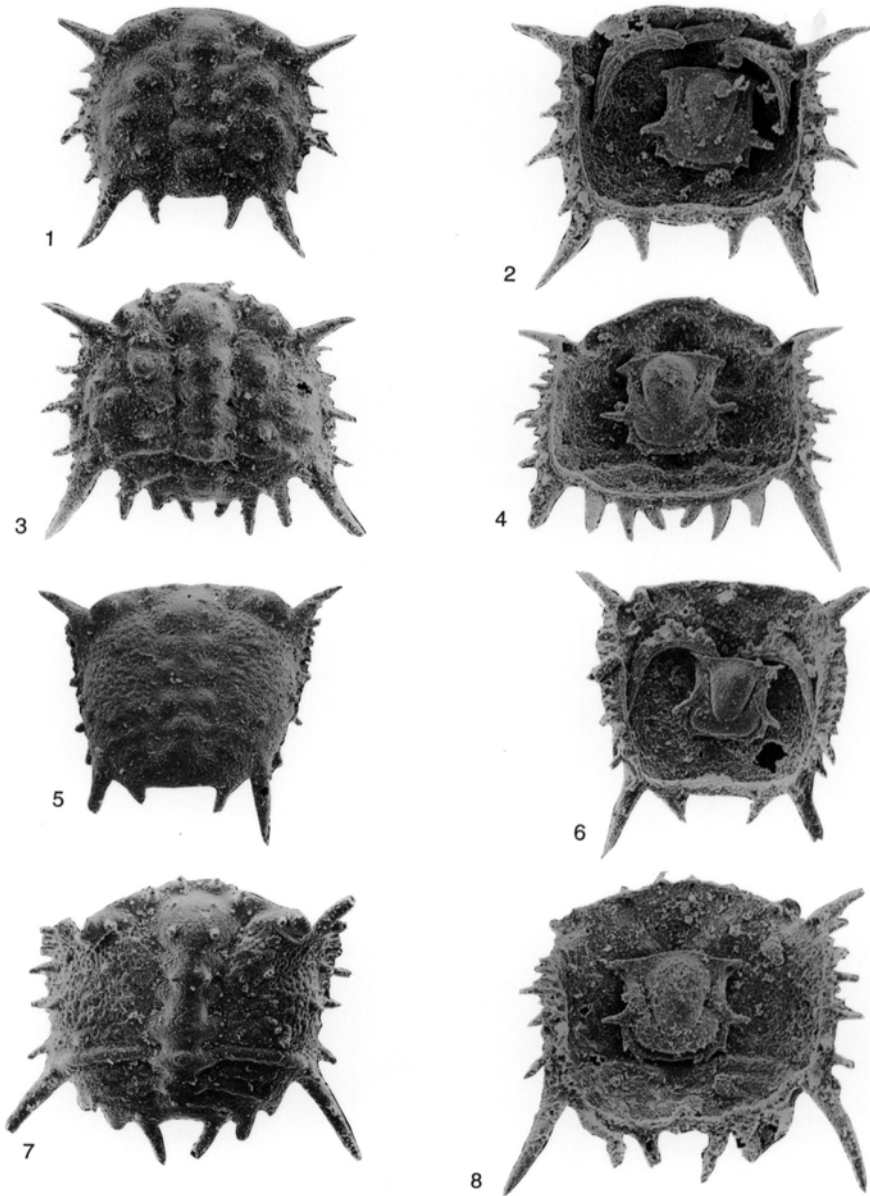
FIG. 176. Phacopida, Encrinuridae. All specimens from the Crown Point Formation, Middle Ordovician, New York (locality PB81). *1–4,* Protaspides of *Physemataspis insularis* SHAW; *1,2,* dorsal and ventral views of small protaspid stage; note attached hypostome, rostral plate, and free cheeks; *1,* NYSM 16353, ×63.5; *2,* NYSM 16354, ×74; *3,4,* dorsal and ventral views of larger protaspid stage; note attached hypostome; *3,* NYSM 16355, ×55.5; *4,* NYSM 16356, ×55.5 (new). *5–8, Cybeloides prima* (RAYMOND); *5,6,* dorsal and ventral views of small protaspid stage; note attached hypostome and free cheeks; *5,* NYSM 16357, ×62.5; *6,* NYSM 16358, ×62.5; *7, 8,* dorsal and ventral views of larger protaspid stage; *7,* NYSM 16359, ×60; *8,* NYSM 16360, ×62.5 (new).

Holia	CHATTERTON, 1980
Hyrokybe	CHATTERTON & PERRY, 1984
Libertella	HU, 1971; EVITT & TRIPP, 1977
Lyrapyge	FORTEY & MORRIS, 1978
Mackenziurus	EDGECOMBE & CHATTERTON, 1990a
Perryus	EDGECOMBE, SPEYER, & CHATTERTON, 1988 (=*Cromus*)
Physemataspis	EDGECOMBE, SPEYER, & CHATTERTON, 1988 (=*Encrinuroides insularis*)
Pseudocybele	ROSS, 1951a; WHITTINGTON, 1959b; FORTEY & CHATTERTON, 1988
Rossaspis	ROSS, 1951b (=*Protopliomerops*)
Sphaerexochus	?CHATTERTON, 1980; CHATTERTON & PERRY, 1984

EDGECOMBE, SPEYER, and CHATTERTON (1988) redescribed and discussed most known encrinurid larval stages. An important autapomorphy of this group is the presence of IV-1 and V-1 glabellar tubercles. Midfixigenal spines are apparent in early encrinurid larvae but are usually indistinguishable on later growth stages.

Larvae of Cheirurina may be divided into early and late stages. The early stages may have the glabella partly divided sagittally into two pairs of lobes behind an undivided frontal lobe, a plesiomorphic trait shared with some Ptychopariina, Redlichiina, and Calymenina. The later protaspides, without the paired glabellar lobes, are usually characterized by the following features: a proparian facial suture; eye lobes present anterolaterally; a narrow anterior border sagittally; a glabella that expands slightly forward and may be subdivided by a distinct occipital furrow and up to three glabellar furrows that are distinct laterally and usually indistinct medially; pitted genae; large anterior and posterior fixigenal spines and slightly smaller midfixigenal spines; a narrow, incurled doublure with a small number of terrace lines; prominent, sharp tubular marginal spines on the protopygidium; paired tubercles or short spines that may be present on the axis and genae; a distinct marginal furrow and posterior border usually delineating the junction between the protopygidium and the cranidium; three pairs of marginal spines occurring posterolaterally on the shield-shaped hypostome, which is usually pitted; a sculpture that usually consists of pits but may also include small tubercles; and a rostral plate that is separate and transversely widened.

Suborder Calymenina

Protaspides of this suborder have been described by workers listed below (see also Fig. 179).

Apocalymene	CHATTERTON, 1971 (only largest of three protaspides belongs to this genus)
Brongniartella	CHATTERTON & others, 1990
Calymene	CHATTERTON & others, 1990
Flexicalymene	HU, 1971; CHATTERTON & others, 1990
Platycoryphe	LU & WU, 1982
phacopoid	WHITTINGTON, 1957b

SIVETER (1983) provided some information on allometric growth of meraspid and holaspid stages of a species of *Calymene.*

Nonadult-like protaspides (Fig. 179.1–2,11) assigned to the Calymenina are characterized by (1) a globular-quadrate form; (2) a fused rostral-hypostomal plate that lies under much of the ventral surface and has sharply pointed marginal spines (usually nine, but the number may be lower and varies intraspecifically, always with a posteromedial spine); (3) three pairs of prominent, sharp, conical submarginal cranidial spines (anterior, middle, and posterior fixigenal spines); (4) a pair of palpebral lobes adjacent to the glabella running along the anterior margin; and (5) a glabella composed of an undivided frontal lobe that extends to the anterior margin, there being no anterior border, two pairs of glabellar lobes separated by sagittal and transverse glabellar furrows, and an occipital lobe that is not obviously separated from any possible protopygidial axis that may be present. The outline of the glabella is barrel-shaped, and it is narrowest toward the back of the frontal lobe.

Adult-like protaspides succeed nonadult-like larvae in some Calymenina (Fig. 179.3–4). In the adult-like protaspides, the exoskeleton remains fairly strongly arched (tr.);
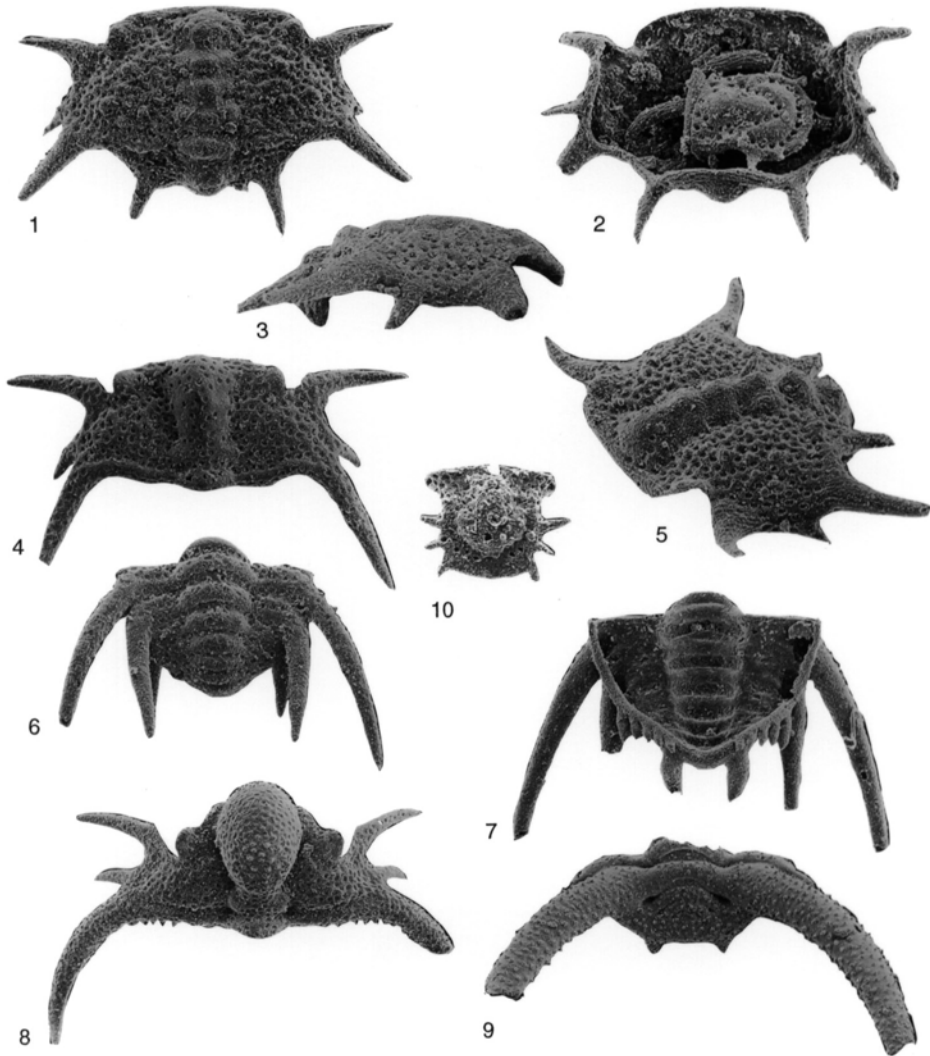
FIG. 177. Phacopida, Cheiruridae. *1–9, Sphaerocoryphe* sp. from the Crown Point Formation, Middle Ordovician, New York (locality PB 81); *1,* dorsal view of protaspis, NYSM 16361, ×47.5; *2,* ventral view of protaspis, NYSM 16362, ×50; *3,* lateral view of protaspis, NYSM 16027, ×65; *4,* dorsal view of small meraspid cranidium, NYSM 16363, ×36.5; *5,* anterodorsolateral view of protaspis, NYSM 16364, ×57.25; *6,* dorsal view of transitory pygidium, NYSM 16365, ×36.5; *7,* ventral view of transitory pygidium with six unreleased protothoracic segments, NYSM 16366, ×36.5; *8,* dorsal view of small cranidium, NYSM 16367, ×25.5; *9,* dorsal view of pygidium, NYSM 16368, ×19. *10, Deiphon* sp. from the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T), ventral view of hypostome, UA 8451, ×47 (new).

the sagittal glabellar furrows have disappeared and the glabella is semicylindrical; the hypostomal suture is functional; the marginal spines of the hypostome are shorter and the median spine is lost; fine marginal spines appear on the anterior border, rostral plate, and cheeks, and the submarginal spines of earlier stages (particularly the anterior and midfixigenal spines) are relatively less prominent; an occipital ring with a tubercle is distinguishable from more anterior parts of the glabella and a protopygidial axis; the eyes are
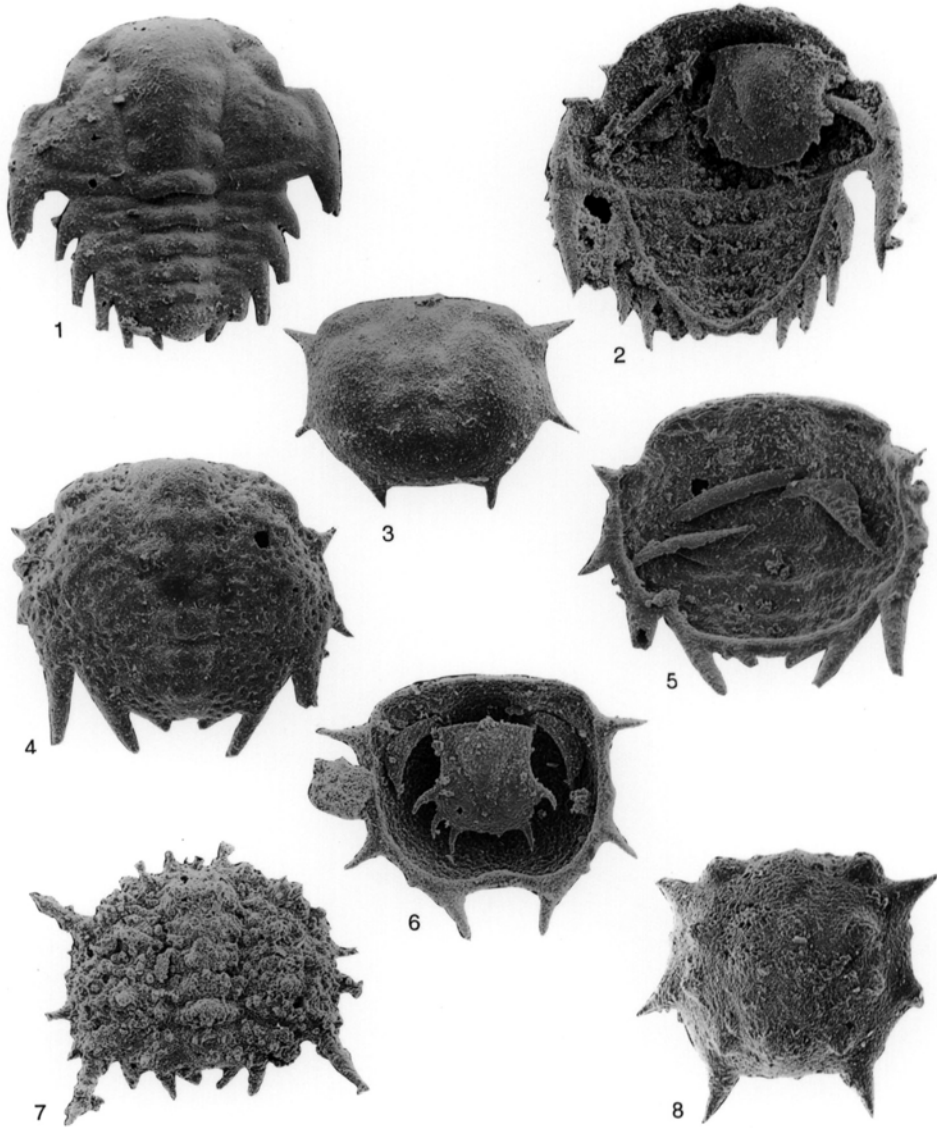
Fig. 178. Phacopida. *1–6,* From the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1,2,* dorsal and ventral views of large protaspides of *Ceraurinella latipyga*? Shaw, Cheiruridae; note attached free cheeks and hypostome; *1,* NYSM 16369, ×39; *2,* NYSM 16370, ×42; *4,5,* dorsal and ventral views of small cheirurid protaspides (possibly *Acanthoparypha* or *Ceraurinella*); note presence of hypostome and free cheeks; *4,* NYSM 16371, ×61; *5,* NYSM 16372, ×75; *3, 6,* dorsal and ventral views of smaller protaspis of *Ceraurinella latipyga?,* NYSM 16373, ×62 (new). *7,8,* From the Wenlock Delorme Formation, northwestern Canada (locality AV4 126T); *7,* dorsal view of protaspis of *Balizoma* sp., Encrinuridae, UA 7826; *8,* dorsal view of small protaspis of *Hyrokybe* sp., Cheiruridae, UA 8452, ×47 (new).

comparatively far forward and opposite the frontal lobe of the glabella; an eye ridge is separated from the anterior margin by a short anterior border; a protopygidium is large and distinct, with marginal spines (two in more mature specimens) at the distal ends of the segments; paired tubercles are visible on the fixed cheeks and sometimes on the glabella; three pairs of glabellar furrows are present as shallow marginal indentations;
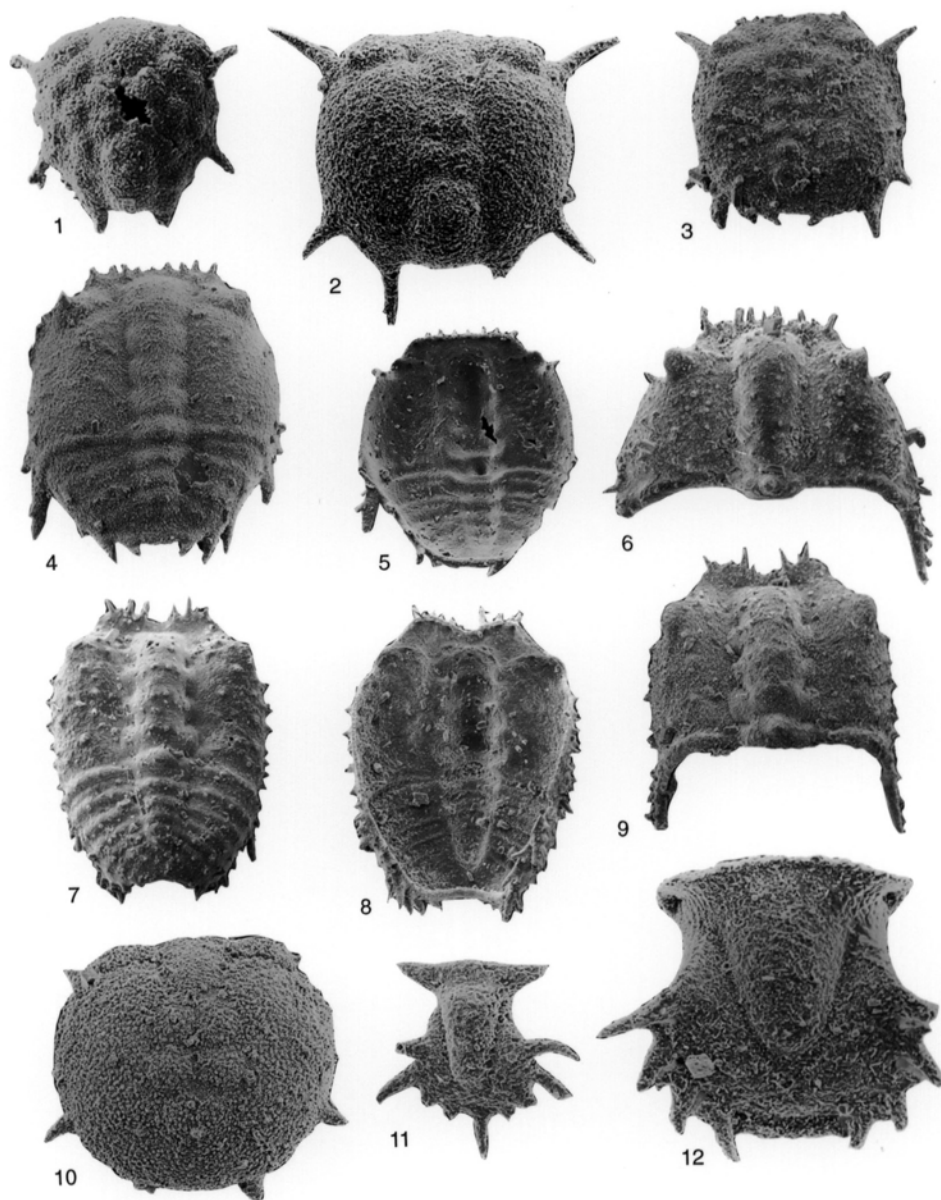
Fig. 179. Phacopida. Protaspides of species in this order may (life-history strategy II) be planktonic (P1, P2) in early stages, benthic in later stages (B1, B2); see CHATTERTON and others (1990, p. 257) for this terminology. *1–4, 11, 12, Flexicalymene senaria* (CONRAD), Calymenidae, from the Martinsburg Formation, Middle Ordovician, Virginia; *1,* dorsal view of smallest protaspis (P1), AMNH 43943, ×75; *2,* dorsal view of second protaspid stage (P2), AMNH 43938, ×75; *3,* dorsal view of third protaspid stage (B1), NYSM 16374, ×41.7; *4,* dorsal view of fourth protaspid stage (B2), NYSM 16375, ×42.5; *11,* ventral view of fused hypostome and rostral plate from last pelagic protaspid stage (P2), AMNH 43939, ×63; *12,* ventral view of small hypostome from benthic protaspid stage, AMNH 43942, ×130 (new). *5,6, Calymene* sp., Calymenidae, from the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T); *5,* ventral view of last protaspid stage (B2), UA 7928, ×33.5; *6,* dorsal view of small cranidium, UA 8453, ×34 (new). *7–9, Brongniartella* sp., Homalonotidae, from the Martinsburg Formation, Middle Ordovician, Virginia; *7,* dorsal view of protaspis (B2), AMNH 43960, ×31.4; *8,* ventral view of protaspis (B2), AMNH 43961, ×31.4; *9,* dorsal view of small cranidium, NYSM 16376, ×29 (new). *10, Apocalymene quadrilobata* (CHATTERTON), Calymenidae, from the Emsian *Receptaculites* Limestone of New South Wales, Australia; dorsal view of protaspis, UA 8454, ×36.8 (new).

and the doublure is narrow, curved inward, and without obvious terrace ridges.

Meraspides of Calymenina have been described by a number of workers (for details, see CHATTERTON & others, 1990; see also RABANO, 1990, *Colpocoryphe*). The facial suture, although it migrates backward during ontogeny, stays proparian until quite late in the ontogeny and becomes gonatoparian only in mature stages of certain taxa.

ORDER PROETIDA

Protaspides of this order have been described by the following authors (see also Fig. 180–182).

Bathyurus	CHATTERTON, 1980
Carrickia	CHATTERTON & LUDVIGSEN, 1976; CHATTERTON, 1980 (=*Phorocephala*)
Cyphaspis	CHATTERTON, 1971
Dimeropyge	HU, 1976; CHATTERTON, 1980; TRIPP & EVITT, 1983; SPEYER & CHATTERTON, 1989
Licnocephala	ROSS, 1953
?Mesotaphraspis	HU, 1976
Phaseolops	HU, 1971
Proetus	CHATTERTON, 1971; HU, 1975b (as *"Proetus"*)
Scharyia	OWENS, 1974; ŠNAJDR, 1980, 1981a, 1990; SPEYER & CHATTERTON, 1989
Tricornotarion	CHATTERTON, 1971
proetid	BEECHER, 1893b, 1895a

There is some confusion regarding the assignment of sclerites to *Dimeropyge* and *?Mesotaphraspis* by HU (1976): e.g., the hypostomes belong to Cheirurina. A protaspis assigned by HU (1975b, fig. 1a, pl. 1, fig. 1) to *Otarion trilobus* HU is an encrinurid, *Encrinuroides* cf. *E. tholus* (see EDGECOMBE, SPEYER, & CHATTERTON, 1988, p. 780).

There may be as many as four different protaspides in the ontogeny of Proetida (e.g., *Scharyia*, Fig. 180). The earliest is very small (about 0.3 to 0.4 mm long) and has a re-entrant posterior margin, usually between two sharp, spinose projections. There may be also a spinose projection anteromedially. Later protaspides lack the re-entrant posterior and have an entire protopygidial margin.

Characteristics of later protaspides include an opisthoparian facial suture; functional connective sutures; a very flat ventral profile and an elliptical to ovoid outline in dorsal view; an anterior border and usually a preglabellar field; eyes located near or just in front of the midlength of the glabella; an axis weakly defined but usually distinguishable; a glabella divided by a transverse occipital furrow but with other furrows usually shallow (e.g., S1 in largest protaspides) to indistinct; genal spines that may (*Dimeropyge*) or may not (*Scharyia*) project outward to affect the outline in dorsal view; sculpture that is smooth, finely granulose, or has a pattern of larger, paired tubercles on the axis and pleurae; a hypostome of even width; and a relatively flat doublure that is sharply turned inward and upward at the margins, with no or few terrace ridges. The hypostome is usually small and without spines or otherwise subdivided posterolateral margins in protaspid stages of this order. One feature that appears to be distinctive of protaspides of Proetida is the very early development of a preglabellar field, a feature that does not develop until the meraspid period in the otherwise rather similar Ptychopariina.

Meraspides of Proetida have been described by several workers, apart from those listed above, including ROSS (1951b, 1953), HINTZE (1953), WHITTINGTON and EVITT (1954), WHITTINGTON (1963), and WHITTINGTON and CAMPBELL (1967). FORTEY and OWENS (1975) used similarities between meraspid cranidia to support their concept of a new order Proetida. FORTEY (1990a) diagnosed this order on the basis of ontogenetic similarities. CHATTERTON (1980) argued that there appear to be two lineages within the Proetida, one with small growth stages having smooth protaspid and early meraspid growth stages (*Proetus, Phaseolops, Licnocephala,* and *Bathyurus*), and one with distinct, organized patterns of tubercles (hystricurinids, telephinids, dimeropygids, glaphurids, aulacopleurids, and *Scharyia*). Phylogeny and ontogeny in Proetida have been insufficiently studied, however, to
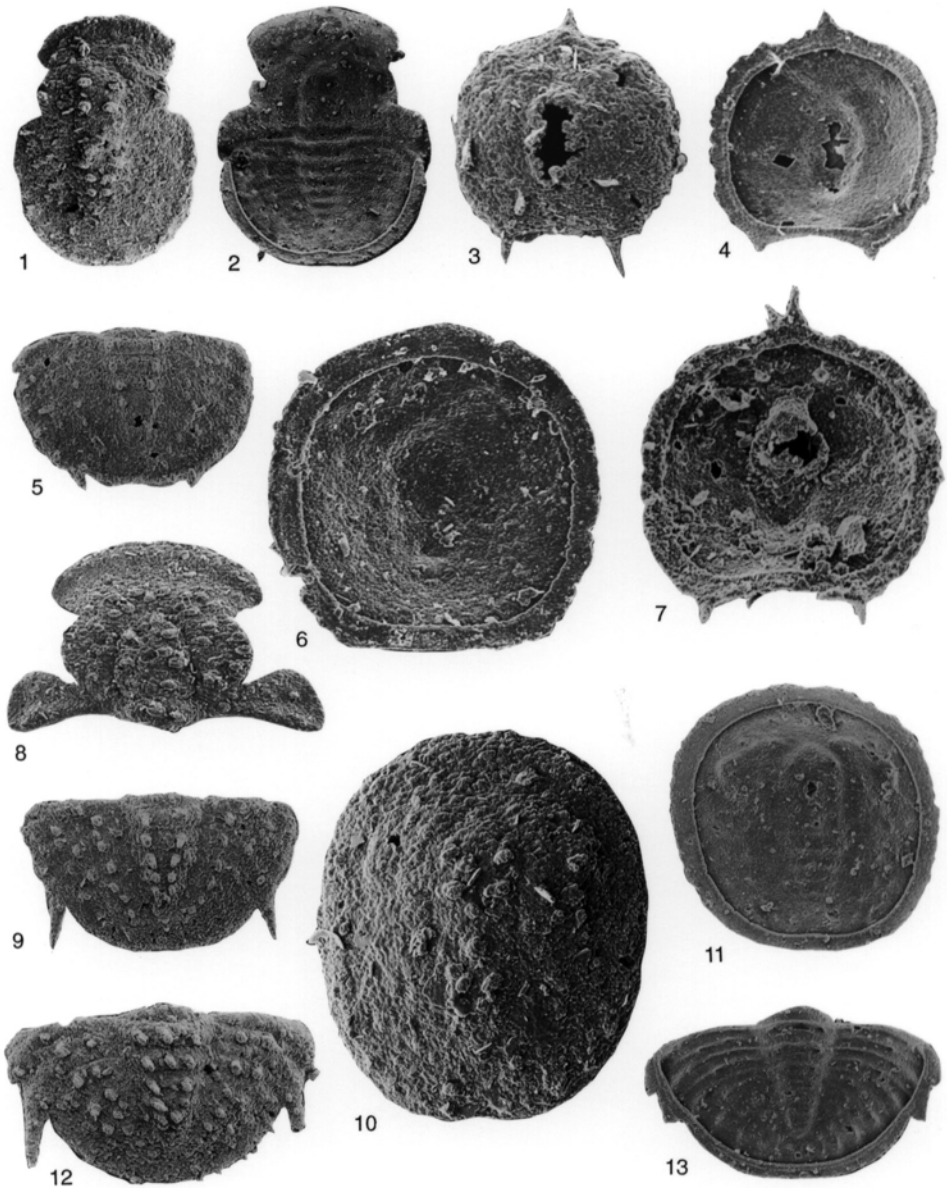
Fig. 180. Proetida. All specimens are of the brachymetopid *Scharyia* aff. *S. redunzoi* Perry & Chatterton from the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T). *1,2,* Dorsal and ventral views of the largest protaspid stage (of at least three and probably four stages); *1,* UA 8455, ×32.5; *2,* UA 7901, ×30.5; *3,4,* dorsal and ventral views of the smallest protaspid stage; note free cheeks and rostral plate still attached; *3,* UA 8456, ×91; *4,* UA 8457, ×91; *5,* dorsal view of an early transitory pygidium, UA 8458, ×30.5; *6,* ventral view of an intermediate protaspid stage; note free cheeks and rostral plate attached; genal spine not apparent, UA 8459, ×91; *7,* ventral view of smallest protaspis; note that free cheeks and rostral plate are attached and the possibly natant position of hypostome is close to inferred life position, UA 8460, ×112; *8,* dorsal view of small cranidium, UA 8461, ×31; *9,* dorsal view of transitory pygidium, UA 8462, ×32.5; *10,11,* dorsal and ventral views of last protaspid stage; note attached free cheeks and absence of genal spine; *10,* ×62.5; *11,* UA 7902, ×126; *12,13,* dorsal and ventral views of transitory pygidia belonging to penultimate meraspid degree; *12,* UA 8463, ×32.5; *13,* UA 8464, ×32.5 (new).
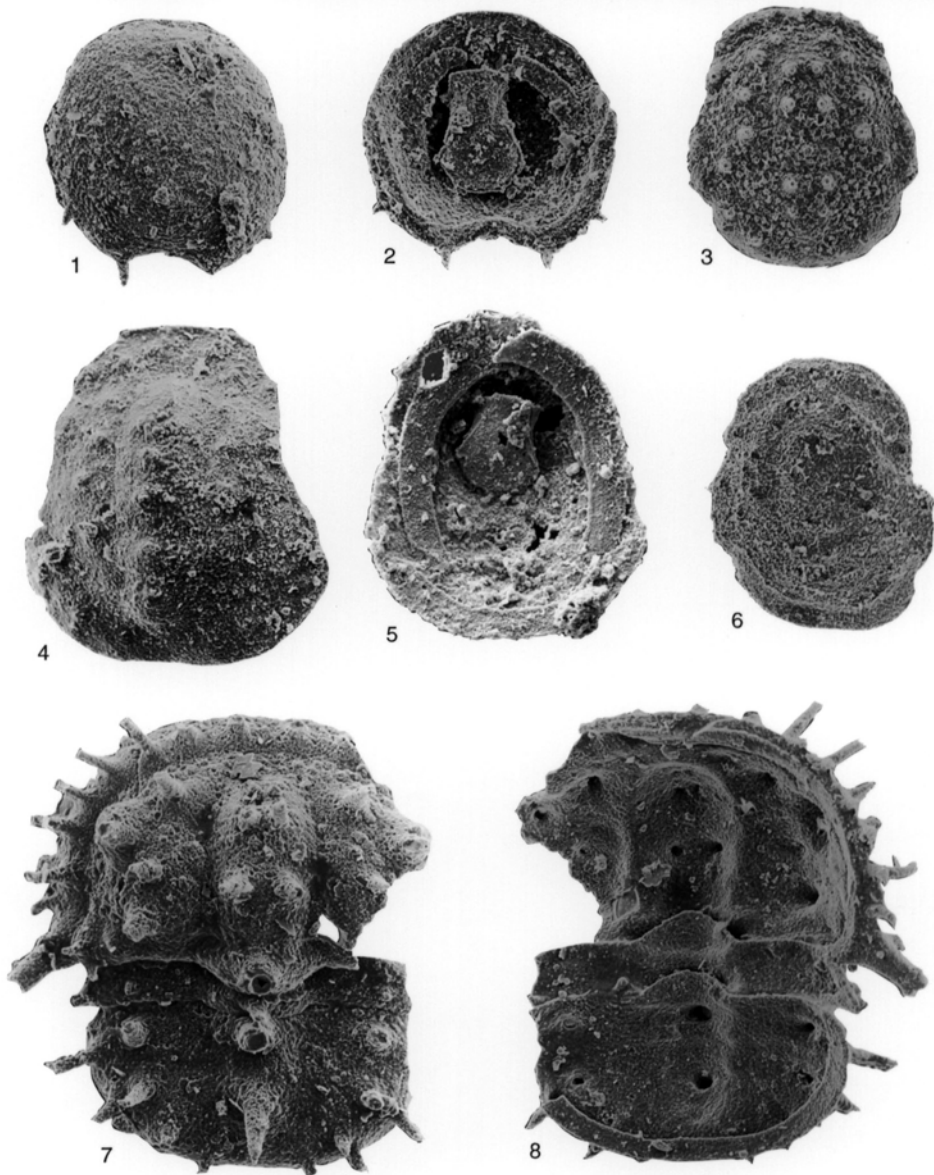
FIG. 181. Proetida, Aulacopleuridae. *1,2,4,5,* Specimens of "*Otarion*" *spinicaudatum* SHAW from the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1,2,* dorsal and ventral views of small protaspides; note out-of-place free cheeks and hypostome attached to ventral surface; *1,* NYSM 16377, ×133; *2,* NYSM 16378, ×135; *4,5,* dorsal and ventral views of later protaspid stages; note out-of-place free cheeks and hypostome still attached to ventral surface; *4,* NYSM 16379, ×107; *5,* NYSM 16380, ×107 (new). *3,6,* Dorsal and ventral views of protaspides of *Dimeropyge* sp., Dimeropygidae, from lower Edinburg Limestone of Virginia (locality 4); *3,* NYSM 16381, ×62.5; *6,* NYSM 16382, ×62.5 (new). *7,8,* Dorsal and ventral views of meraspid degree 1 of *Conopareia* n. sp. from the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T), UA 8465, ×88 (new).

judge whether these are separate lineages. Certainly, prominent spines of early growth stages are often lost secondarily and perhaps sometimes regained. It is unwise to recognize large phyletic groups using a single character that may be homoplasous.

ŠNAJDR (1990, p. 40) illustrated a slab of shale from the Wenlock Liten Formation

covered in late meraspid molts and carcasses of one species, *Aulacopleura koncki.* ŠNAJDR believed this sample to be representative of a site where a large number of individuals of this species molted. He suggested that some of the molts that are disarticulated may have been disturbed by other molting individuals.

ORDER LICHIDA, FAMILY LICHIDAE

Ordovician to Devonian protaspides of this family have been described by workers listed below (see also Fig. 183–184).

Acanthopyge	WHITTINGTON, 1956c; CHATTERTON, 1971
Amphilichas	CHATTERTON, 1980; HU, 1974a; TRIPP & EVITT, 1981
Hemiarges	CHATTERTON, 1980; HU, 1974a; TRIPP & EVITT, 1981; SPEYER & CHATTERTON, 1989

Some problems of protaspid assignments were resolved by TRIPP and EVITT (1981). Lichid protaspides are so similar to one another and so different from those of other taxa that they strongly support the monophyletic nature of this group. Protaspides have been found for members of the Lichinae (*Dicranopeltis*), Tetralichinae (*Amphilichas*), and Ceratarginae (*Hemiarges* and *Radiolichas*). The later protaspides are adultlike, very similar to meraspides of the same taxa, and clearly had a benthic life mode. It is now apparent to us that lichids (Fig. 166.1,2) may also have had an earlier nonadult-like, planktonic growth stage. As with all small stages that are separated from later growth stages by a radical metamorphosis, some uncertainty attends associating these with adult stages. CHATTERTON originally assigned larvae, which we now consider may belong to a lichid (*Acanthopyge*) planktonic stage, to one growth stage of *Apocalymene quadrilobata* (CHATTERTON, 1971, fig. 18h,i, pl. 19, fig. 8–10, pl. 21, fig. 1–3). This reassignment is still controversial, since similar stages have not been found for all other lichid ontogenies.

Features of the more adult-like protaspides of lichid trilobites were described by CHATTERTON (1980, p. 12) and include an

opisthoparian facial suture; distinct axial and pleural regions; a comparatively wide (sag. and exsag.) anterior border; a posterior border and posterior marginal furrows to the cranidium; distinct palpebral lobes just in front of or close to the midlength of the cranidium; an occipital tubercle and a pattern of larger tubercles that is usually present on the axis and pleurae (see CHATTERTON, 1971 and Fig. 149 for terminology); a librigenal spine is usually absent; three or five pairs of marginal spines present on the protopygidium; interpleural furrows present on protopygidium; a doublure with terrace ridges distally and a sharp ridge around the proximal ends of marginal spines; and a hypostome with blunt-ended marginal spines that make the margins appear to be subdivided by four pairs of slits.

The distinctive anterolateral glabellar lobes or bullae of adult lichids may be absent in protaspides or present as small lobes along the axial furrows (*Acanthopyge* in CHATTERTON, 1971). After they appear as small lobes in or proximally adjacent to the axial furrows of later protaspid or early meraspid cranidia, they expand forward and outward but apparently remain glabellar, with the axial furrows surrounding them. The posterolateral cranidial lobes also expand outward from early meraspid stages onward and may incorporate genal as well as glabellar material as they expand (see detailed arguments in CHATTERTON, 1971; and THOMAS & HOLLOWAY, 1988). A sequence of developmental stages of an Ordovician species of *Hemiarges* is shown in Figure 184.

ORDER LICHIDA, FAMILY ODONTOPLEURIDAE

Protaspides of this family have been described by the workers listed below (see also Fig. 185.1,2,5,11,12).

Ceratocephala	CHATTERTON, 1980
Ceratocephalina	CHATTERTON, 1971
Diacanthaspis	WHITTINGTON, 1956d; HU, 1974b
Dudleyaspis (Taemasaspis)	CHATTERTON, 1971

Small odontopleurid meraspides have been described by the above workers as well
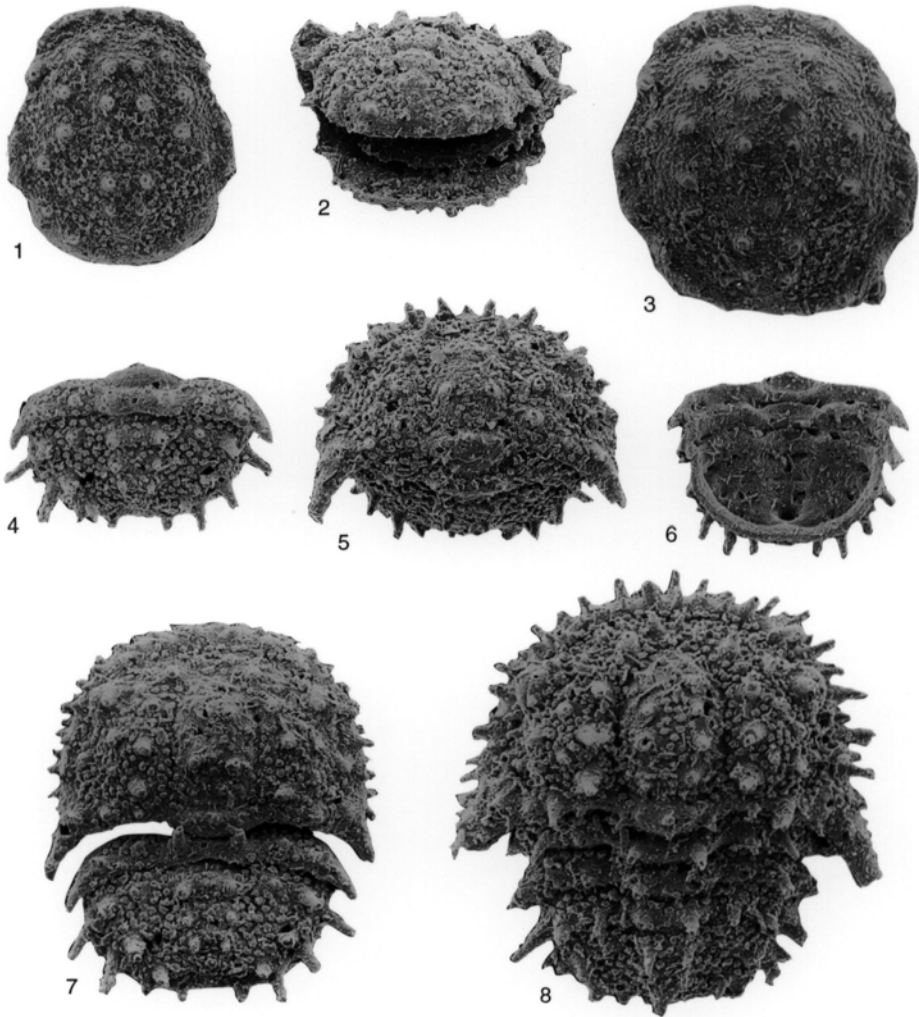
FIG. 182. Proetida. Specimens of *Dimeropyge* aff. *D. clintonensis,* Dimeropygidae, from the Esbataottine Formation, Middle Ordovician, northwestern Canada (locality P17.2); compare Figure 160. *1,* External view of protaspis P2, lacking free cheeks, UA 8466, ×80; *2,* external view of enrolled meraspid degree 0, UA 8467, ×64; *3,* dorsal view of late protaspis, UA 8468, ×97.5; *4,* dorsal view of small meraspid thoracic segment and transitory pygidium (degree 1?), UA 8469, ×63; *5,* external view of partly enrolled meraspis (degree 1), UA 8470, ×64; *6,* ventral view of meraspis (degree 2 or more), UA 8471, ×49; *7,* dorsal view of reconstructed meraspis (cephalon found separate from thoracic segment and transitory pygidium), UA 8472 and UA 8469, ×71; *8,* dorsal view of meraspid degree 2, UA 8473, ×72 (new).

as WHITTINGTON and EVITT (1954), SHAW (1968), WHITTINGTON and CAMPBELL (1967), CHATTERTON and PERRY (1979, 1983), and RAMSKÖLD and CHATTERTON (1991). Protaspides for this group are small and adult-like. No nonadult-like protaspides have been associated with this family.

The Dameselloidea are regarded as a sister group of Odontopleuroidea by FORTEY (1990a) and herein. ENDO (1939a, 1939b) provided poor illustrations considered to be of protaspides of the damesellid *Blackwelderia* from the Cambrian of China. Restudy of this material will be necessary before
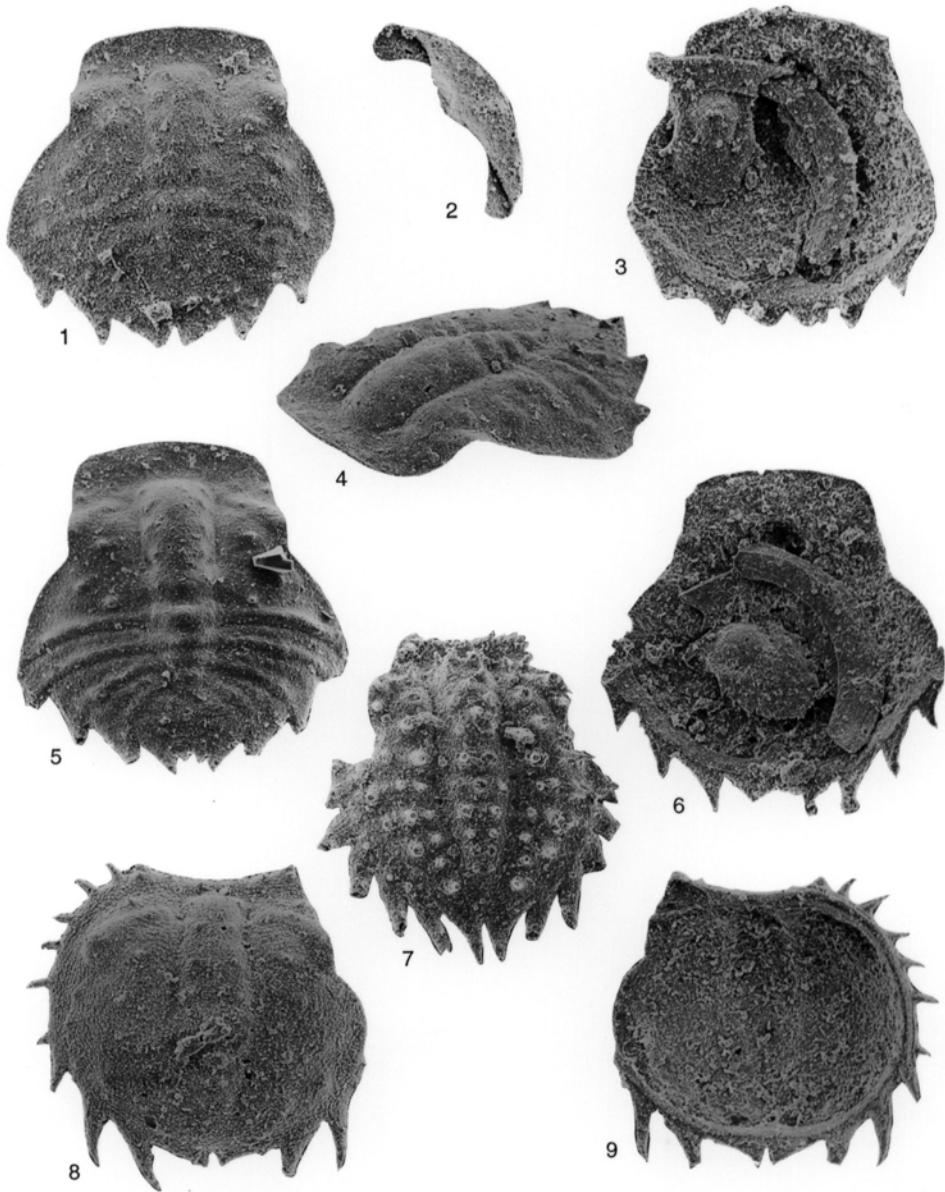
Fig. 183. Lichidae. *1–6,* Protaspides of *Hemiarges* aff. *H. turneri* CHATTERTON & LUDVIGSEN from the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1,* dorsal view of small protaspis, NYSM 16383, ×62; *2,* dorsal view of protaspid free cheek, NYSM 16384, ×63.5; *3,* ventral view of small protaspid growth stage; rostral plate, hypostome, and free cheek are attached, NYSM 16385, ×62.5; *4,* anterodorsolateral view of small protaspis, NYSM 16386, ×67; *5,* dorsal view of large protaspid stage, NYSM 16387, ×53.5; *6,* ventral view of large protaspid stage, NYSM 16388, ×50. *7,* Dorsal view of large protaspid stage of *Amphilichas* sp. from the Lower Edinburg Formation, Middle Ordovician, Virginia (locality 4), NYSM 16389, ×37. *8,9,* Dorsal and ventral views of *Amphilichas minganensis?* (BILLINGS), small protaspid growth stage with single free cheek attached, from the Crown Point Formation, Middle Ordovician, New York (locality PB81), NYSM 16390, ×61.5 (new).
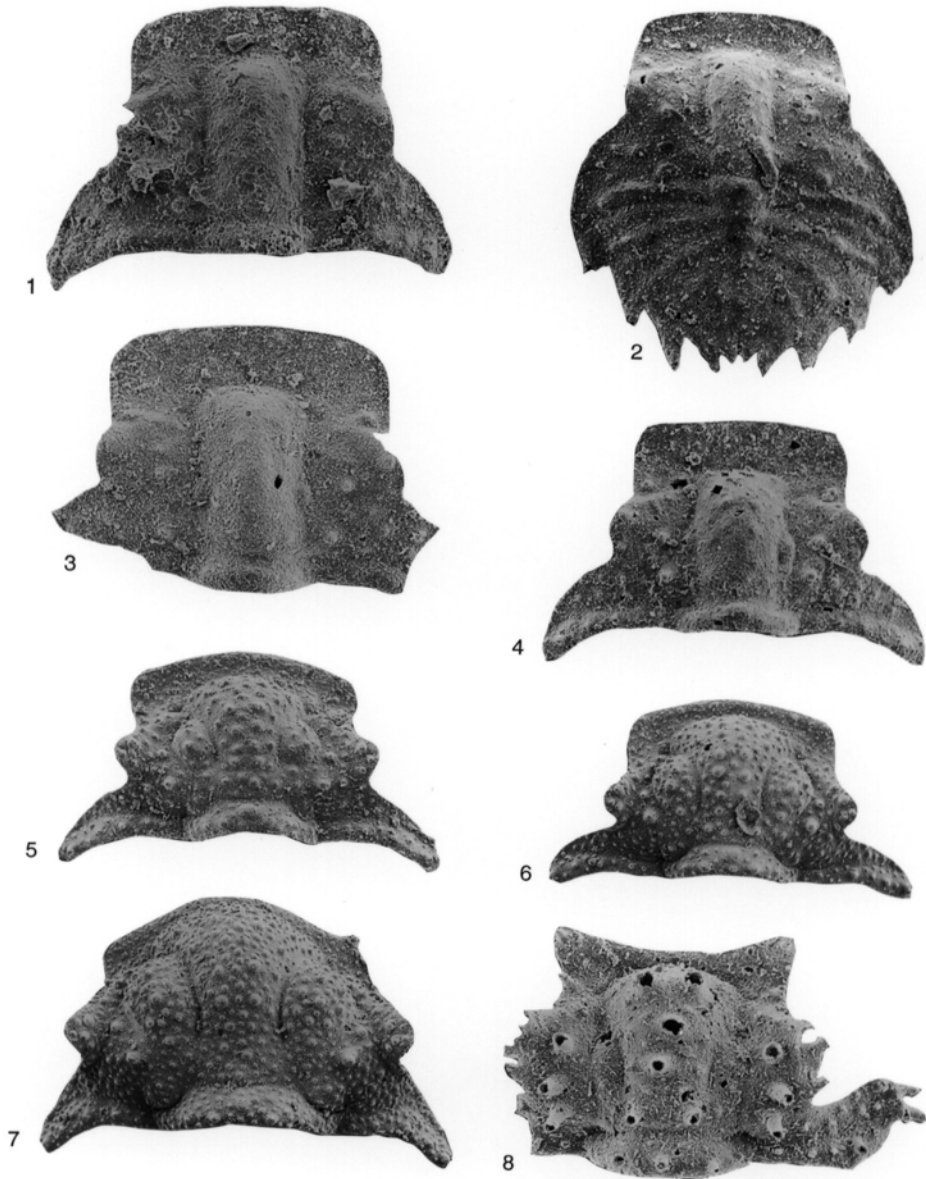
FIG. 184. Lichidae. Development of cranidial lobation in lichids. All specimens are from the Crown Point Formation, Middle Ordovician, New York (locality PB 81). *1–7,* Dorsal views of cranidia and protaspis of *Hemiarges* aff. *H. turneri* CHATTERTON & LUDVIGSEN; *1,* cranidium (bullae very small but distinguishable on glabellar side of axial furrow in L2 position), NYSM 16391, ×62; *2,* last protaspid stage (cranidial lobes indistinct; note that this is not NYSM 16014 as in SPEYER & CHATTERTON, 1989, fig. 4e), NYSM 16392, ×56.25; *3,* small cranidium (bullae expanded transversely to affect outline of glabella; posterolateral lobes barely distinguishable in L1 position as part of sides of glabella), NYSM 16393, ×62.5; *4,* small cranidium (bullae expanded outward and slightly forward; posterolateral lobes (L1) expanding slightly outward behind bullae), NYSM 16394, ×44.6; *5,* small cranidium (bullae expanded farther outward and forward to opposite at least part of L3; posterolateral lobes expanded outward but not quite as far as bullae; transverse width of glabella apparently slightly reduced towards front of posterolateral lobes, opposite fixigenal spine pair A1 of CHATTERTON, 1971), NYSM 16395, ×31.25; *6,7,* larger cranidia (bullae and *(Continued on facing page.)*

it may be used to clarify this relationship. ENDO's drawings (1939b, fig. 1b, 5b) are of larvae that show little similarity to post-Cambrian odontopleurid protaspides and a greater similarity to those of Redlichiina.

The protaspides assigned to post-Cambrian odontopleurids are similar to one another and support the thesis that these taxa form part of a monophyletic group. They share the following characteristics: the facial suture is initially proparian, then changes to opisthoparian between protaspid and meraspid periods or within the meraspid period; the librigenae have marginal spines; paired spines occur on the glabella and anterior border (see Fig. 149), an exception being *Dudleyaspis* and perhaps *Acidaspis;* the glabella is distinct and subparallel-sided to barrel-shaped, with a shallow occipital furrow and up to three indistinct transglabellar furrows farther forward; glabellar furrows often appear to constrict the glabella slightly locally; sculpture between tubercles may be absent or granulose; an occipital spine or node is present with or without subsidiary occipital spines; a distinct pattern of prominent, paired spines occurs on the genae and posterior border; sharp, tubular marginal spines are found on the protopygidium with or without spinules; the doublure is narrow, incurled to inturned, and without terrace ridges; the hypostome is slightly transverse with entire margins or very short spines; the hypostomal doublure is often embayed just behind the shoulder, sometimes later forming a hole in the doublure that is separate from its interior margin; the posterior margin of the protocranidium is delineated by a distinct furrow; and the ventral profile is subhorizontal.

The glabellar lobes of odontopleurids appear to have originated through lateral expansion of the glabella, with the glabellar furrows deepening and lengthening; and the individual glabellar lobes sometimes swell so as to be separated from the median part of the glabella by sublongitudinal furrows. Their proximity to the palpebral lobe in some taxa appears to be a combination of expansion of the glabella and migration inward of the eye. The movement of the facial suture from a proparian pattern to an opisthoparian pattern between protaspid and meraspid periods or during the early part of the meraspid period (Fig. 186) is well documented.

CLASSIFICATION UNCERTAIN

Ontogenies of Cambrian taxa that have not been placed with confidence into any superfamily or order include those of Plethopeltidae (HU, 1986, *Arapahoia*), *Plagiura* (HU, 1985b), *Missisquoia* (HU, 1971; see also under Corynexochida, Leiostegiina above), and *Paranumia* HU (1973).

HU (1986) commented on the similarity of the protaspides of the plethopeltid *Arapahoia* to those of the norwoodiid *Norwoodella* (Ptychoparioidea) and the cedariids *Cedaria* and *Cedarina* (Ptychoparioidea). We agree with HU that the morphological similarities of early growth stages of these taxa imply relative recentness of common ancestry; the Plethopeltidae should be included with the Norwoodiidae and the Cedariidae in the Ptychoparioidea.

FIG. 184. *Explanation continued from facing page.*

posterolateral lobes slightly more expanded than in smaller cranidia; axial furrows shallow, particularly opposite A1; posterolateral part of fixigena in front of border furrow slightly swollen so that boundary between anterior part of posterolateral lobe and fixigena is not very distinct); *6,* NYSM 16396, ×21.5; *7,* NYSM 16397, ×21. *8, Amphilichas conradi* CHATTERTON & LUDVIGSEN from the lower Esbataottine Formation, Middle Ordovician, northwestern Canada (locality P17.2); bullae not delineated posteriorly by distinct furrow, but longitudinal furrow separating bullae from rest of glabella is very shallow to indistinct behind L2, and axial furrows are distinct, UA 8474, ×47 (new).
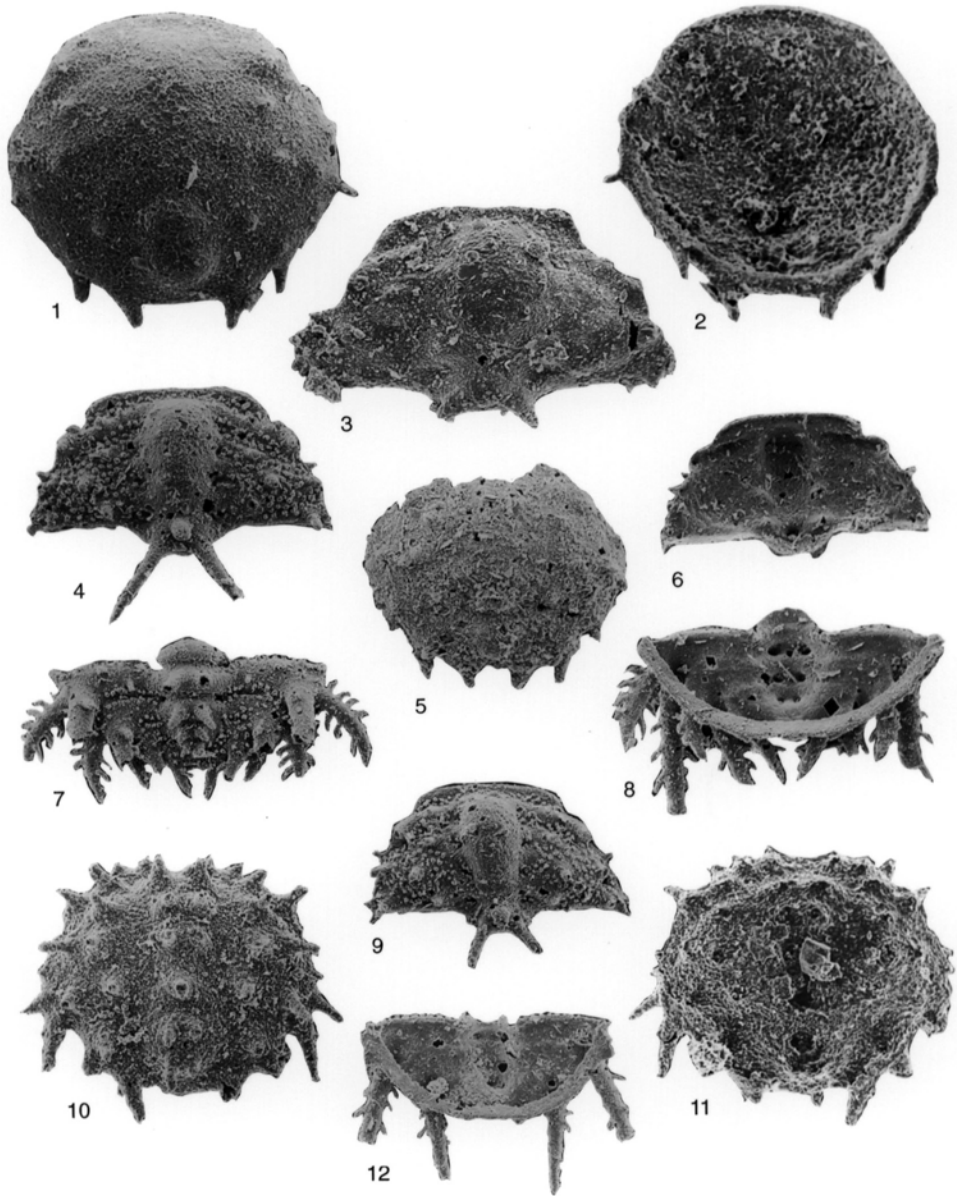
FIG. 185. Odontopleuridae. *1–9,12, Ceratocephala triacantheis* WHITTINGTON & EVITT; *1–3,* from the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1,2,* dorsal and ventral views of protaspis, NYSM 16398, ×117; *3,* small cranidium, NYSM 16399, ×67 (new). *4–9,12,* from the Esbataottine Formation, Middle Ordovician, northwestern Canada (locality P17.2); *4,* dorsal view of small cranidium, UA 8175, ×64; *5,* dorsal view of incomplete protaspis, UA 8475, ×65; *6,* ventral view of cranidium, UA 8173, ×64; *7,* dorsal view of transitory pygidium (lost specimen), ×50; *8,* ventral view of transitory pygidium, UA 8179, ×64; *9,* dorsal view of small cranidium, UA 8174, ×64; *12,* ventral view of transitory pygidium, UA 8176, ×64. *10,11,* Dorsal and ventral views of protaspis of *Diacanthaspis secretus* WHITTINGTON from the lower Edinburg Limestone of Virginia (locality 4), NYSM 16400, ×80 (new).
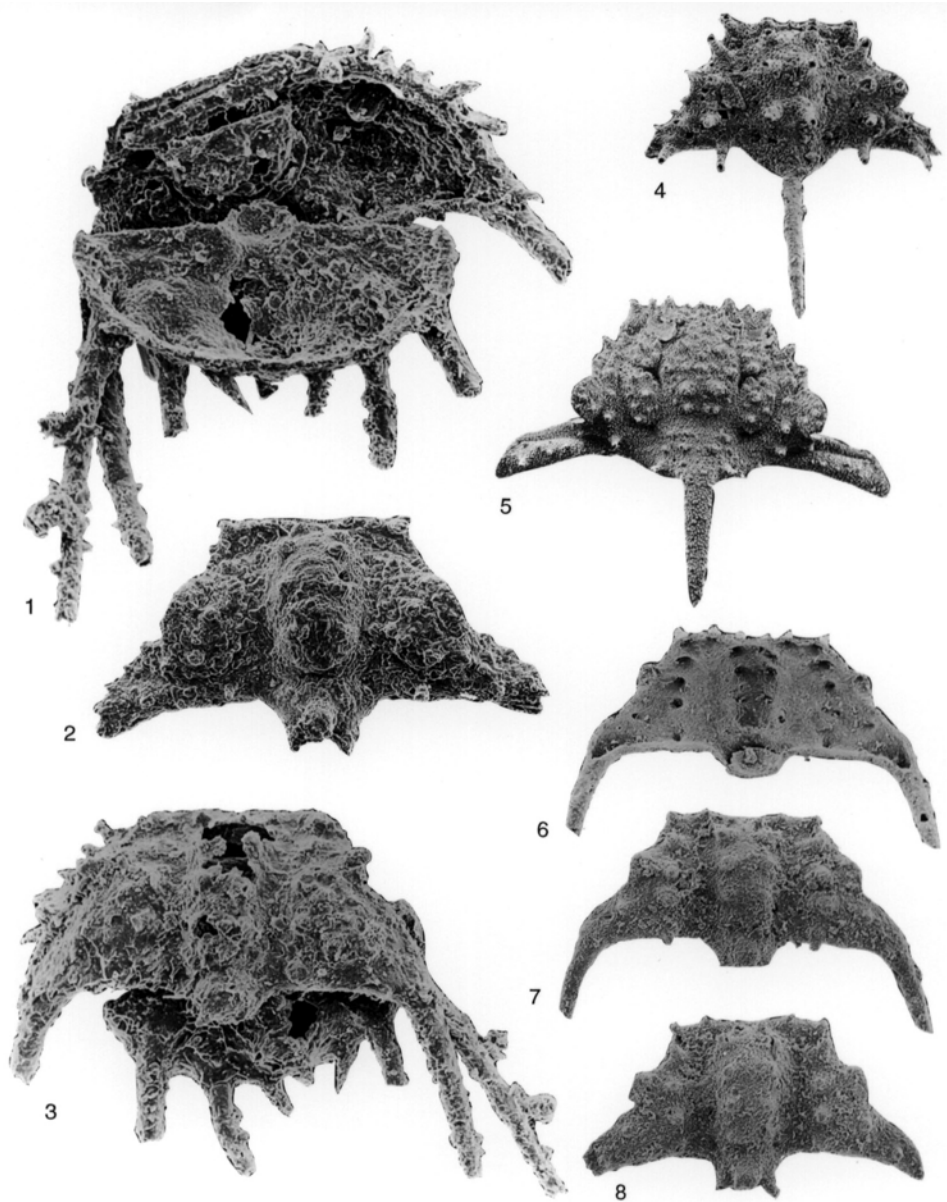
FIG. 186. Odontopleuridae. *1–3,* From the Mackenzie Mountains, early Llandovery, northwestern Canada (locality AV1-95.5); *1,3,* ventral and dorsal views of meraspid degree 0 of *Kettneraspis jaanussoni* CHATTERTON & PERRY, with genal spine on fixigena, not on free cheek, and attached rostral plate and hypostome, UA 8271, ×86; *2,* dorsal view of meraspid cranidium of *K. jaanussoni;* facial suture has migrated inward so genal spine is now on free cheek, UA 8476, ×60 (new). *4–8,* From the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T); *4,5,* dorsal views of cranidia of *K. longstaffei;* in this clade of *Kettneraspis* small cranidia have a large occipital spine and reduced or absent subsidiary occipital spines; *4,* UA 8477, ×32.5; *5,* UA 8478, ×13.9; *6,7,* ventral and dorsal views of small meraspid cranidium of *K. lenzi,* UA 8273, ×45.5; *8,* dorsal view of meraspid cranidium of *K. lenzi.* Note that in *K. lenzi* the facial suture migrates inward to displace the genal spine from the fixed cheek to the free cheek. Also, it is quite clear from the similarities of the small cranidia of *K. jaanussoni* and *K. lenzi* (including prominent pairs of subsidiary occipital spines and a short, knoblike occipital tubercle) that they form part of a clade that is distinct from the clade that includes *K. longstaffei* (and *K. belli* CHATTERTON & PERRY, *K. besti* CHATTERTON & PERRY and *K. boltoni* CHATTERTON & PERRY) and has a prominent, long, sharp occipital spine in small cranidia. The patterns of the other prominent spines or tubercles on the cranidia of both of these clades are essentially the same, UA 8479, ×45.5 (new).

EVOLUTIONARY HISTORY

Richard A. Fortey and Robert M. Owens

The history of the trilobites extends through some 300 million years. There is evidence that trilobites were capable of rapid evolutionary change, and refined zonal schemes of wide geographical application have been based on successions of species, especially in the Cambrian and Ordovician. Where these zones can be compared with those based on other organisms, trilobites appear to have changed relatively rapidly. For example, in the Upper Ordovician (Ashgill) Ingham (1970) recognized as many as eight shelly zones, largely based on trinucleid trilobites, spanning an interval equivalent to perhaps three graptolite zones and extending through approximately 7 to 8 million years. The Upper Cambrian zonation of Scandinavia (Henningsmoen, 1957a) is based on species of olenid trilobites (Fig. 187), and the average duration of these zones may be from one to two million years, depending on which absolute age assessment is accepted for the Cambrian. Given such rapid change over so long a time period, no short summary of trilobite evolutionary history can do justice to its complexity. Some general features of trilobite history are addressed here, together with examples of evolutionary change that can be studied directly from the stratigraphic record. The problems of trilobite phylogenetics are not considered further, and emphasis will be placed on those aspects of trilobite history that do not depend on having a completely resolved phylogenetic classification (Fortey & Owens, 1990a).

CHANGES IN MORPHOLOGY THROUGH TIME: GENERAL FEATURES

Primitive morphology is exemplified either by such Olenellina as *Olenellus* or by Redlichiina, such as *Eoredlichia* and *Redlichia.* Olenellina and Redlichiina share many features that are presumed to be primitive for the Trilobita, the main difference being the absence of facial sutures in Olenellina. This absence is regarded as primitive by most authors (Fortey & Whittington, 1989), and the presence of facial sutures, unique to trilobites, is considered to be a characteristic of Redlichiina and all higher trilobites, except where they are again secondarily lost.

Most Redlichiina and Olenellina share the following features, which may be taken as an inventory of the primitive condition in the trilobites. They have relatively low dorsoventral convexity and typically the oval exoskeleton is about two-thirds as wide as long. Genal spines are present. The thorax is composed of a large number of spinose segments, of which the third may be macropleural; the articulation was nonfulcrate (Whittington, 1990) and allowed considerable arching of the body, if not complete enrollment. The pygidium is small but appears to be composed of more than one segment. Eyes are long and extend close to the glabella anteriorly; the eye ridge and eye lobe form a continuous structure (the ocular lobe) that may be subdivided by one or more furrows (Pillola, 1991). The visual surface is surrounded by a circumocular suture, so that the eye surface is rarely found in place. Palmer and Halley (1979) have shown that the visual surface may be attached in some early olenellid growth stages, implying that the circumocular suture may not have been functional early in ontogeny. The primitive glabella tapers forward and is relatively long (sag.), with the frontal lobe bosslike or acuminate and three pairs of long (tr.) glabellar furrows that may be transglabellar; the occipital ring is defined. Fortey (1990a) maintained that the primitive hypostomal condition is conterminant (or attached by a pronglike doublural extension in some *Olenellus* species); primitive hypostomes have narrow borders, lack such features as posterior forks, and have small maculae. Olenellina, for which few ontogenies are

known, apparently did not have a calcified protaspis; the development of *Redlichia* from protaspis to adult (W. ZHANG, LU, & others, 1980) was gradual without a metamorphosis at any stage.

From this bauplan the range of trilobite morphology was derived by modification of one or more features. These modifications became more extreme and more pervasive after the Cambrian, which is often described as a time when morphology was generally conservative. The changes are not easy to demonstrate quantitatively, but FOOTE (1991) has succeeded in showing that the range of morphology exhibited by post-Cambrian trilobites increased considerably, as revealed by the complexity of morphological maps of cranidia (Fig. 188). The same is shown by the appearance of more instances of those morphotypes associated with pelagic habits, trilobites with fringes, and other distinctive morphologies. Such changes were pervasive and tended to recur in several unrelated phylogenetic lineages.

CHANGES FROM PRIMITIVE MORPHOLOGY

Important changes from the primitive morphology as exemplified by *Eoredlichia* are summarized in Figures 189 and 190.

SHAPE OF EXOSKELETON

The general form of the exoskeleton may become transverse, i.e., wide in relation to length (*Gastropolus,* some trinucleoids), or elongate (*Opipeuter, Remopleurides*). The transverse shape may be accompanied by reduction in number of thoracic segments and widening (tr.) of the pleurae, while in elongate forms the pleurae may be reduced in width (tr.). A transverse outline is not common, but it is most typical of Trinucleoidea in the Ordovician; its most extreme manifestation is found in the Chinese genera *Taklamakania* and *Pseudampyxina* (W. ZHANG, 1980) in which the thoracic segments are reduced to as few as three. Some Cambrian genera were elongate, such

as *Bathynotus, Elvinia,* and some paradoxidids and Agnostina, as were many Ordovician genera, especially those associated with pelagic habits (FORTEY, 1974a, 1985). The extreme in pleural reduction is attained in the bizarre trilobite *Bohemilla,* which was excluded from the class Trilobita in the last edition of the *Treatise* (WHITTARD in MOORE, 1959), not least because it apparently lacked pleurae completely. Early bohemillids, however, retain remnants of the pleurae, and their trilobite affinity is no longer in dispute. Very elongate trilobites are uncommon after the Ordovician, which may reflect the loss of pelagic habits. The nearest proportions to those of the Ordovician forms are probably to be found in such cheirurids as *Crotalocephalus,* but in this case the long, narrow appearance is in part attributable to steep downturning of the thoracic pleurae. The vast majority of post-Ordovician trilobites have an elongate-elliptical outline not greatly different from that of a typical early trilobite.

CONVEXITY

Convexity is highly variable in trilobites. Some species, especially illaenids (OWEN & BRUTON, 1980) and such Upper Cambrian genera as *Plethometopus* (STITT, 1975), are both effaced and with the cephalic shield especially convex in the sagittal direction. Such convexity may be associated with the bumastoid stance (WESTROP, 1983), in which the trilobite is supposed to have burrowed backwards into the sediment, leaving only the convex cephalic shield projecting, the eyes being horizontal in this attitude. Other convex trilobites are greatly vaulted across the thorax but not especially so across the cephalon and may be generally smoother; this is particularly characteristic of Homalonotidae (Ordovician to Devonian). HAMMANN (1983) argued that this morphology is consistent with a burrowing habit. In many trilobite families all or part of the glabella becomes particularly convex and expanded (especially in Phacopida, Cheiruridae, Cybelinae), and this may have been associated with an expansion of the foregut be-

ZONES	SUBZONES
Acerocare	*Acerocare ecorne* *Westergaardia spp.* *Peltura costata* *Peltura transiens*
Peltura scarabaeoides	*Peltura paradoxa* *Parabolina lobata* *Ctenopyge linnarssoni* *Ctenopyge bisulcata*
Peltura minor	*Ctenopyge affinis* *Ctenopyge tumida* *Ctenopyge spectabilis* *Ctenopyge similis*
Protopeltura praecursor	*Ctenopyge flagellifera* *Ctenopyge postcurrens* *Leptoplastus neglectus*
Leptoplastus	*Leptoplastus stenotus* *Leptoplastus angostatus* *Leptoplastus crassicorne* *Leptoplastus raphidophorus* *Leptoplastus poucisegmentatus*
Parabolina spinulosa	*Parabolina spinulosa* *Parabolina brevispina*
Olenus with *Homagnostus obesus*	*Olenus scanicus* *Olenus dentatus* *Olenus attenuatus* *Olenus wahlenbergi* *Olenus truncatus* *Olenus gibbosus*

Fig. 187. Biozones in the Upper Cambrian of Scandinavia, based on olenid trilobites, showing fine stratigraphical subdivision (adapted from Henningsmoen, 1957a).

neath it (Eldredge, 1971). Most trilobite families display a range of convexity, and it is not a character of taxonomic importance above the generic level. Even within the Lower Cambrian a few convex genera are known (*Giordanella, Bonnia,* and some earlier eodiscoids), and dorsoventrally flattened and convex trilobites coexisted in most later trilobite faunas.

INCREASED SIZE OF PYGIDIUM

A large pygidium is believed to be an advanced character. In trilobites other than Agnostida the size of the pygidium increases on average through the Cambrian to the Or-

dovician but not greatly thereafter (Fig. 191). Pygidial size is easily modified via heterochronic change (see previous section on ontogeny, p. 173), and increased caudalization is not, perhaps, a character of great importance. This is shown by the fact that pygidial size may vary widely within a single family. In Olenidae the pygidium may be small to almost isopygous. Moreover, if Naraoiidae is the sister group of other trilobites, the pygidium of naraoiids has already attained its largest possible size. By the end of the Early Cambrian, isopygous trilobites had appeared in several groups (Agnostida as well as gigantopygids and yinitids in
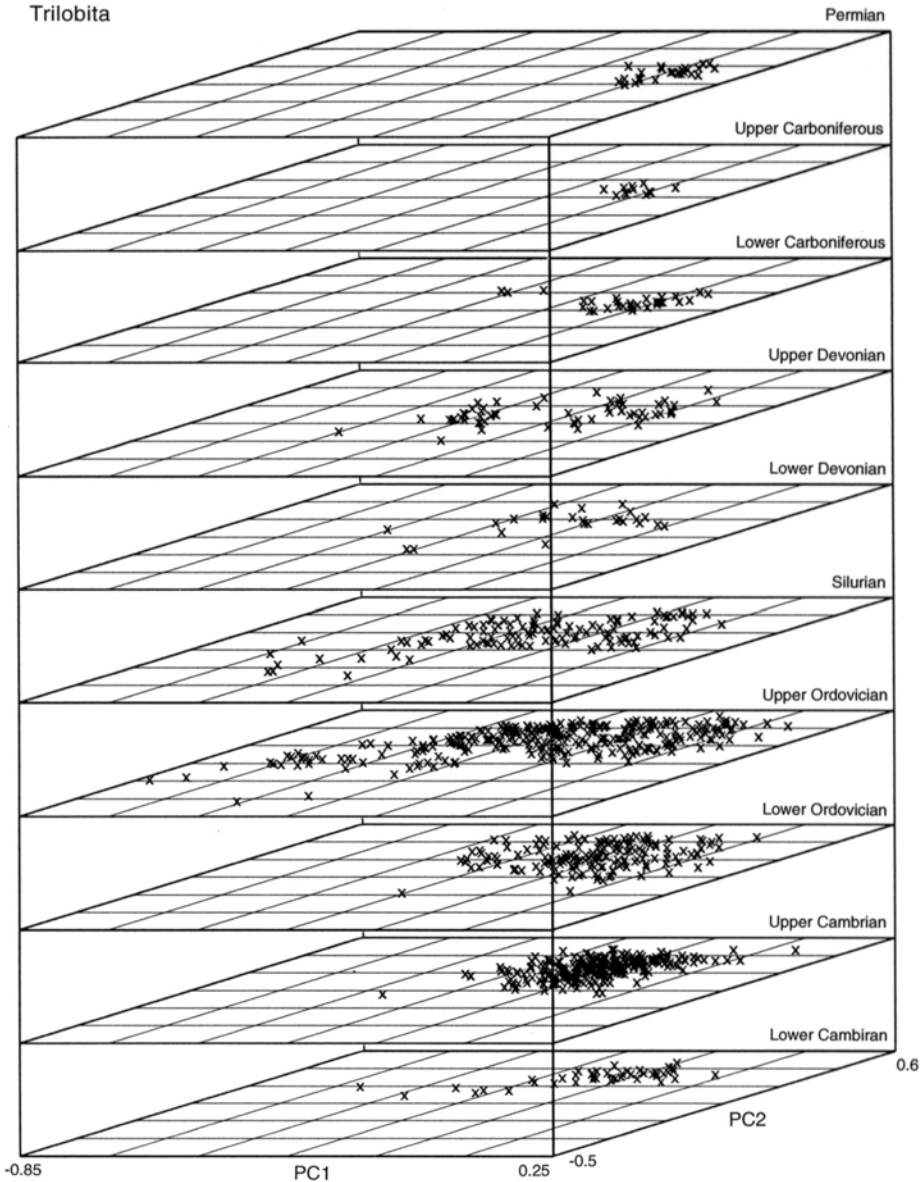
FIG. 188. Post-Cambrian trilobites occupied greater morphospace than Cambrian trilobites, as shown by morpho-logical maps of the first two principal components (PC1 and PC2) (adapted from Foote, 1991, fig. 2).

Redlichiina), and such forms lived alongside species with smaller pygidia. This applies throughout the remainder of the history of Trilobita, although by the Devonian and later periods, elements in the fauna with small pygidia (e.g., *Aulacopleura*) were less numerous. In any case, there is no suggestion

that small pygidia were heavily selected against, because the shift from generally small to generally large pygidia takes place over almost 200 million years. Species with large pygidia tend to be enrolled tightly (BERGSTRÖM, 1973a) because of the coapta-tion of cephalic and pygidial margins. A few
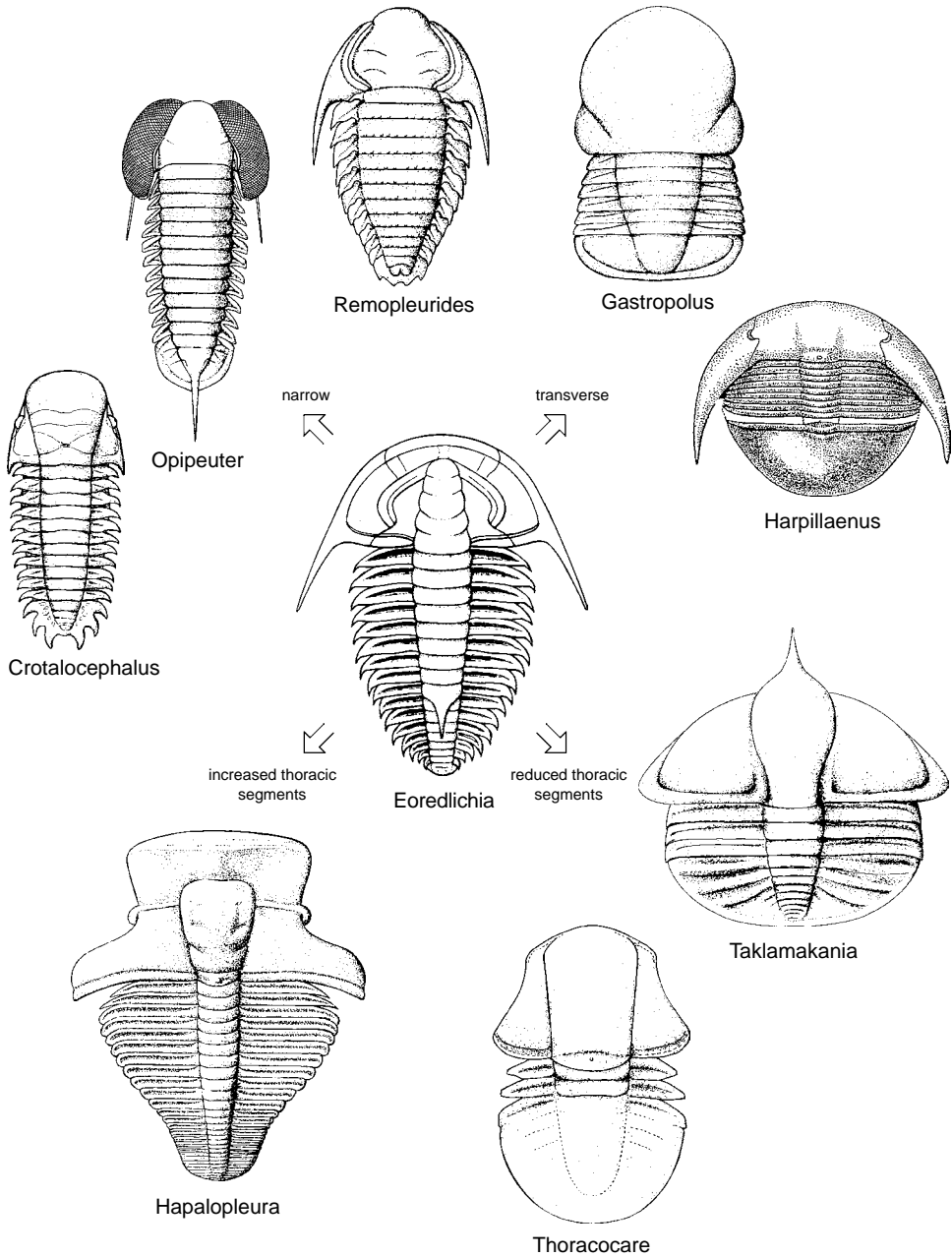
FIG. 189. Changes through time in the trilobite exoskeleton, compared with the generalized and primitive morphology exemplified by *Eoredlichia* (new).

examples are known in which a reversal to a small pygidium has taken place. Primitive remopleuridoids had large pygidia (*Apatokephalus*) with at least four segments, whereas a more derived genus (*Remopleurides*) has a

minute pygidium—usually with two segments. The remopleuridid *Hypodicranotus* from the middle to the upper part of the Ordovician may have but a single segment in the pygidium (LUDVIGSEN & CHATTERTON,
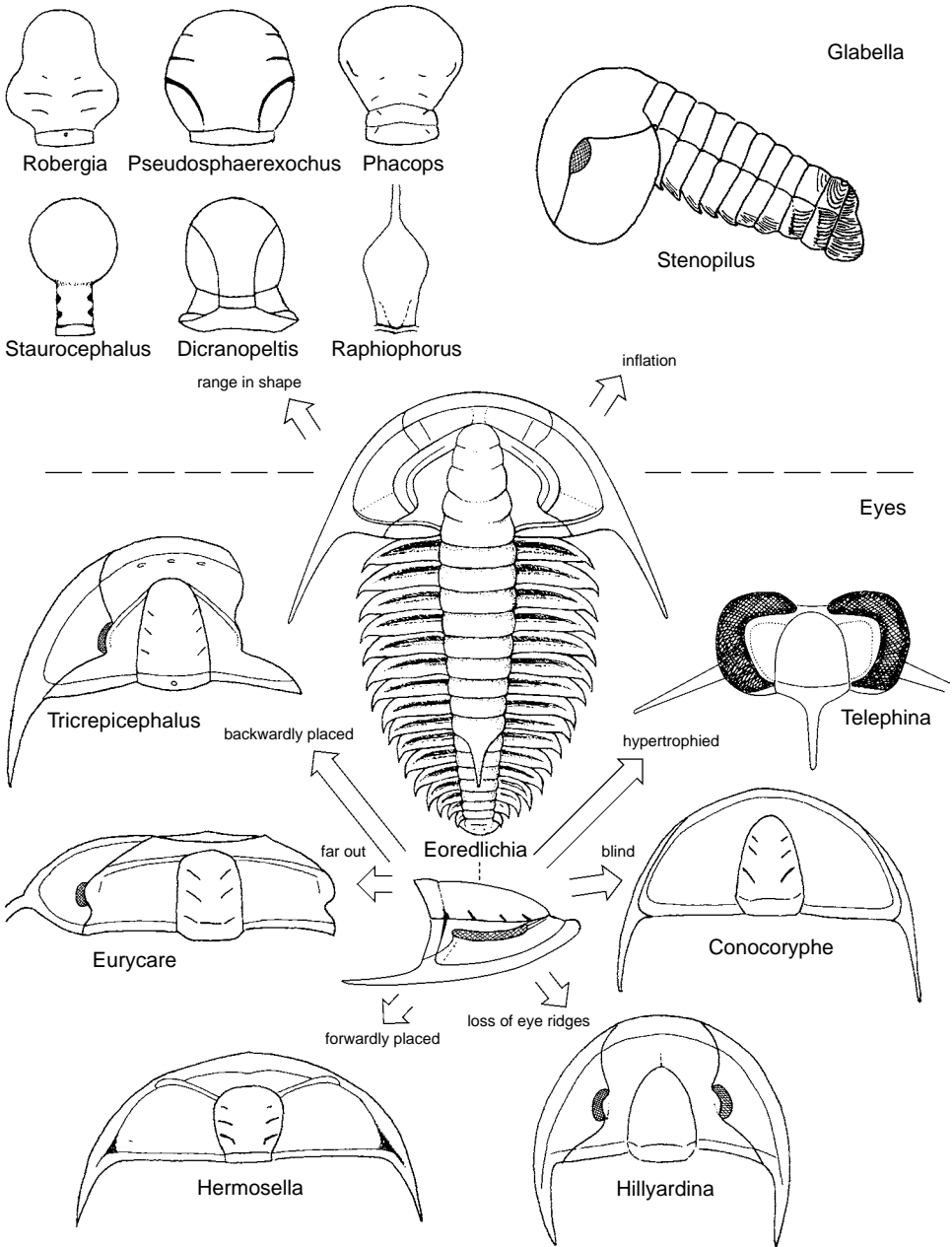
FIG. 190. Changes through time in glabella and eye morphology and position compared with the generalized and primitive morphology exemplified by *Eoredlichia* (new).

1991). It seems likely that a similar reversal has taken place in the Ordovician family Celmidae (*Celmus*), which has an extraordinarily small pygidium (BRUTON, 1983), be-

cause the families to which it may be related all have pygidia of normal proportional size. LANE (1971) has recognized a trend toward reduction in the number of pygidial seg-

ments in cheirurid lineages from the Ordovician and Silurian. However, where the pygidium and cephalic margin attained close peripheral contact in enrollment, as in asaphids and Agnostida, there was little change in pygidial size thereafter. Changes in style of enrollment were accompanied by changes in the pleural articulating facets, which are summarized in Figure 192.

LOSS OF GENAL SPINES

Genal spines were lost repeatedly. In many families the presence or absence of genal spines is of significance only at the generic level, and in some families (e.g., Olenidae) there are genera that span the range between having very long (*Olenus*), short (*Leptoplastus*), or no (*Jujuyaspis*) genal spines (Fig. 193). Short genal spines may be present in small growth stages even when absent in adults (Calymenidae, Nileidae). Nonetheless, some families typically lack genal spines—for example, Calymenidae, Cyclopygidae, Phacopidae, and Illaenidae. Presumably, exceptions (e.g., the illaenid *Thaleops*) may consititute a reversal: the reappearance of the genal spine may be paedomorphic. This has been demonstrated in the nileid *Peraspis* (FORTEY, 1975b). Other families never lost their genal spines; for example, we know of no spineless member of the superfamily Trinucleoidea. In this superfamily the genal spines are presumed to play an obligatory part in the functional morphology, and all trinucleoids have a short body, which the genal spines greatly exceed in length. Normally, genal spines may have assisted in molting, added protective armory (especially in the enrolled condition when the spines increase the diameter of the animal), and prevented yawing as the trilobite sank through the water column (cf. FISHER, 1975). It is likely that several of these functions were combined. The readiness with which spines were lost in many families, however, shows that these functions could be suspended. A common tendency was for genal spines to become advanced, to originate far forwards on the cephalon. This happens early in Lower Cambrian Olenellina and Redlichiina and later in such families as Olenidae (Upper Cambrian species), Remopleurididae (Ordovician), and Telephinidae (Ordovician).

EYES

The eyes of all early trilobites are circumscribed by ocular sutures. The earliest example with the eye surface attached is a meraspid olenellid figured by PALMER and HALLEY (1979), but so far as we know the adults had a circumocular suture. By contrast, nearly all post-Cambrian trilobites had the visual surface attached to the free cheek. It is virtually certain that the circumocular suture was lost polyphyletically, having disappeared in parallel in several lineages (in Asaphida, in Olenina, and in Phacopida). After the Ordovician, the Calymenidae were alone in retaining the primitive condition. It is curious that loss of this suture happens in several clades within a short interval of time from the Late Cambrian to the Early Ordovician.

CLARKSON has discussed evolution of the eye in an earlier section. It was primitively large, close to the glabella anteriorly, and probably had a striplike profile. Even in some Early Cambrian species the eye had moved away from the glabella (*Metadoxides*; see PILLOLA, 1991) to take up a position midway across the cheek; this position is highly characteristic of plesiomorphic ptychoparioids and, indeed, of most Middle to Late Cambrian trilobites. In such forms the eye ridge remains prominent and runs inwards to a homologous point near the anterolateral corner of the glabella. In many later, Ordovician to Devonian trilobites the eye ridge is effaced, but in some groups (Odontopleurida and some Aulacopleuridae) it remains distinct, even in species with stalked eyes. Species in which the eye is so far forward that the eye ridge runs inwards and backwards are very rare but occur in the Hapalopleuridae (*Jegorovaia*) and Olenidae (*Remizites*). Hypertrophied eyes and blindness are discussed below as typical evolutionary trends. Eye size
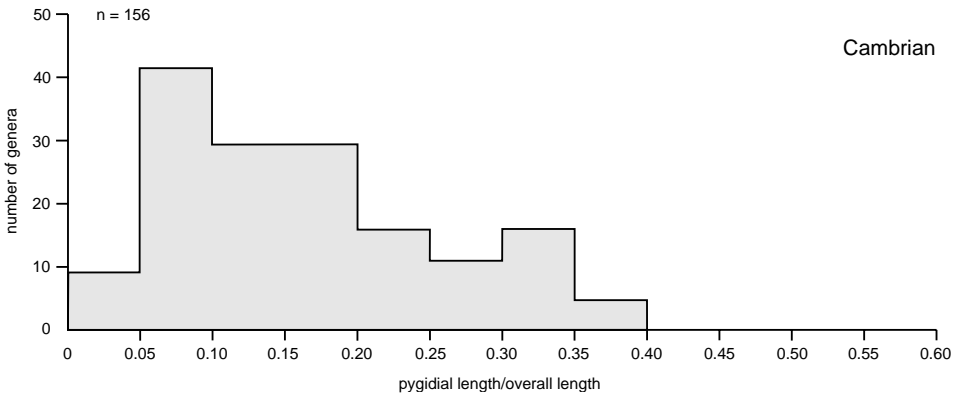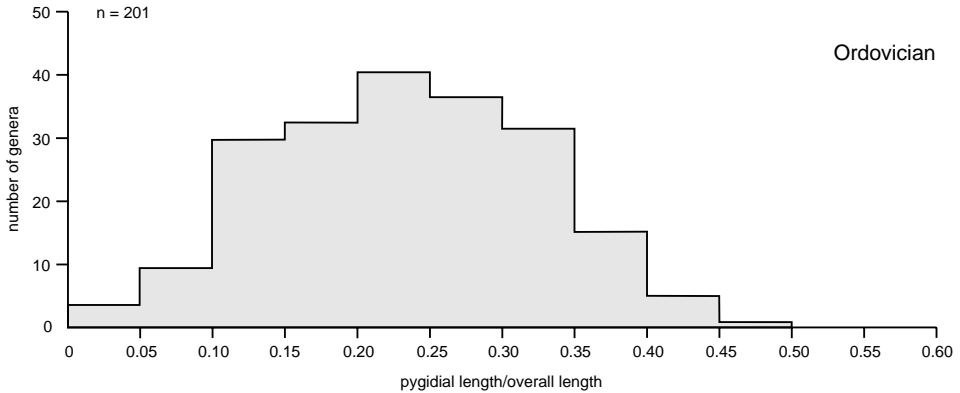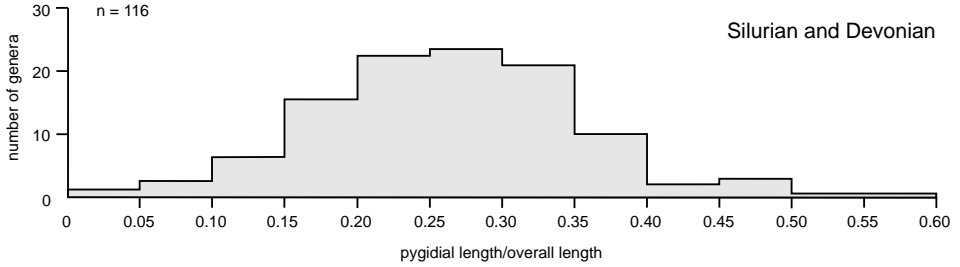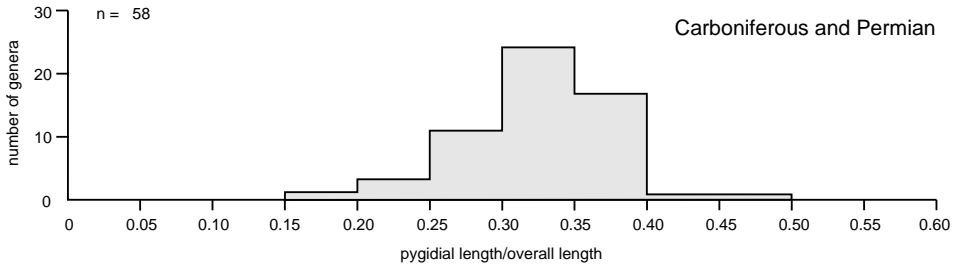
FIG. 191. General increase in the size of the pygidium through time in trilobites other than Agnostida as shown by the proportion of the total exoskeletal length occupied by the pygidium, measured from entire exoskeletons (new).
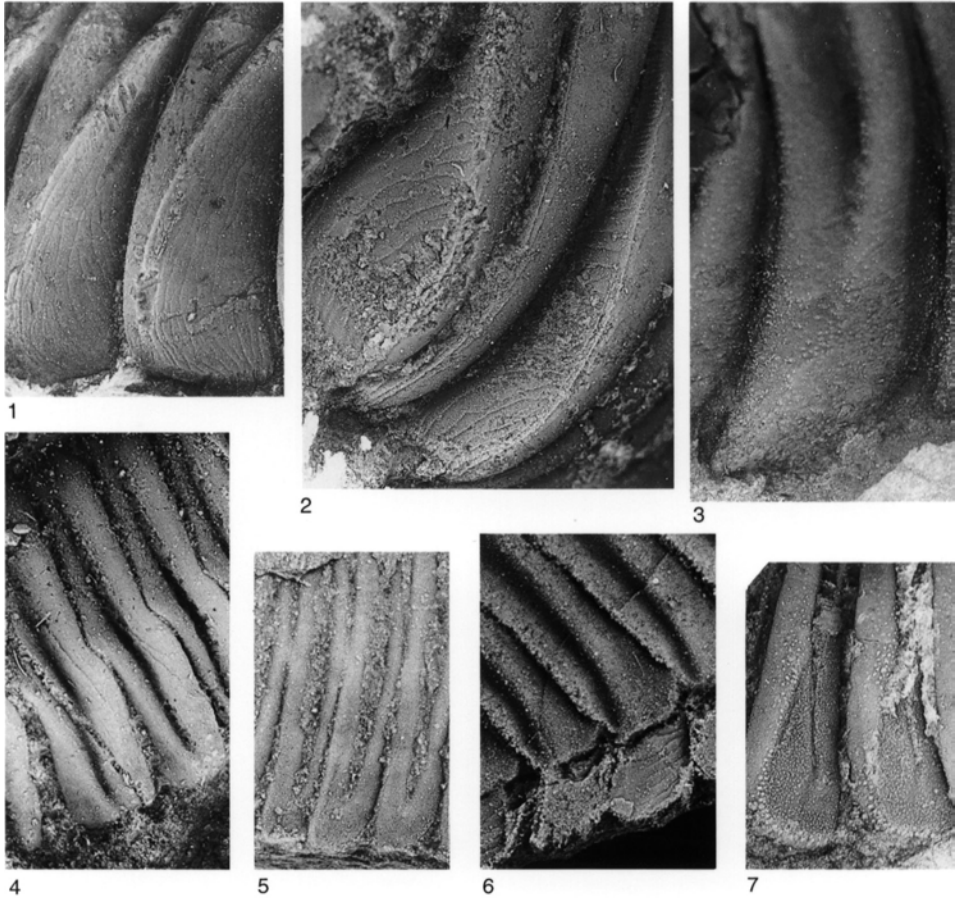
Fig. 192. Advanced and primitive types of articulating facets. *1,* Asaphid, *Asaphus* sp., BM 15430, Middle Ordovician, Russia, ×8. *2,* Nileid, *Symphysurus palpebrosus,* BM It20684, Middle Ordovician, Sweden, ×8. *3,* Granulose dalmanitoid facet, *Dalmanites caudatus,* BM 167a, Silurian, with postfacetal type of pleural furrow, ×8. *4,* Primitive type, smooth, in the Silurian aulacopleuroid *Otarion diffractum,* BM I3603, ×12. *5,6,* Primitive type in the Middle Cambrian ptychoparioid *Elrathia; 5,* BM It5396, dorsal surface, ×12; *6,* BM It5397, narrow doublure with terrace ridges primitive for Asaphina, ×15. *7,* Granulose calymenoid facet, with epifacetal type of pleural furrow, *Calymene* sp., BM It20685, Upper Ordovician, Anticosti Island, ×10 (Fortey & Chatterton, 1988, fig. 13).

is a variable character of trilobites but has been rather widely used in generic diagnoses. Position of the eye in relation to the glabella is constant in many clades; interestingly, after the Late Cambrian there was a reversion to having eyes close to the glabella in several groups, including Proetidae, most Asaphidae, Remopleurididae, and Phacopidae. In several respects remopleuridids look like Olenellina (for example, in the long, curved eye lobe and small pygidium), but we know from phylogenetic analysis that this resem-blance is a product of convergence. At the Permian end of their history, the trilobites had their eyes as close to the glabella as they did at the beginning but with the important difference that these stratigraphically young-est trilobites completely lacked the palpebral furrows and eye ridges of their predecessors.

GLABELLAR FORM

The glabella is one of the most variable of trilobite features and has rightly assumed great importance in taxonomy. Here we only
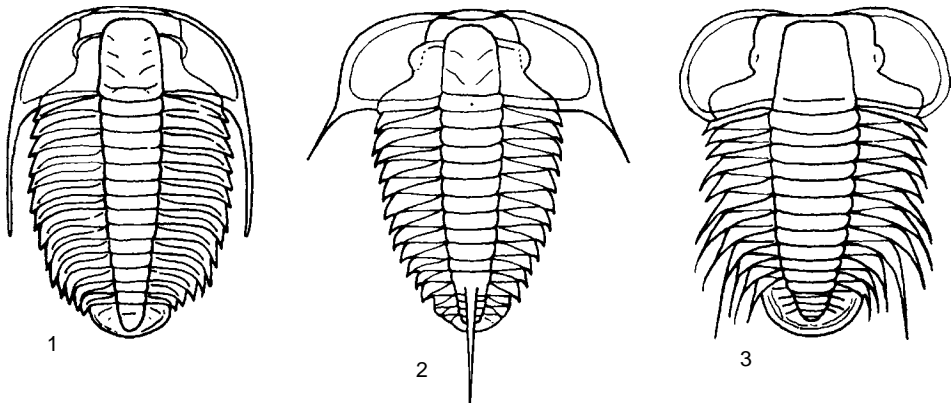
FIG. 193. Loss of genal spines within the monophyletic family Olenidae. *1, Olenus micrurus* SALTER (new); *2, Leptoplastus stenotus* ANGELIN (Henningsmoen, 1957a, pl. 2, fig. 16); *3, Jujuyaspis keideli* KOBAYASHI (Henningsmoen, 1957a, pl. 2, fig. 17).

note some broad evolutionary features. The elongate shape found in Olenellina and the more generalized Redlichiina is probably primitive and is found also in the early Eodiscina. The Agnostina soon acquired glabellar peculiarities of their own, which have led some workers to propose a separate nomenclature for furrows and other cephalic features of these trilobites (Fig. 6). Although inflation of any glabellar lobe can occur, it is perhaps commonest in the frontal lobe and is already displayed by some Early Cambrian Olenellina (*Wanneria*); in Middle Cambrian paradoxidids; in many such Ordovician families as Encrinuridae (*Oedicybele*), Bathyuridae (*Bathyurus*), Dalmanitidae as a whole, and trinucleids; and in the Silurian-Devonian Phacopida and Cheiruridae. After the demise of these groups, phillipsiids acquired similar anterior glabellar inflation in the Permo-Carboniferous. Inflation of the basal glabellar lobe occurred particularly in Ordovician-Silurian Calymenidae. One can find examples where the second glabellar lobe has become particularly inflated (*Chasmops*) or perhaps uncommonly the third lobe (certain Cybelinae). The whole glabella may be inflated in the manner of *Sphaerexochus*. No convincing functional explanation of such inflation has been advanced. A common glabellar modification is

the effacement of glabellar furrows, which proceeds to completion in many families from the Lower Cambrian onwards (Agraulidae, Illaenuridae, Illaenidae, Plethopeltidae). In general, the occipital furrow and 1S are last to become effaced (see *Bollandia*), compared with the more anterior furrows. The question of effacement is considered in more detail below.

The extent to which the glabella of so-called advanced trilobites might incorporate genal material is the subject of some controversy. The ontogeny of several trilobites (Encrinuridae, see EVITT & TRIPP, 1977; Raphiophoridae, *Endymionia,* see WHITTINGTON, 1965) shows that inflated bullar lobes appear in the axial furrows of very small growth stages, and these get larger during subsequent growth stages, growing into the axial region as they do so. In adulthood such lobes would traditionally have been regarded as glabellar—strictly speaking such a glabella would not be homologous with those of other trilobites, because it would incorporate nonaxial material. It is not always clear, however, whether some specialized glabellas include extra-axial material. The curious lateral lobes of lichids (THOMAS & HOLLOWAY, 1988) can be interpreted in several ways—as wholly glabellar, wholly extraglabellar, or partly either. It is clear,

however, that lateral glabellar lobes similar to the bulba have been produced several times in post-Cambrian trilobite history, in several distinctive clades (Monorakidae, Lichidae, Trinucleoidea, Encrinuridae). Bacculae adjacent to the base of the glabella may also have been incorporated into the axial lobe (*Carolinites*, see FORTEY, 1975b). It is probable that all these glabellar modifications were connected with the insertion of musculature for operation of cephalic limbs and, hence, were of fundamental importance for the life of the trilobite. However, trilobites for which limbs are known do not include species with modified glabellar structure, so one cannot say whether peculiar glabellas accompany peculiar cephalic limbs. The only exception may be *Cryptolithus,* which BERGSTRÖM (1972) claimed had appendages that differed from those of other trilobites.

ENROLLMENT

Articulation of the thorax and enrollment have been described in preceding sections. Trilobites having nonfulcrate articulation need further investigation, but this primitive form appears to be known only in Olenellina, some Redlichiina, and rarely in other Cambrian taxa. Nonfulcrate articulation may have allowed complete enrollment but only of the cylindrical type with a lateral gap. Complete enrollment to form a closed exoskeletal capsule characterized Agnostida, is known in the Lower Cambrian *Crassifimbra* (PALMER, 1958) and ellipsocephalids (e.g., WESTERGÅRD, 1936, pl. 11, fig. 9), and may well have become more general among Upper Cambrian trilobites; it is the dominant form of enrollment in the post-Cambrian periods. Presumably enrollment protected trilobites from predation and from sudden changes in the environment. It is now known (BRIGGS, 1994) that large predators capable of inflicting injury on trilobites were present in the Lower and Middle Cambrian. After the Cambrian more varied and swiftly moving predators (cephalopods and, later, fish) may have increased predation pressure and led to the dominance of the closed cap-

sule and the proliferation of coaptative devices (see previous discussion of the evolution of such devices, p. 67). Pleural facets in post-Cambrian trilobites (FORTEY & CHATTERTON, 1988, fig. 13; CHATTERTON & CAMPBELL, 1993, fig. 1d, 1h, 2f, 3g–h) were in some groups large and bore sculpture.

CEPHALIC SUTURES

The opisthoparian facial suture of the Redlichiina is assumed to be primitive, and it is retained by most trilobites. The proparian pattern was derived in the Early Cambrian (Eodiscina), Middle Cambrian (*Schmalenseeia*), Late Cambrian (Norwoodiidae, Loganopeltidae), and Early Ordovician (Olenidae, Phacopida) in what are now known to be independent evolutionary lines. Because a proparian stage is present in early ontogenies of all or nearly all opisthoparian trilobites, the appearance of this feature in a range of adults has been explained as an instance of heterochrony. This appears to be a one-way process, because although opisthoparian sister groups are known or likely for proparian forms (e.g., within Pelturinae in Olenidae, see HENNINGSMOEN, 1957a), we know of no example where a proparian ancestor has been claimed for an opisthoparian trilobite. This implies that once paedomorphosis (broadly interpreted, see MCNAMARA, 1982) has happened it was not possible to revert to the ancestral condition, the later (opisthoparian) phases having been permanently lost from the development program.

On the cephalic doublure, the rostral plate might be interpreted as showing a general tendency towards reduction (Fig. 194): it decreases in width (tr.) through the major trilobite phylogenetic sequence shown by FORTEY (1990a, fig. 14). It comprises the bulk of the venter in Olenellina; in Redlichiina it is frequently still wider than the glabella, but the doublure of the free cheek occupies the rest of the cephalic doublure. In most Ptychopariina it is narrower still, being of the same width (tr.) or less than that of the glabella. The complete loss of the rostral plate followed; the earliest examples are
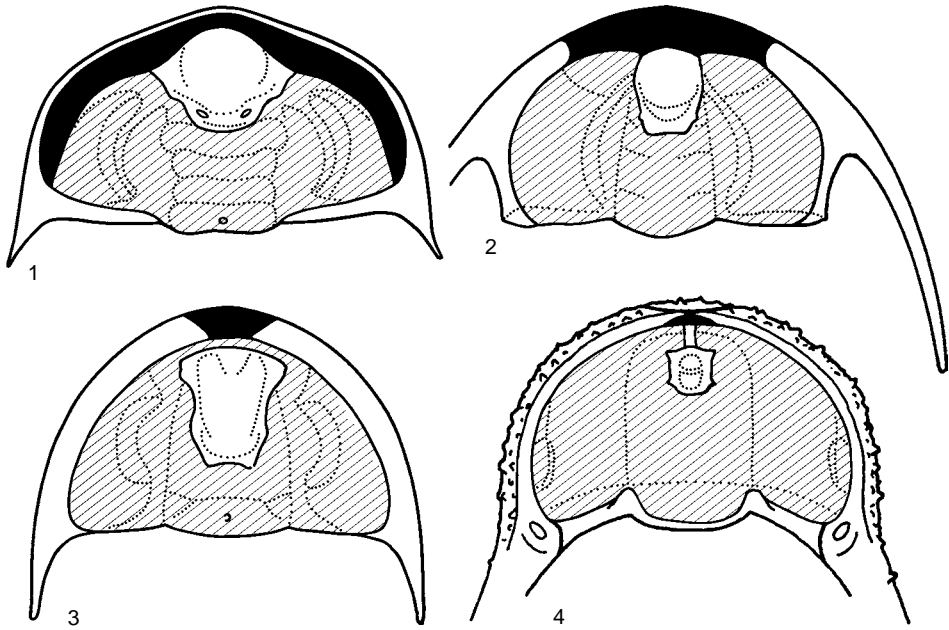
FIG. 194. Reduction in transverse width of the rostral plate (shown by blackened area), as seen in ventral views of *1, Kjerulfia, 2, Redlichia, 3, Proetus,* and *4, Dimeropyge* (*1, 4,* adapted from Moore, 1959, fig. 48b,f; *2,3,* new).

probably Middle Cambrian Anomocaroidea with a median suture (FORTEY & CHATTERTON, 1988). Yoked cheeks, in which ventral sutures have ankylosed, are known in early Late Cambrian Olenidae (*Olenus,* see HENNINGSMOEN, 1957a, fig. 12) and arose independently in numerous later and phylogenetically unrelated families such as Kainellidae, Nileidae, Trinucleidae, Phacopidae, and Shumardiidae.

Most types of ventral sutures, however, persisted side by side after the Middle Cambrian to the end of the Ordovician, when all forms with a median suture became extinct. Wide rostral plates are typical of the Illaenidae, for example, while narrower rostral plates persisted in some Bathyuridae, Odontopleuridae, and Proetidae. The evidence is that the rostral plate was a persistent structure even when it became exceedingly narrow, as it did in Encrinuridae (TRIPP, 1962) and Dimeropgyidae (WHITTINGTON, 1963). On this basis FORTEY and CHATTERTON (1988) believed that its reduction to a median suture was likely to be a character of

major phylogenetic importance. However, fusion or ankylosis of the sutures appears to have happened more readily; for example, fused cheeks are known in some examples of large asaphids where median sutures are present in smaller individuals of the same species (*Isotelus*). Fused cheeks derived from loss of the median suture look identical to those derived from ankylosis of the connective sutures, and phylogenetic analysis is needed to reveal the history. We believe that the Olenidae, Shumardiidae, and Phacopidae were derived from ancestors having rostral plates, whereas Nileidae, Kainellidae, Cyclopygidae, and probably Trinucleoidea were derived from ancestors having a median suture.

HYPOSTOMAL ATTACHMENT

Different modes of attachment of the hypostome remain constant through whole trilobite clades: Odontopleurida and Lichida are always conterminant, Ptychopariina natant, and Phacopidae impendent, for example. However, it is clear that there is an

evolutionary sequence in some trilobites from natant to conterminant to impendent. This is because advanced members of well-established clades have attached hypostomes, and primitive ones have natant hypostomes. Particularly good examples are known from the Remopleuridoidea and Proetida (Fig. 195). Furthermore, trilobites having impendent hypostomes were more advanced than those with conterminant hypostomes. There is no known instance of trilobites with such secondarily attached hypostomes having given rise to trilobites with natant hypostomes. Trilobites with the natant hypostomal condition correspond broadly with Ptychopariida in the sense of the 1959 *Treatise* (MOORE, 1959).

It is known that Redlichiina had conterminant hypostomes (W. ZHANG, LU, & others, 1980, pl. 20, fig. 9), and if it is assumed that this represents the primitive trilobite morphology, it is then apparent that the Ptychopariina (having a natant hypostome) were themselves a derived group. The derivation of the detached, natant hypostome can be traced to the upper Lower Cambrian, where some protolenids were undoubtedly natant but which otherwise retained many of the primitive characters of the Redlichiina. Hence, the conterminant hypostomal condition can be either primitive (primary conterminant condition) or secondarily derived from a natant condition. Primary conterminant trilobites include such important Cambrian groups as the Corynexochida and probably the Lichida, Odontopleurida, and Illaenina. Secondarily conterminant trilobites appear in the geological record after the appearance of the natant condition, as would be expected. The earliest secondary attachment of the hypostome to the doublure is probably the ceratopygid *Proceratopyge* in the upper Middle Cambrian (RUSHTON, 1983). In Proetida all known early species from the Ordovician were natant, and the conterminant and impendent forms only became prevalent in the later (Carboniferous to Permian) history of the group, after all other conterminent and
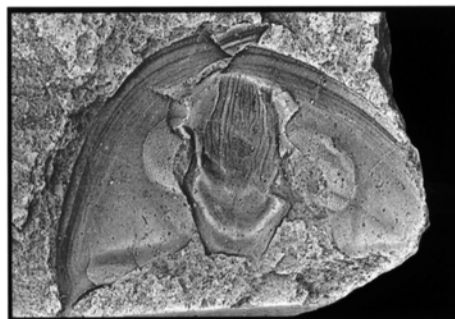
FIG. 195. Examples of secondary attachment of the hypostome in Carboniferous (Dinantian) Proetida. Primitive sister groups of these trilobites all had natant hypostomes, and the attachment of hypostome to doublure is secondary. *1,* Impendent condition in *Griffithides acanthiceps* WOODWARD, from Derbyshire, England (NMW 86.25G.2332), ×5. *2,* Secondary conterminant condition in *Archegonus (Phillibole)* sp. aff. *A. (P.) aprathensis* (RICHTER & RICHTER) from Lancashire, England (NMW 88.36G.10), ×3 (Fortey, 1990a, fig. 5b,c).

impendent trilobites belonging to other trilobite orders had died out. Clearly, the hypostomal attachment condition closely reflected the feeding mode of the trilobite, and such Proetida were presumably filling niches that were previously occupied by styginid (conterminant) or phacopoid (impendent) trilobites.

The sequence of events is illustrated in Figure 196. The paraphyletic redlichiids gave rise both to derived groups of trilobites with primary conterminant hyopstomal attachment (Corynexochida, Lichida, etc.) and to the first natant forms. The latter speciated
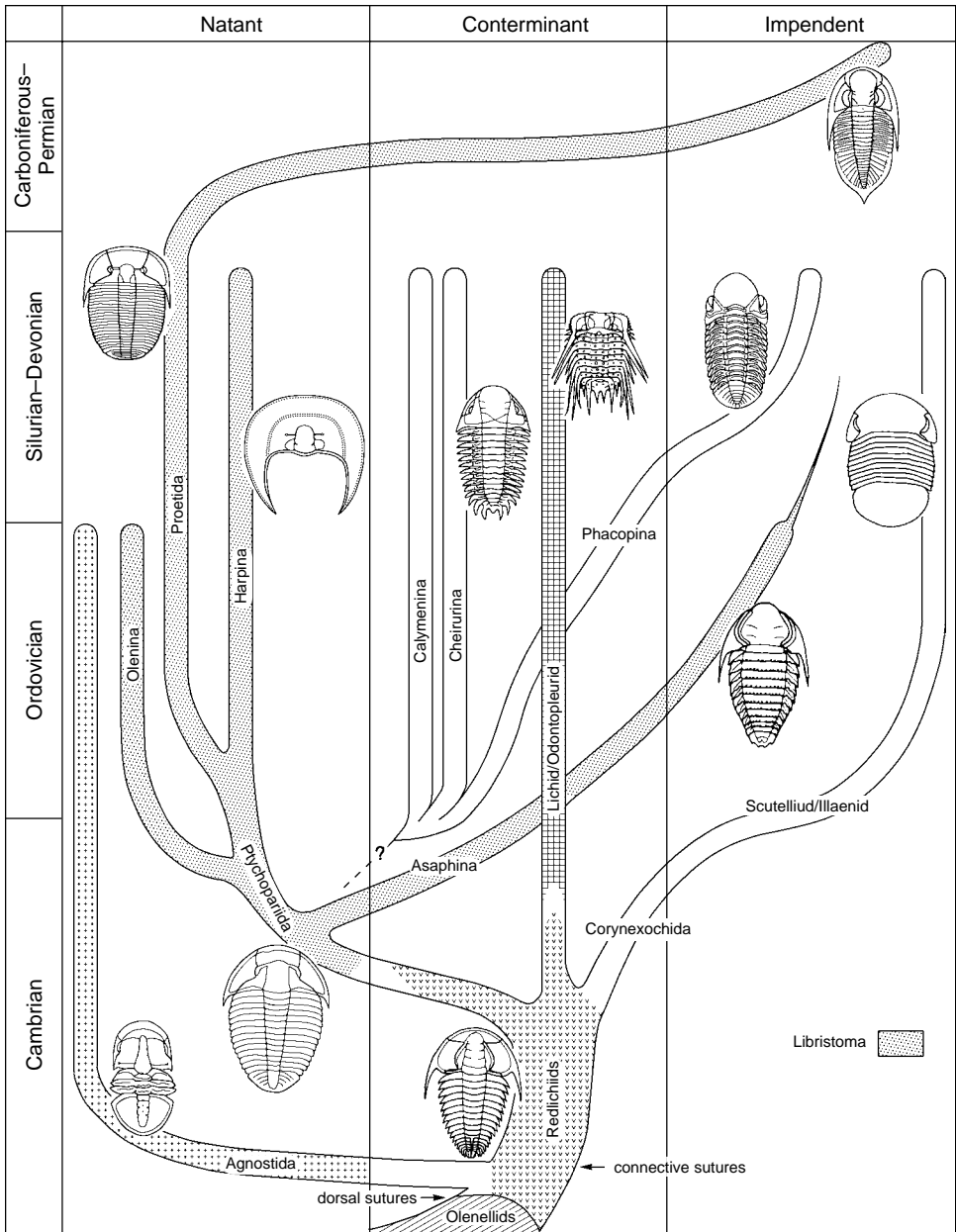
F<small>IG</small>. 196. Summary of the history of hypostomal attachment and the phylogeny of the Trilobita (adapted from Fortey, 1990a, fig. 19).

rapidly in the Middle to Late Cambrian, but quite soon secondary attachment of the hypostome occurred in some groups, so that by the Ordovician primary conterminant, natant, and secondary conterminant trilo-bites lived side by side. Impendent trilobites became common at this time. Some of the secondarily conterminant families of Asaphina became extinct at the end of the Ordovician. Later, some of the groups of
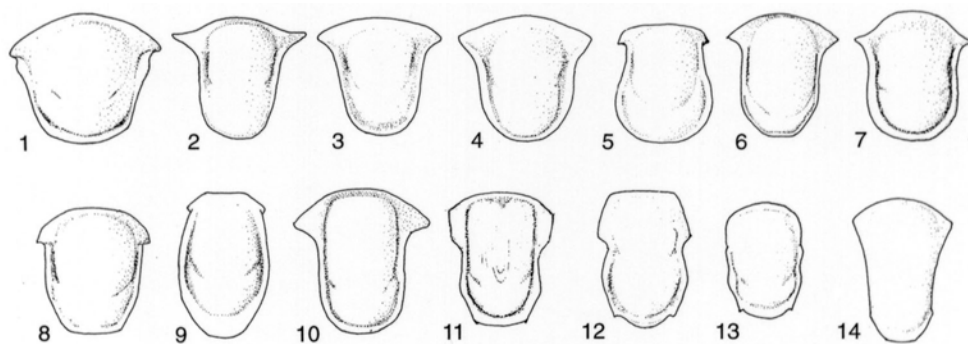
FIG. 197. Lack of morphological change through time in natant hypostomes; examples from several families ranging in age from Lower Cambrian (*2*) to Carboniferous (*14*). *1, Drepanopyge* (Yinitidae), Lower Cambrian, a primitive example of an attached hypostome, showing that this early morphology is retained in natant forms, ×2; *2, Crassifimbra* (Ptychopariidae), Lower Cambrian, ×10; *3, Conocoryphe* (Conocoryphidae), Middle Cambrian, ×4; *4, Ptychoparia striata* (Ptychopariidae), Middle Cambrian, ×2.5; *5, Dunderbergia* (Alokistocaridae), Upper Cambrian, ×10; *6, Aphelaspis* (regarded as Pterocephaliidae), Upper Cambrian, ×5; *7,* a hystricurid, Lower Ordovician, ×9; *8, Parabolinella* (Olenidae), Lower Ordovician, ×4; *9, Bathyurellus* (Bathyuridae), Lower Ordovician, ×3; *10, Paraproetus* (Proetidae), Upper Ordovician, ×7; *11, Proetus* (Proetidae), Silurian, ×4; *12, Koneprusites* (Proetidae), Devonian, ×6; *13, Voigtaspis* (Proetidae), Devonian, ×3; *14, Gitarra* (Phillipsiidae), Carboniferous, ×3 (Fortey, 1990a, fig. 11).

Proetida became secondarily conterminant, and following the Late Devonian extinctions, this group alone was the source of all modes of hypostomal attachment.

HYPOSTOMAL SPECIALIZATION

This specialization is connected with hypostomal attachment because all the known specialized hypostomal forms are associated with the conterminant or impendent condition. Natant hypostomes are remarkably similar in the many different groups in which they occur, from the Lower Cambrian to the Carboniferous (Fig. 197). They are also similar to many hypostomes of Redlichiina, characteristic features being an elongate middle body with short middle furrows, narrow borders, and the lack of prominent forks, distinctive maculae, coarse sculpture, or other specializations like the rhynchos. Hypostomes attached to the doublure were usually rigidly braced (WHITTINGTON, 1988a, 1988b). Regardless of whether they were primarily or secondarily attached, modifications of the Redlichiina bauplan follow a number of directions. Appearance of posterior forks is doubtless polyphyletic, being known from asaphids,

lichids, calymenids, remopleuridids, and late Proetida. The deepest known forks are in the remopleuridid *Hypodicranotus* and the asaphid *Lycophron.* Hypostomes that are wider (tr.) than long are uncommon; the widest known is that of the cyclopygid *Degamella,* but hypostomes of some nileids (*Nileus*) and *Remopleurides* are also wide (tr.). In Nileidae much of this width is accounted for by wide lateral borders, and wide borders occur also in the hypostomes of several other families, especially Dameselloidea, Asaphidae, and Lichida. The macula is found principally upon attached hypostomes (Fig. 198). Many rigidly attached hypostomes developed a strong surface sculpture on the middle body. In some Asaphidae, Nileidae, and Illaenidae, strong terrace ridges run continuously from the cephalic doublure to the hypostome, and it is clear that together the two comprise a single functional unit. This may be the best known instance in which terrace ridge systems had a sediment-gripping function (see SCHMALFUSS, 1981). Other hypostomes may be granulose (invariably so in Cheiruroidea, and in most Phacopina and Odontopleurida) or even coarsely tuberculate. The inner edge of the
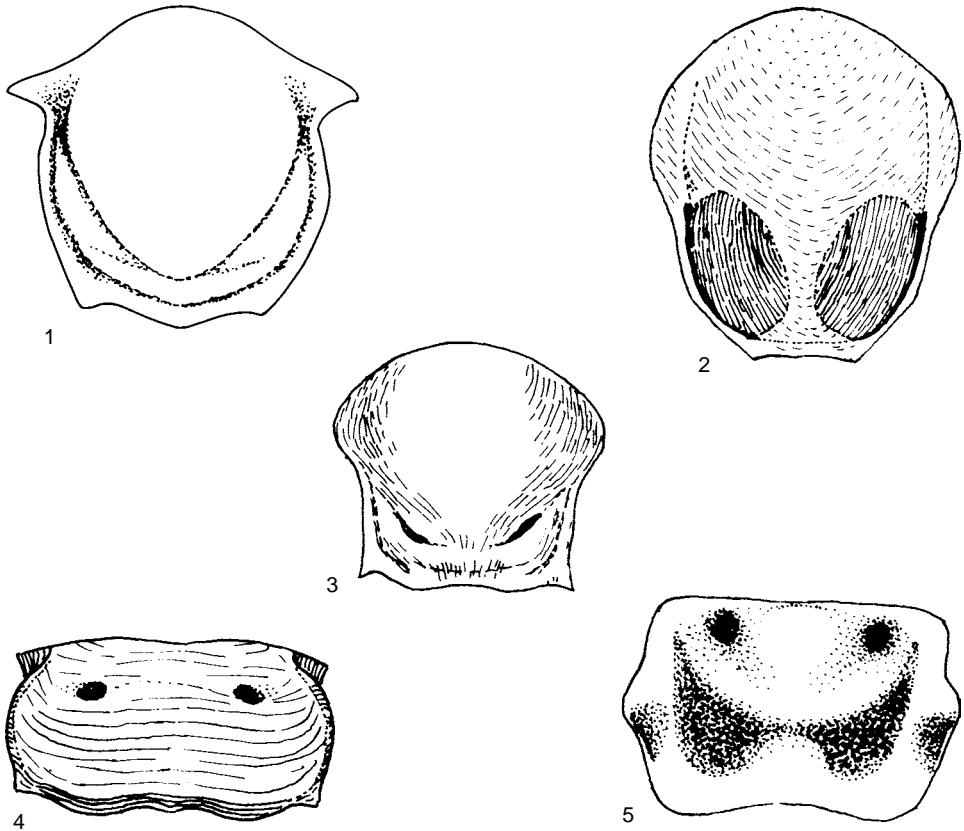
FIG. 198. Maculae in attached hypostomes. *1, Hypermecaspis latigena* FORTEY; *2, Robergia schlotheimi* (BILLINGS); *3, Paradoxides minor* (BOECK); *4, Nileus affinis* BILLINGS; *5, Ceratocephala plummeri* CHATTERTON & PERRY (new).

fork may be equipped with grinding surfaces (Silurian Odontopleurida, CHATTERTON & PERRY, 1983) or rasping surfaces (the Ordovician asaphid *Isotelus*). It is clearly not fanciful to suppose that in these trilobites the margin of the hypostome assisted in the maceration and preparation of food, and it is reasonable to add that tougher or bulkier items could be handled by trilobites equipped with these hypostomal modifications. While the hypostome (both conterminant and natant) primitively occupied quite a small part of the cephalic venter (e.g., *Elrathia,* see FORTEY, 1990a, pl. 1), in derived forms with forks and the like the hypostome can occupy a much larger area, the maximum possibly being in the Lichida. This suggests that, in addition to playing a fuller part in the preparation of food, the hypo-

stome also protected the delicate underside of the head. Conversely, natant hypostomes remained proportionately rather small, regardless of geological age. This, coupled with their conservatism, is additional evidence that natant forms probably habitually dealt with small particles and may have included the detritivores and filter feeders among the trilobites.

SCULPTURE

Sculptural type is exceedingly variable in the trilobites. FORTEY and WILMOT (1991) showed that thicker cuticles (greater than 200μ) tend to be associated with inshore sites, at least in the Early Ordovician. Because coarse tuberculation is associated with thick cuticle, it is not surprising that this sculptural type is commonest in epeiric habi-

tats (many Phacopidae, Brachymetopidae, etc.). However, such sculpture appears to have been relatively rare before the Late Cambrian, regardless of habitat. It may be that most early Cambrian trilobites had thin cuticles, but there are few data.

Many trilobite families have species characterized by different surface sculptures: granules, raised lines, terrace ridges, fine pits, smooth, or any combination of these. WHITTINGTON (1959a) and NIKOLAISEN (1983) have shown that various species of Ordovician Remopleurididae are typified by such sculptures. FORTEY (1974b) recognized different species of the Ordovician olenid *Balnibarbi* by their different surface sculpture. In life, sculptural patterns may have been enhanced by color patterns and functioned in species recognition or camouflage; some tubercles and pits may also have been associated with sensory organelles.

Most surface sculpture is surficial (as the name implies), and internal surfaces of the cuticle are comparatively smooth. However, in some trilobites (see illaenids in WHITTINGTON, 1965) different sculptures occur on internal and external cuticular surfaces. The smaller kinds of granules and ridges are considered to be too small to have had much function in strengthening the cuticle. They also tend to be absent over so-called muscle insertion areas. The evolution of sculptural types, if they functioned in species recognition, may have been somewhat haphazard; certainly there is no consistent progression from smooth to granulose to ridged. Some higher taxa of trilobites are broadly typified by one sculptural type. The granulose-reticulate sculpture of the cheiruroid genae is one example, the Bertillon pattern of Styginidae another. With a little experience most observers recognize the typical lichid sculpture of variously sized pustules. Nonetheless, the function of these particular kinds of surface sculpture remains obscure.

Concentric terrace ridges are present on the doublure of most trilobites, including Redlichiida, and they were probably lost in only two groups: Phacopida and Odontopleurida, where they were replaced by pustules or small, scalloped ridges. The function of terrace ridges is controversial, and hence the signficance of their loss is difficult to interpret. MILLER (1975) claimed that terrace ridges functioned as part of a system for monitoring currents. If, as claimed by SCHMALFUSS (1981), terrace ridges gripped the sediment during the creation of a filter chamber beneath the trilobite, then their loss would indicate abandonment of filter-feeding habits. MILLER (1976) and MCNAMARA (1980) have suggested that some Phacopida may have been predators, for example. On the other hand, some terrace ridges on the doublure cannot have gripped the sediment, especially in those species where the doublure is broad and reflexed against the dorsal exoskeleton to extend close to the axis, at which the appendages articulated (*Symphysurus*, FORTEY, 1986). In most Cambrian species, especially primitive libristomates, ventral terrace ridges are feeble. They become strongly developed in some younger families, especially on the cephalic doublure: Asaphidae (*Niobe*), Illaenidae, Nileidae, Brachymetopidae. In such forms the ridges may have rested on, restrained, or shoveled sediment. It does not seem possible for this function to have applied to odontopleurids with a border of downward-pointing spines, and perhaps this explains the loss of terrace ridges in this family.

EVOLUTION OF REPEATED MORPHOTYPES IN TRILOBITE HISTORY

During the course of trilobite history some designs appeared repeatedly. What is known of the phylogenetics of the group indicates that these designs appeared independently within different major taxa. FORTEY and OWENS (1990a) described these distinctive designs as morphotypes. Some morphotypes can be linked with a specific life habit; for others this habit is unknown or is the subject of debate.

Many trilobites become effaced—that is, they lose defined dorsal furrows. Often glabellar furrows are effaced first (*Eremiproetus*),

followed by the occipital furrow (*Platy-peltoides*), and then the axial furrows (*Illaenus*). In some trilobites effacement first occurs at the front of the glabella (*Parvigena, Geragnostella*), resulting in an entirely smooth cephalon. In others (e.g., *Leiagnostus*) the entire dorsal exoskeleton becomes effaced. As Lane and Thomas (1983) observed, such effacement is polyphyletic, and highly effaced trilobites come to resemble one another. This causes taxonomic problems: do effaced end members really deserve the generic status they are often accorded? In some groups (Styginidae and Agnostina especially) almost any genus appears to be capable of becoming effaced. The oldest example we know of is the Early Cambrian genus *Giordanella;* the youngest is *Paraphillipsia* from the Permian. Ontogenies of effaced trilobites show that early growth stages are less effaced (e.g., *Leurostega,* Robison & Pantoja-Alor, 1968), and effacement was therefore of benefit to the adult, but what advantage it conferred is not known. Effacement may have resulted from more than one selection pressure because it is found in trilobites that lived in widely different habitats with completely different morphology. It occured in deep-water, benthic olenids with thin exoskeletons, supposedly planktonic Agnostina, and comparatively inshore illaenids and asaphids having thick cuticles. It does not contribute in any obvious way to streamlining, and although effaced trilobites are frequently convex, there are examples of effacement of trilobites of low convexity (Styginidae). Hence, effacement may not have been in response to a common external cause in all instances and is not one of the simpler examples of homeomorphy.

MORPHOTYPES AND THEIR STRATIGRAPHIC DISTRIBUTION

Fortey and Owens (1990a) distinguished eight trilobite morphotypes, which are common and distinctive morphologies appearing in several phylogenetic lineages. More morphotypes can be recognized, but this sample provides some measure of evolutionary activity in the trilobites because there were times at which these morphotypes were numerous and others when they are rare. The morphotypes are summarized as follows (Fig. 199–200).

PHACOMORPH

These are convex trilobites that are nearly isopygous and have tuberculate sculpture in many species. Other characteristics include a tumid glabella, which expands forward, with the posterior glabellar furrows (when present) forming the intercalating ring and a pygidium with strongly furrowed pleural fields and prominent axis. Large-eyed phacomorphs are typical shelf inhabitants. As the name implies *Phacops* is the typical representative, but phacomorphs are derived from other families such as Bathyuridae (*Bathyurus, Petigurus*), Asaphidae (*Norasaphus*), Hammatocnemidae (*Ovalocephalus*), and Phillipsiidae (*Ditomopyge*).

PELAGIC

This morphology was described by Fortey (1985). Hypertrophied and often convex eyes and reduced (tr.) thoracic pleurae are typical features. Telephinidae, Bohemillidae, and Cyclopygidae are exemplars of this morphotype (Fig. 199.1–2).

ILLAENIMORPH

These trilobites are among the most highly effaced of all trilobites, and they are characterized by lack of a marked change in convexity between the axial and pleural areas as well as by effacement of glabellar and ring furrows. The eyes are relatively far back. Typically the sagittal convexity of the cephalon exceeds that of the thorax and pygidium, which may have been partly buried in soft sediment in the bumastoid stance described by Westrop (1983). Illaenidae (Fig. 199.3–4) provide the type examples, but there is also a confusing range of similar forms from Plethopeltidae, Koldinioididae, Styginidae, and Proetidae.
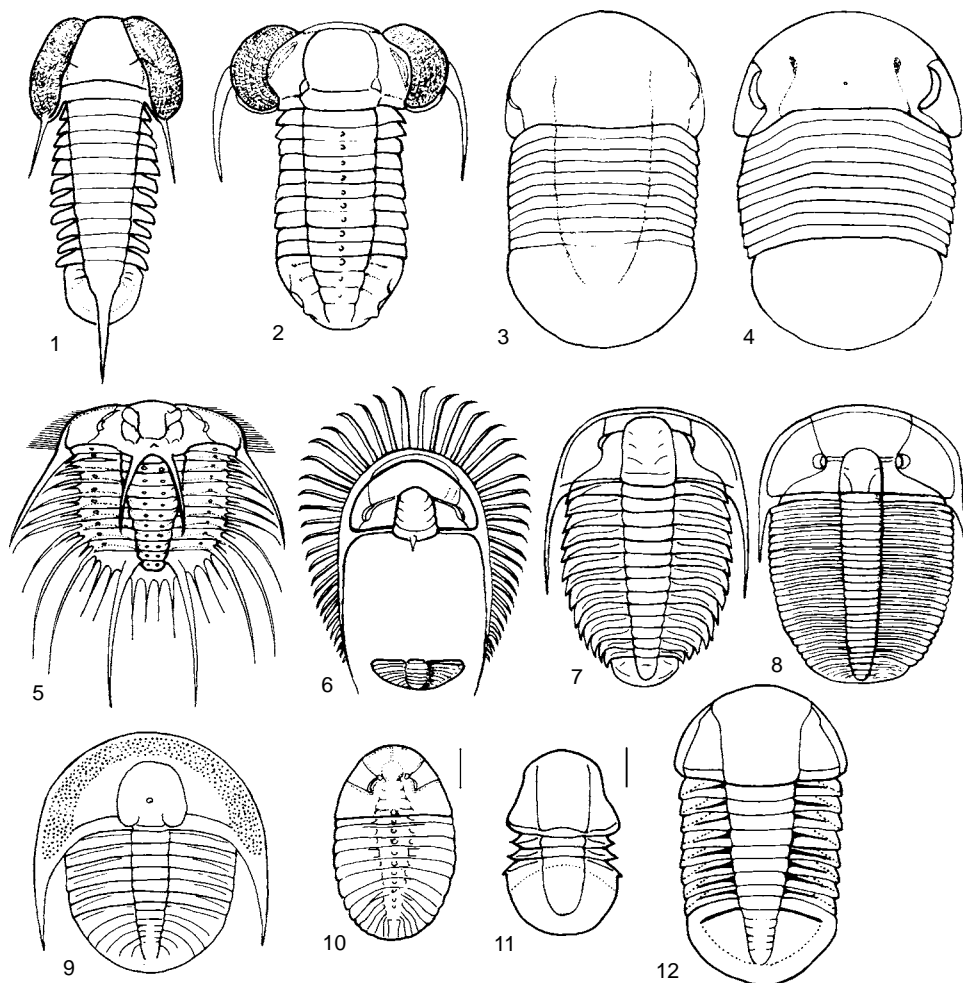
FIG. 199. Major morphotypes that have appeared several times from separate phylogenetic origins in the history of the Trilobita. *1–2,* Pelagic: *Opipeuter inconnivus* FORTEY and *Carolinites genacinaca* ROSS; *3–4,* Illaenimorph: *Illaenus sarsi* JAANUSSON and *Bumastus barriensis* MURCHISON; *5–6,* Marginal cephalic spines: *Odontopleura ovata* EMMRICH and *Bowmania americana* (WALCOTT); *7–8,* Olenimorph: *Olenus micrurus* SALTER and *Aulacopleura koninckii* (BARRANDE); *9,* Pitted fringe: *Dionide levigena* FORTEY & OWENS; *10–11,* Miniaturization: *Schmalenseeia amphionura* MOBERG and *Thoracocare minuta* (RESSER); *12,* Atheloptic: *Illaenopsis harrisoni* (POSTLETHWAITE & GOODCHILD). Magnifications range from approximately ✕0.5 to ✕2.5, except for views 10 and 11, where the scale bars represent 1 mm (Fortey & Owens, 1990a, fig. 5.4).

ATHELOPTIC

These trilobites have greatly reduced eyes although their close relatives are known to have had normal eyes (FORTEY & OWENS, 1987). (Agnostina are not atheloptic because eye reduction typifies the whole clade.) They are often but not invariably associated with deeper-water biofacies. The dalmanitinoid *Ormathops* is typical, but this is a common morphotype from the Middle Cambrian onwards.

MINIATURIZATION

Miniature trilobites, which achieve maturity at a millimeter or two in length, are possibly always the product of progenesis

(Fig. 199.10,11). *Shumardia* is a typical example.

PITTED-FRINGE TRILOBITES

The trinucleid trilobite is typical of this morphotype, in which a fringe is formed by more than one row of pits in the dorsal cephalic margin, which are opposed by a wide, lower lamella carrying corresponding pits on the external surface. Harpetids and dionidids are similarly constructed (Fig. 199.9).

OLENIMORPH

These are *Olenus*-like trilobites with thin cuticle, narrow axis, wide (tr.) but short (exsag.) thoracic pleurae, and many thoracic segments. Olenimorphs were probably adapted to cope with low oxygen concentrations, the numerous segments and the wide pleural regions increasing both the number and length of respiratory exites. Stratigraphically early examples include *Mexicella,* while the latest example is probably the aulacopleurid *Aulacopleura* (Fig. 199.8).

MARGINAL CEPHALIC SPINES

Trilobites with an array of spines around the cephalic margin are typically odontopleurid, but a similar morphology has been derived from other sources, e.g., the Upper Cambrian entomaspidid *Bowmania* (Fig. 199.5–6).

A plot of the distribution of these morphotypes through time (Fig. 200) shows that more examples were contributed by more families during the Ordovician than at any other time, after a build-up in the Late Cambrian. The end-Ordovician extinction produced a drastic decline in the number of families providing the morphotypes, and the pelagic morphotype disappeared forever. The Silurian had fewer families than the Devonian. Several more of the morphotypes,

including olenimorphs and pitted fringes, disappeared at the Frasnian-Famennian extinctions. Proetida alone continued to provide several of the morphotypes until the end of the Permian.

This history of morphotypes provides, in microcosm, a pattern such as has been described for trilobite morphology as a whole and for hypostomal attachment: increase in variety through the Cambrian, a burst in the Ordovician that is curtailed by the end-Ordovician extinction, and subsequent recruitment of similar morphotypes from other families until the Late Devonian extinctions, after which the Proetida alone simulated earlier morphologies.

SPECIES-LEVEL EVOLUTION: CASE HISTORIES

In view of the number of trilobites known, there are very few well-supported examples of species-level change through stratigraphic sequences. Even fewer are supported by plausible scenarios giving a functional explanation of claimed trends. In contrast, there are many phylogenies of families, usually given at the end of a monographic treatment of the group in question in the form of a tree linking genera by dotted lines. Such phylogenetic diagrams have been proposed for the following families: Phacopidae (CHLUPÁČ, 1977), Cheiruridae (LANE, 1971), Encrinuridae (STRUSZ, 1980), Olenidae (HENNINGSMOEN, 1957a), Lichida (THOMAS & HOLLOWAY, 1988), Calymenoidea (HAMMANN, 1983), and Proetinae (LÜTKE, 1980). Such analyses are useful summaries, but they are, nonetheless, theoretical constructs. Cladistic analyses of the same taxa may produce different patterns, which can also be interpreted phylogenetically. Here we refer only to case histories that are alleged to represent the evolutionary history itself, species by species.

FIG. 200. The distribution of important trilobite morphotypes through geological time, showing periods of optimal diversity of design, especially during the Ordovician, with major reduction following the late Ordovician extinction event and subsequent recovery (adapted from Fortey & Owens, 1990b, fig. 7.6).
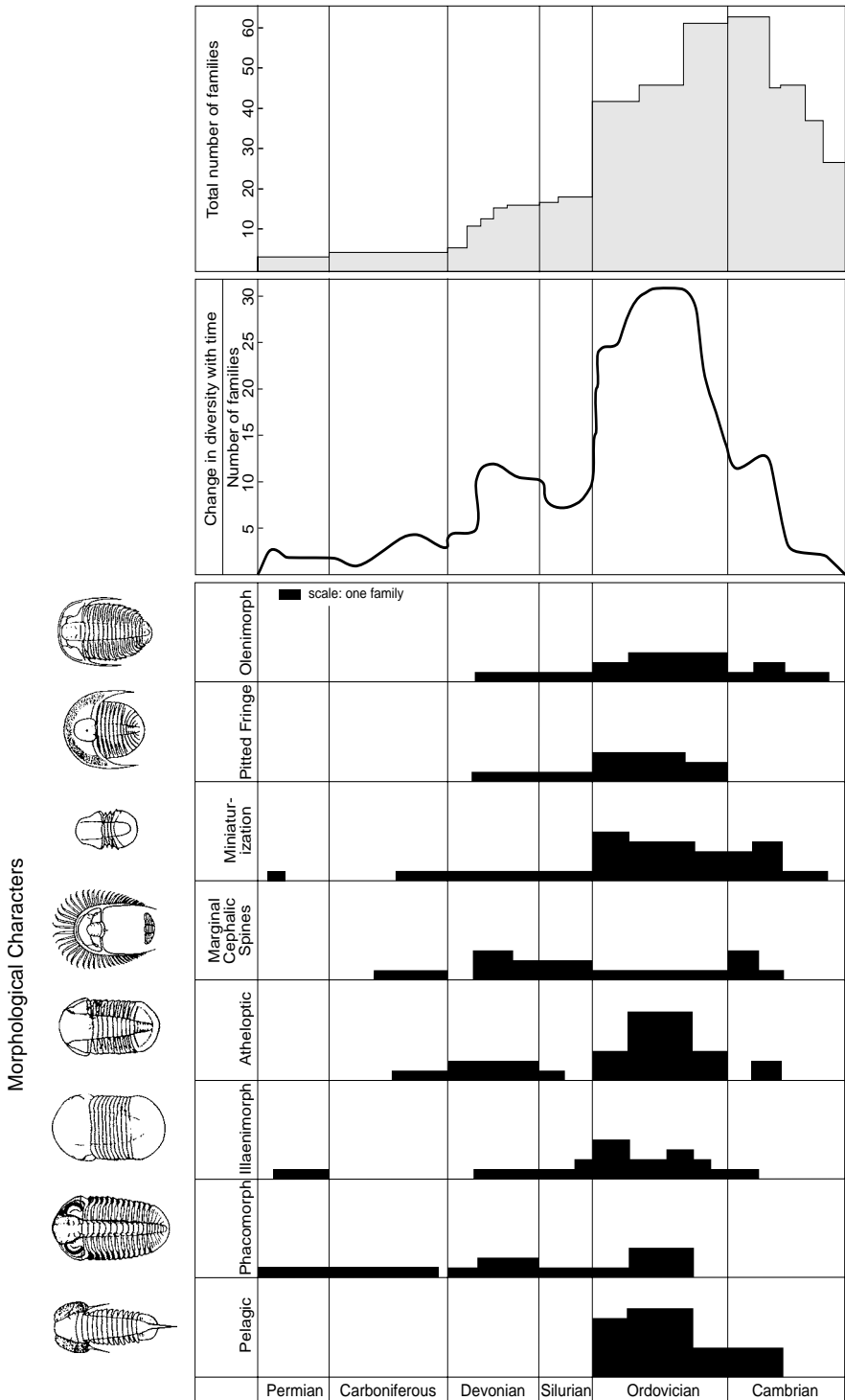
FIG. 200. *For explanation, see facing page.*

LOSS OF EYES AND BLINDNESS

Loss of eyes and blindness occur as a repeated trend in trilobite evolution. In Phacopoidea it is known to be highly polyphyletic (Fig. 201; see also Fig. 118) and can happen in two ways: the eye can migrate to a marginal position to become eventually eliminated or the number of lenses can be progressively reduced. Few examples from phacopoids, however, include all stages from ancestors with eyes to blind descendant species; most are plausible morphological series. Figure 119 gives an example of a true lineage in which much of the rest of the morphology of the trilobite remains the same, and it is clear that loss of the eyes does not involve major genetic restructuring. It is known that cave-blindness happens readily among living, aquatic arthropods.

ANTERIOR FUSION OF HYPERTROPHIED EYES

The pelagic morphotype has enlarged eyes, and there are several examples in which the eyes migrated anteriorly. In its extreme development, the eyes eventually touch on the midline to form one enormous visual organ. This morphology has its analogue in the living hyperiid crustacean *Cystosoma.* These monocular trilobites are always stratigraphically younger than closely related species with normal paired eyes, and hence this is another example of a polyphyletic trend. In the Ordovician Cyclopygidae (MAREK, 1961) such anterior fusion occurs in three genera, *Cyclopyge, Pricyclopyge,* and *Microparia.* However, a species-to-species lineage recording this fusion is known only in *Pricyclopyge* through an apparently gradualistic series of subspecies of *P. binodosa* (SALTER) collected from successive zones in the late Arenig to Llanvirn (Fig. 202). Although there is variation in the separation of the eyes within any one population of the earlier subspecies, the eyes are eventually conjoined in *P. binodosa synophthalma* (KLOUČEK). Anterior enlargement and fusion of the eyes was presumably particularly useful to pelagic trilobites and occurs exclusively in this morphotype.

OLENID EVOLUTION

Olenidae often lived in oxygen-poor environments that preserve an exceptionally complete stratigraphic record. Bed-by-bed collecting through olenid-rich sequences has yielded plausible phyletic series of species (HENNINGSMOEN, 1957a) that have been studied in great detail. KAUFMANN (1933) described the succession of *Olenus* species in the earlier part of the Scandinavian Upper Cambrian, using quantitative analysis of large samples. A series of olenid species could be identified using cranidial characters that appeared suddenly in the stratigraphic record, but within these species rapid change in pygidial characters occurred. Although KAUFMANN regarded the species as having been derived from a conservative stock not present in the sections studied, the succession of species could equally be regarded as an example of rapid change, i.e., punctuated equilibrium (see, however, HOFFMAN & REIF, 1994). FORTEY (1974b) used the latter explanation to describe a lineage of olenid species from the Lower Ordovician (Arenig) of Spitsbergen, but in this lineage more aspects of morphology changed between species than in *Olenus,* including width of preglabellar field, eye position, and pygidial size. An interesting feature of the lineages from Spitsbergen was that different, closely related species were typified by different surface sculpture patterns, which may have functioned during sexual selection. Changes of surface sculpture are commonly seen in trilobites and are not otherwise readily explicable.

COAPTATIVE DEVICES IN ENROLLMENT

Changes in coaptative devices in lineages such as that of species of *Placoparia* (Fig. 69) are particularly persuasive as evolutionary examples because most of the other morphological features were little changed. The species in this series are described as part of a

punctuated lineage. The inference that the evolutionary changes resulted in the capacity for tighter enrollment is a reasonable one.

TRINUCLEID FRINGES

The size, number, and arrangement of pits in the Ordovician trinucleid fringe vary greatly and provide important criteria for systematics (C. P. Hughes, Ingham, & Addison, 1975). Changes in species of *Onnia* were described by Owen and Ingham (1988), but no functional hypothesis explains the kind of changes that occurred.

GRADUALISTIC CHANGE IN PYGIDIAL RIBBING

Sheldon (1987) described sequential changes in pygidial ribs through a British Ordovician sequence based on very large quantitative samples. Similar increases in number of pygidial ribs at the population level take place in several co-occurring lineages from different trilobite families. Within the general trend, Sheldon observed short-lived reversals in the ribbing number. This work is important because it is one of the few quantitatively based studies where apparently gradualistic change has been demonstrated in more than one genus at one time. The fact that similar changes occur in several lineages might argue for some ecophenotypic control (rather than speciation), but Sheldon correctly noted that end members would certainly be regarded as species in conventional trilobite taxonomy.

HETEROCHRONIC CHANGES

Heterochronic lineages of species of Cambrian olenellids were described by McNamara (1978). Heterochrony has been invoked as an important source of evolutionary novelty, but there are comparatively few examples where species-by-species evolution by means of heterochrony has been demonstrated, although it is plausible in many instances. See, for example, comments on origins of Agnostida in the section on classification (p. 297) and the cases of evolutionary reversal discussed above.

EVOLUTION IN RELATION TO PALEOGEOGRAPHY

Trilobites inhabited marine environments from equatorial to polar paleolatitudes. The dalmanitoid *Mucronaspis,* for example, accompanied the Late Ordovician glaciation and was adapted to cool temperatures (Jaanusson, 1979). Conversely, the Early Ordovician family Bathyuridae was confined to paleoequatorial regions (Whittington, 1963; Cocks & Fortey, 1982). Trilobite niches extended from inshore, even intertidal, habitats to deep-marine, continental slope habitats. Probably no other Paleozoic group of organisms had such a wide geographic spread. This leads to the possibility of evolution within different habitats and on separate continental plates. Because the Paleozoic included periods when continents drifted apart or converged, as well as major climatic fluctuations, there is a complex pattern of evolution that reflects shifting biofacies and changing paleogeography.

TRILOBITE BIOFACIES

Onshore to offshore biofacies patterns (Fig. 137) are typical of much of the history of the trilobites. These patterns may occur in relation to a former continent edge—that is, they record a transect from inner shelf to continental slope—or they may reflect paleoenvironments within intracratonic basins. There may be no genera in common between contemporaneous faunas occupying inshore and deep-water sites; these faunas from different biofacies may be as different as those from different faunal provinces (Fortey, 1975a). Of the various terms that have been applied to describe the constant association of genera in relation to paleoenvironmental site—community, community type, constant generic association (CGA), realm, and so on—biofacies is probably most commonly used and least confusing.

Lower Cambrian faunas show some differentiation into biofacies across the carbonate shelf (W. Zhang, Lu, & others, 1980). However, deeper-water sites with trilobites are
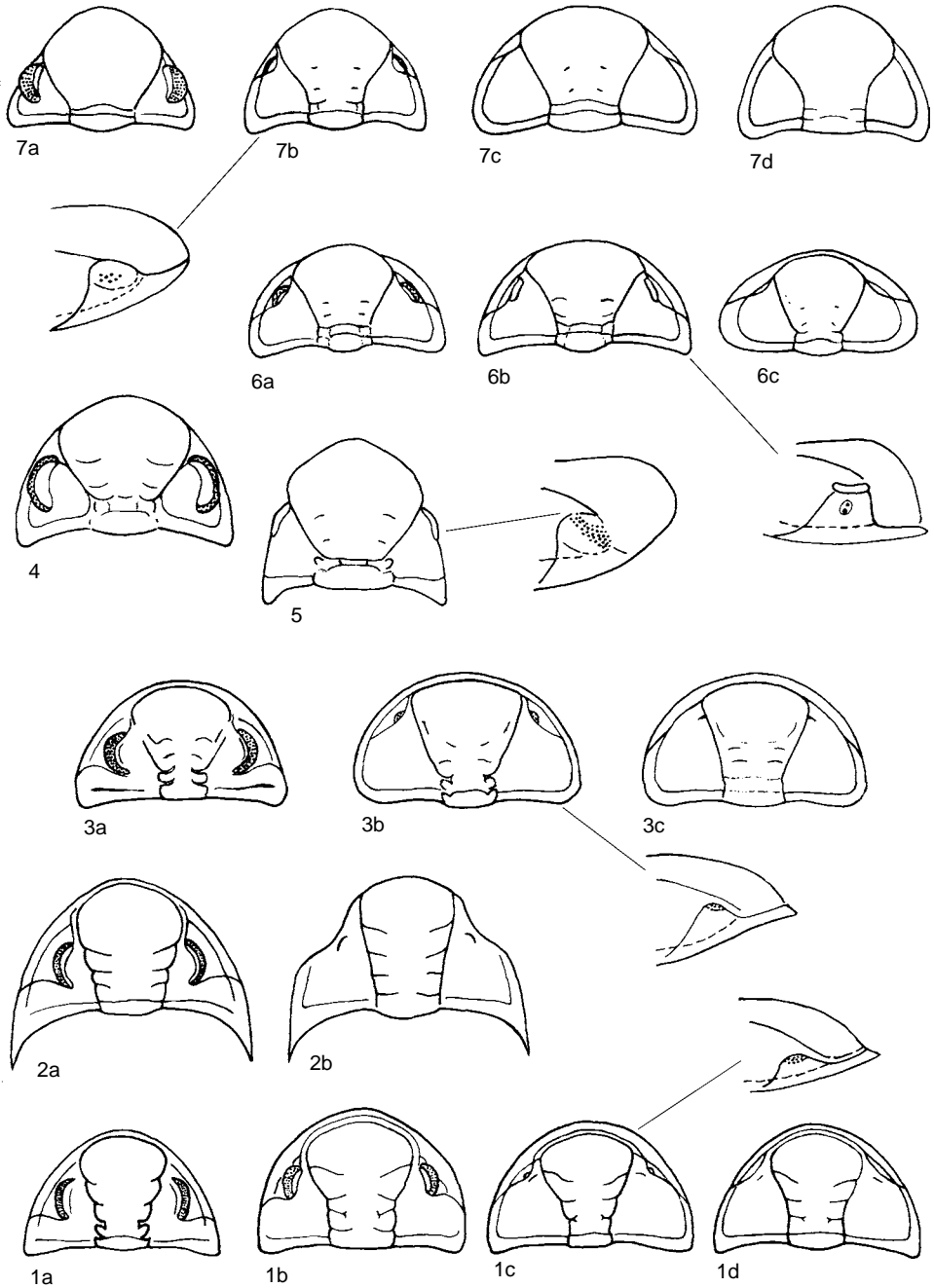
FIG. 201. Loss of eyes in Phacopoidea as an example of a polyphyletic evolutionary trend. The selected examples do not necessarily represent evolutionary lineages but illustrate the kinds of successive change that occurred.——*1a–d, Ormathops,* Ordovician, Arenig and Llanvirn series; *1a, O. borni* DEAN; *1b, O. atavus* (BARRANDE); *1c, O. llanvirnensis* (HICKS); *1d, O. nicholsoni* (SALTER).——*2a,b, Mucronaspis* and *Songxites,* Ordovician, Ashgill Series; *2a, M. mucronata* (BRONGNIART); *2b, Songxites* sp.——*3a–c, Phacopidella* and *Denckmannites,* Silurian, Wenlock and Ludlow series; *(Continued on facing page.)*

almost unknown at this early time in trilobite history, although some of the earlier Agnostina (late Early Cambrian) may already have occupied sites marginal to former continents (RASETTI & THEOKRITOFF, 1967), and by the late Early Cambrian *Atops* may represent the first atheloptic trilobite (Fig. 139). By mid-Cambrian times the whole inshore to deep-water range of biofacies was occupied by trilobites, with Agnostina particularly common in more oceanward sites (ROBISON, 1972a), where they may have been accompanied by the diverse atheloptic assemblages attributed to the Conocoryphidae.

Similar inner-shelf to outer-shelf transects have been described by LU (1974), who recognized what he termed bioenvironmental control of Cambrian trilobite distribution in China. PALMER (1972) has described how North American Late Cambrian trilobites relate to distribution of the inner detrital belt, carbonate belt, and outer detrital belt. In all these cases the Cambrian pattern is a comparatively simple one relating to more or less concentric facies belts running approximately parallel to an inferred shoreline (Fig. 203). Carbonate ramps in the tropical belt may have developed steep margins, thus providing a rather abrupt contact between shelf and marginal biofacies, as in the Upper Cambrian of parts of the western United States (COOK & TAYLOR, 1975). The deeper biofacies are often associated with olenid trilobites, as was appreciated already by WILSON (1957); at that time such biofacies were attributed to an association with geosynclines, which would now be understood to indicate proximity to a Cambrian ocean. However, the olenid sea of Scandinavia (HENNINGSMOEN, 1957a) extended more widely over shelf areas, and this may be a reflection of the stratified nature of the Upper Cambrian oceans. Cambrian trilobites may have subdivided the habitat much more finely than is indicated by the broad shelf-to-ocean transect. Such associations of genera have been recognized by WESTROP (1986b) and LUDVIGSEN, WESTROP, and KINDLE (1989) using Q- and R-mode analysis of Upper Cambrian faunas from Alberta and western Newfoundland, respectively. Such analyses may reveal something about niche width in these early faunas. It is also clear that fidelity to a biofacies was an important factor in trilobite evolution.

Similar shelf-to-ocean Ordovician biofacies were recognized by FORTEY (see Fig. 137) in Spitsbergen, which was in a paleoequatorial position at that time (Fig. 204). The olenid biofacies persisted from the Cambrian and comprised the most oceanic biofacies. The open-shelf nileid biofacies was named after one of its dominant families, although shumardiids, asaphids, remopleuridids, and raphiophorids were also typical. A carbonate-mound biofacies, which may have developed at the edge of a carbonate platform in tropical areas, was typified by illaenids and cheirurids. The inner-shelf, carbonate bathyurid biofacies (FORTEY, 1979) was dominated by the eponymous trilobite family but also had restricted asaphids, dimeropygids, pliomerids, and other such trilobites. LUDVIGSEN (1978b) recognized a similar suite of biofacies for mid-Ordovician

FIG. 201. *Explanation continued from facing page.*

3a, P. glockeri (BARRANDE); *3b, D. volborthi* (BARRANDE); *3c, D. caecus* SCHRANK.——*4, Phacops (Phacops) degener* BARRANDE, Devonian, Emsian Stage, a typical phacopid with well-developed eyes, the kind that probably lies at the beginning of the lineages shown in parts 5, 6, and 7.——*5, Phacops (Prokops) prokopi* CHLUPÁČ, Devonian, Pragian Stage.——*6a–c, Nephranops,* Devonian, Frasnian and early Famennian stages; *6a, N. miserrimus* (DREVERMANN); *6b, N. incisus incisus* (RÖMER); *6c, N. incisus dillanus* (RICHTER & RICHTER).——*7a–d,* Devonian, Frasnian and Famennian species; *7a, Phacops granulatus* (MÜNSTER); *7b, Cryphops acuticeps* (KAYSER); *7c, Trimerocephalus mastophthalmus* (Reinhard RICHTER); *7d, Dianops griffithides* (RICHTER & RICHTER) (adapted from Fortey & Owens, 1990b, fig. 5.2).
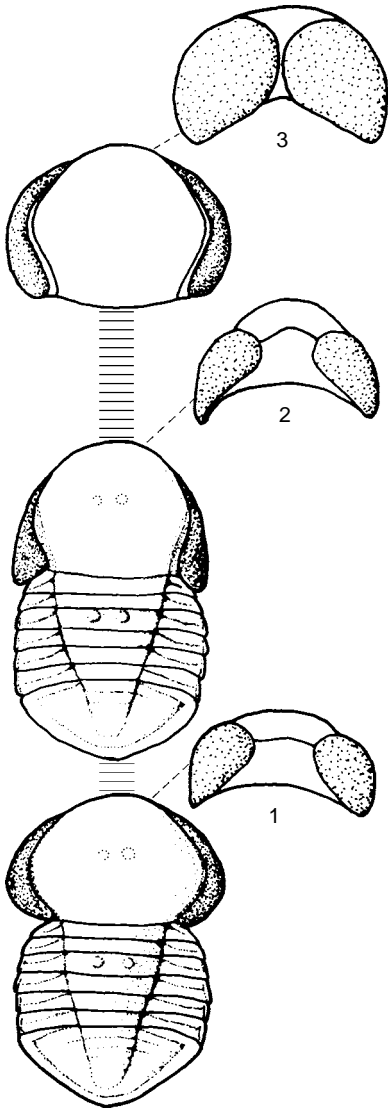
FIG. 202. Anterior convergence of the eyes of *Pricyclopyge:* an evolutionary trend repeated in several lineages of pelagic trilobites; in its extreme development the eyes are fused. *1, P. binodosa eurycephala* FORTEY & OWENS; *2, P. binodosa binodosa* (SALTER); *3, P. synophthalma* (KLOUČEK) (Fortey & Owens, 1990a, fig. 5.1b).

western Laurentia, and CISNE and others (1980) noted the influence of paleoenvironments on the evolution of some species of *Flexicalymene* and other trilobites in eastern Laurentia. A comparable suite of biofacies has been recognized off Ordovician Gondwana (FORTEY & OWENS, 1978, 1987),

but because Gondwana was at a high paleolatitude, a different selection of trilobites was generally dominant in the biofacies there (see Fig. 209). The Olenid biofacies, however, could be found in deeper-water sites off both Laurentia and Gondwana—indeed, it is virtually pandemic (COCKS & FORTEY, 1990). Similar biofacies patterns persisted to the Ashgill (e.g., PRICE & MAGOR, 1984) but appear to have broken down at the Late Ordovician extinction event.

The early Silurian is regarded as a time when trilobite faunas are not well differentiated into biofacies. We know of no unequivocal deep-water trilobite biofacies from the Llandovery, for example. However, depth- and facies-related trilobite associations have been reported widely from the later Silurian (Fig. 205) and Devonian [CHLUPÁČ, 1987 (Silurian of Bohemia), CHLUPÁČ, 1983 (Devonian of Bohemia), THOMAS, 1980 (Silurian of Great Britain), MÄNNIL, 1982 (Silurian of East Baltic), CHATTERTON and PERRY, 1983 (Silurian odontopleurids of arctic Canada), and G. ALBERTI, 1969, 1970, 1981 (Devonian of Morocco)]. The most diverse of these are the Bohemian examples described by CHLUPÁČ, who matched many of the benthic associations he recognized with those defined by BOUCOT (1975). He noted persistence through time of some environmentally related assemblages but identified change in their taxonomic composition. For example, the illaenid-cheirurid assemblage was replaced in the Devonian by a styginid-proetid community.

The Old World Province in Europe and adjacent areas comprises the Rhenish and Hercynian (or Bohemian) magnafacies (ERBEN, 1964), dominated respectively by nearshore clastics and offshore carbonates (Fig. 206). The former contain a restricted trilobite fauna with homalonotids, acastomorphs, and asteropyginids dominating, while the latter contains a diverse fauna with proetids, tropidocoryphids, cheirurids, phacopids, odontopleurids, and lichids. Various subprovinces, which are probably
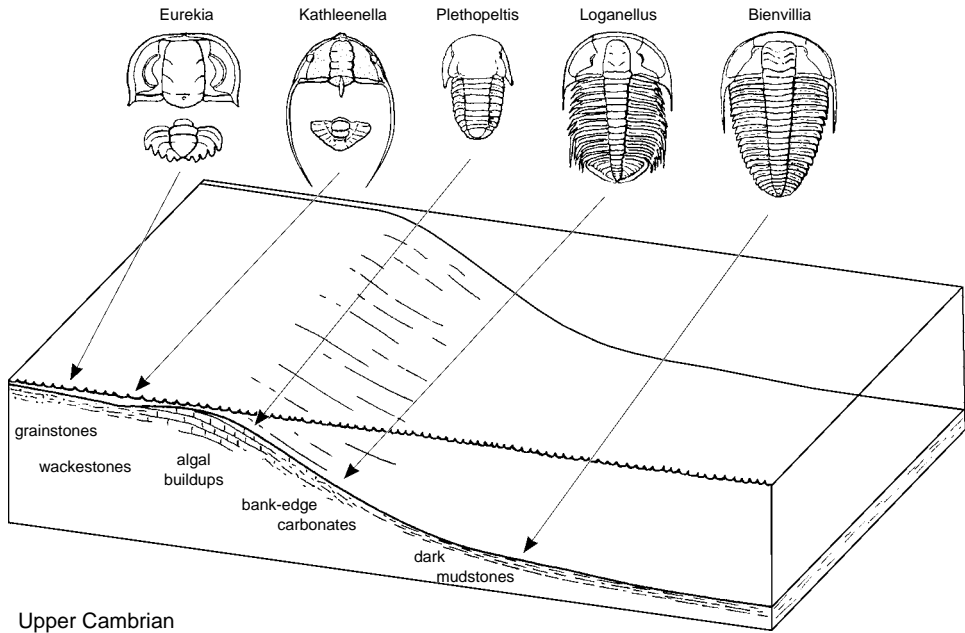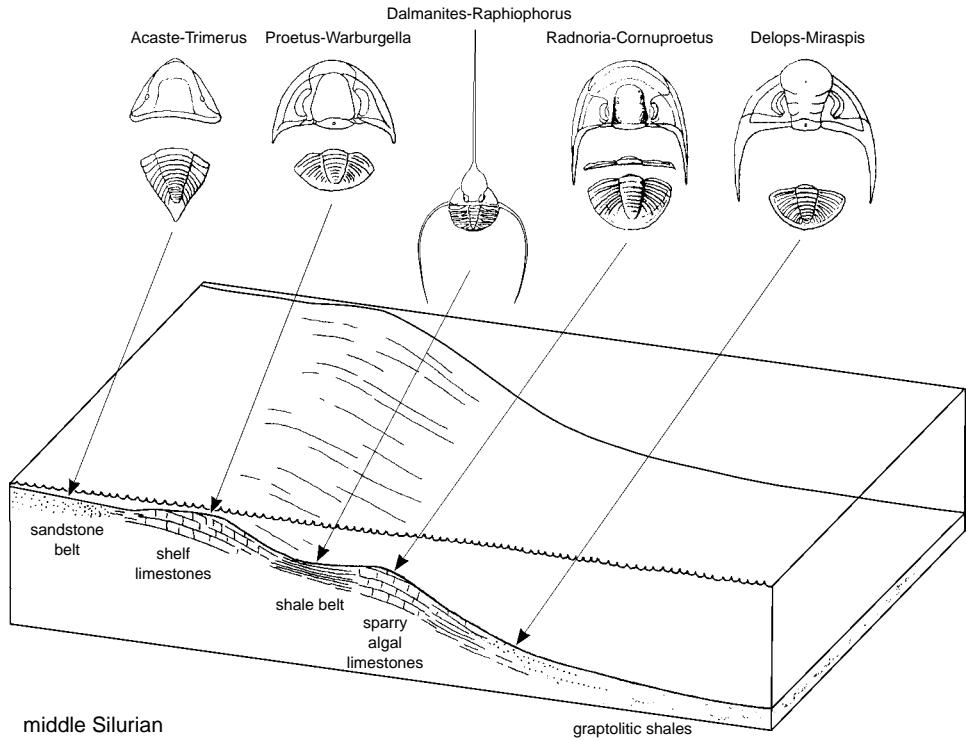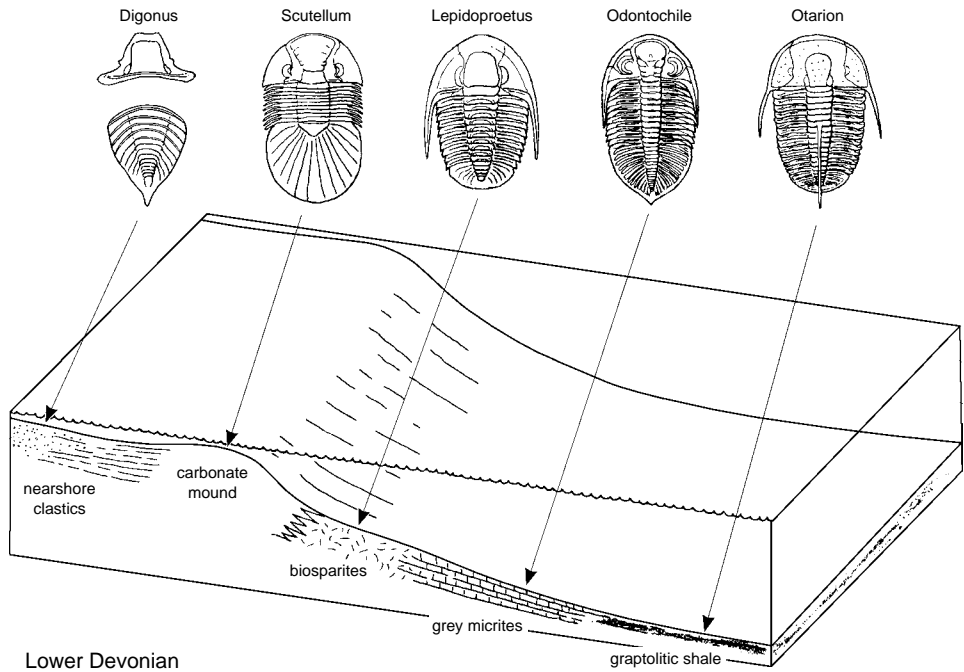
FIG. 203. Biofacies of Upper Cambrian continental shelf of Laurentia. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (adapted from Ludvigsen & others, 1986).

facies-controlled, have been discriminated and include Uralian (with some Appalachian elements), Tasman, and New Zealand (see HOUSE, 1979 for summary).

Figure 207 illustrates biofacies of the Lower Carboniferous of northern England. Few benthic trilobite associations have been described from the Carboniferous and Permian, but BREZINSKI (1986b) gave a detailed analysis for the Lower Carboniferous (Mississipian) of Missouri in which he recognized three such natural associations of species. He also noted variations in surface sculpture of one species that depended on the enclosing lithology. HAHN and HAHN (1988) briefly discussed associations from the Dinantian of Belgium and northeastern Germany. BREZINSKI (1992) described depth-related associations in the Permian of Texas, and CISNE (1971) observed decreasing taxonomic and numerical diversity with increase in depth in a Permian sequence in the western United States.

For the evolution of trilobites the importance of biofacies is threefold. (1) Evolution may have proceeded within biofacies, as has been described for the Olenidae above. Indeed, some families appear to have been remarkably loyal to a biofacies. LANE (1972) and FORTEY (1980a) noted the persistence of the carbonate-mound, illaenid-cheirurid biofacies from Early Ordovician until Devonian times. It is not surprising that some of the most long-lived trilobite genera (*Scotoharpes, Decoroproetus*) favored this habitat. (2) Deeper-water biofacies include more pandemic species and genera (TAYLOR & FORESTER, 1979; FORTEY, 1980b) and hence have a more limited capacity for provincial speciation. WILSON (1957) presciently noted the almost worldwide relationship of occurrences of Cambrian olenid trilobites to what were then termed geosynclinal habitats. These would now be recognized as oceanward environments fringing paleocontinents. Deep-water genera may also be long lived (FORTEY, 1980a). (3) By contrast, inshore biofacies tend to include endemics, which respond to local conditions of substrate, temperature, water chemistry,
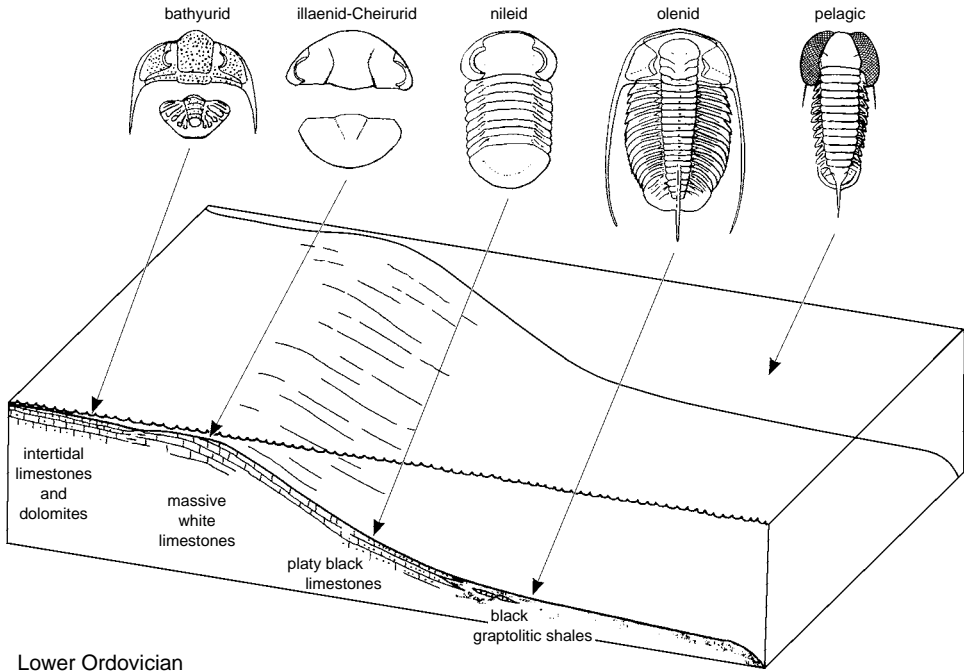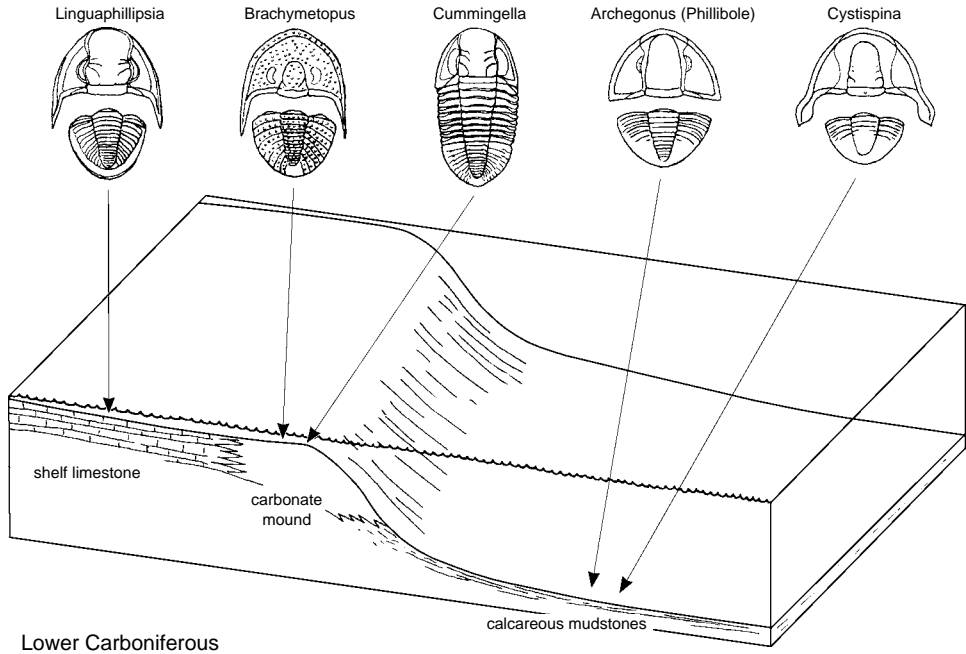
FIG. 204. Biofacies of Lower Ordovician continental shelf of Laurentia. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (adapted from Fortey, 1975a).

and the like. Speciation among these was more likely to relate directly to the distribution of paleocontinents by paleolatitude or to geographic separation. This has resulted in what have usually been termed trilobite provinces.

DISTRIBUTION OF ANCIENT CONTINENTS AND TRILOBITE EVOLUTION

That some kinds of trilobites were characteristic of extensive paleogeographic areas has been recognized for a long time. The application of plate tectonics to the Paleozoic to produce more reliable paleogeographic maps has made new sense of such provincial distributions, especially when they are taken in conjunction with biofacies patterns within a single paleocontinent (for example, COCKS & FORTEY, 1988, referring to Gondwana). Indeed, trilobite distributions themselves have played a part in deducing the distributions of paleocontinents, especially in the

early Paleozoic (WHITTINGTON & HUGHES, 1972; COCKS & FORTEY, 1982). Because the inshore biofacies are more likely to be confined to a single paleocontinent, the distribution of such biofacies is the best guide to former distribution of continents, and evolution inshore is most likely to have proceeded as an endemic phenomenon. Some degree of endemism characterizes the greater part of trilobite history, because the climatic gradient, combined with the effects of separation of continental plates, produced endemic faunas. Hence the evolution of trilobites may have been driven as much by extrinsic, paleogeographic factors as by intrinsic, morphological change. No doubt this accounts, in part, for the repeated appearance of morphotypes, as described above.

Geographic separation of trilobite faunas is apparent from the Lower Cambrian (Atdabanian) onwards (RICHTER & RICHTER, 1941b; COWIE, 1971). The differentiation into major realms characterized by Olenel-

Fig. 205. Biofacies of middle Silurian continental shelf of Gondwana. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (adapted from Thomas, 1979).

lina (especially in Laurentia) and Redlichiina (especially in China and Australia) must, therefore, have happened in pre-Atdabanian times, but this phase of differentiation and vicariance has left no record. Hardly any genera are common to both regions, so that geographic differentiation was implicated early in the diversification of faunas (Fig. 208). There are characteristic Eodiscina and Redlichiina in China and distinctive Olenellina in Laurentia, and these are assumed to be the product of *in situ* evolution in those areas. Mixed faunas occur in Morocco and Siberia, but there are also endemics in these localities as in Scandinavia, which may indicate that there were already in the Early Cambrian still further biogeographic subdivisions. These early faunas were almost entirely inhabitants of shelves.

Later Cambrian faunas were also differentiated paleogeographically. By this time shelf faunas were differentiated from more marginal biofacies. Generally widespread faunas occur at some times, however—for example, at the *Glyptagnostus reticulatus* Zone as Kobayashi (1949) observed. Such widespread faunas resulted from onlap of more cosmopolitan faunas onto shelf regions at times of marine transgression. In general, Middle to Upper Cambrian trilobites differ at the generic or even familial level among biogeographic areas, and Öpik (1967) even described one superfamily (Rhyssometopoidea) endemic to Australia in the Mindyallan fauna. A sample horizon taken about the level of the Middle-Upper Cambrian boundary shows rich endemic eastern Gondwanan faunas characterized by Damesselloidea, Laurentian endemics especially in shelf limestones, and another suite of genera in platform Siberia, while the North Atlantic realm of authors marks the inception of the olenid

FIG. 206. Biofacies of Lower Devonian continental shelf of the Old World Province. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (adapted from Chlupác, 1987).

sea. There may be an element of taxonomic artifice in this pattern; for example, a critical comparison of Siberian with North American trilobites has not yet been made. Nonetheless, it seems probable that paleocontinental distribution was a prime control of trilobite speciation and distribution.

The Early Ordovician was a time of wide continental dispersal, with the north pole in present-day North Africa. Strong faunal provinciality was the result (Fig. 209). Paleoequatorial Laurentia and Siberia were typified by trilobites of the family Bathyuridae (WHITTINGTON, 1963), which were confined to inshore carbonates and which did not survive the Ordovician. Tropical sediments at the eastern edge of Gondwana (South China, central Australia, Argentina) were not colonized by bathyurids, but a whole suite of endemic asaphids (*Lycophron*), dikelokephalinids (*Asaphopsis, Hungioides, Dactylocephalus*), dalmanitoids (*Prosopiscus*), and leiostegiids (*Annamitella*) were typical of

this area. By contrast, inshore, high-latitude Gondwana (HENRY, 1980a; COCKS & FORTEY, 1988) was dominated by a calymenoid-dalmanitoid fauna including *Ormathops, Zeliszkella, Neseuretus, Calymenella,* and *Plaesiacomia.* Baltica was in temperate latitudes and was occupied by another suite of endemics, especially genera belonging to the families Asaphidae (Megistaspidinae, Ptychopygiinae) and Nileidae (*Varvia*). Enough is known about the Early Ordovician platform faunas for us to be sure that knowledge of these paleogeographic areas is not the product of biased monographic coverage. They hold their integrity through much of the Ordovician, but by the upper Caradoc the distinctions are somewhat less clear. This is because of a complex interaction between several factors: notably, the proto-Atlantic Ocean (Iapetus) had partly closed; the Caradoc transgression had brought some of the more widespread, deeper-water faunas into shelf environments; and climatic dete-

FIG. 207. Biofacies of Lower Carboniferous continental shelf of northern England. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (new).

rioration may have begun. Even in the late Caradoc, however, trilobite faunas are not pandemic: some genera remain restricted to eastern Gondwana (*Paraphillipsinella*), western Gondwana (*Mucronaspis*), or Laurentia (*Isotelus*).

The glaciation at the end of the Ordovician, which culminated during the Hirnantian Stage (BRENCHLEY, 1984), profoundly affected trilobite faunas. The relatively impoverished, cool-water, shelf faunas, with *Mucronaspis* (Fig. 210) and *Brongniartella,* spread at the expense of warmer-water faunas. The tropical belt was severely restricted, but reef environments survived in a few places, such as Anticosti Island.

Following the extinction of many trilobite clades at the end of the Ordovician, Llandovery trilobites are reported as showing relatively little provincial differentiation. For a while, the faunal composition was apparently dominated by those taxa that survived the Ashgill crisis. Such trilobite-based Sil-

urian provinces as have been claimed (KOBAYASHI & HAMADA, 1974; SCHRANK, 1977) are of broad extent and embrace several paleocontinents. COCKS and FORTEY (1990) noted the generally cosmopolitan nature of Silurian faunas but discriminated several biogeographic regions in the upper part of the system. A circumpolar, low-diversity *Clarkeia* fauna, named for a characteristic brachiopod, included also a few homalonotid trilobites and is perhaps analogous to the Ordovician calymenoid-dalmanitoid fauna (Fig. 209). Temperate paleolatitudes tended to be dominated by deposits of terrigenous clastics, and there was once again a tropical carbonate belt; both of these included some endemic forms. Many Silurian trilobite genera are widespread, as are some species: the cheirurid *Sphaerexochus mirus,* for example, under several different names, occurs in North America, Europe, Japan, and eastern Australia. Those genera with a more restricted distribution were
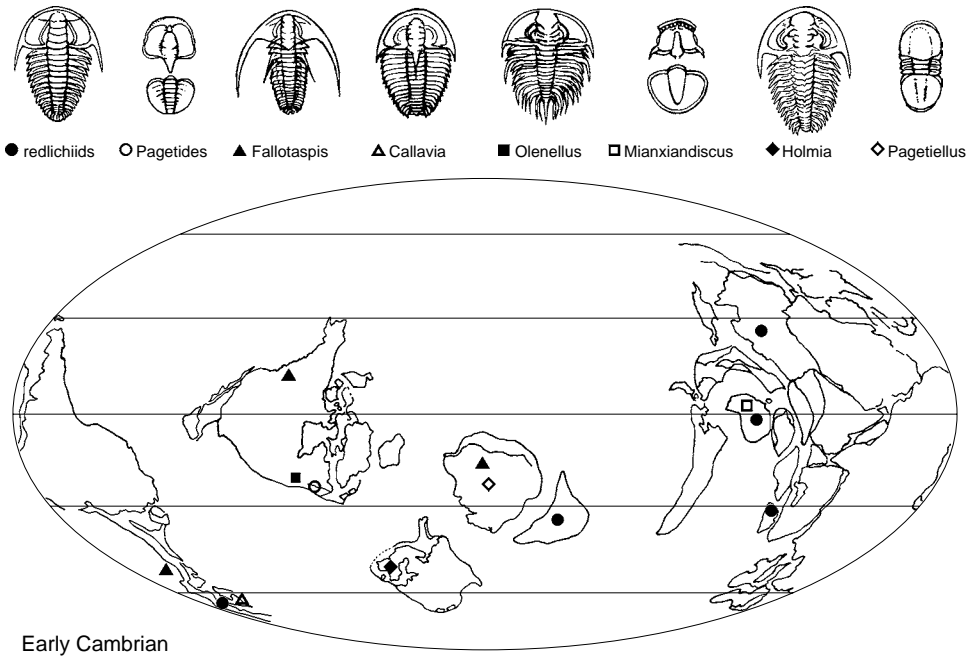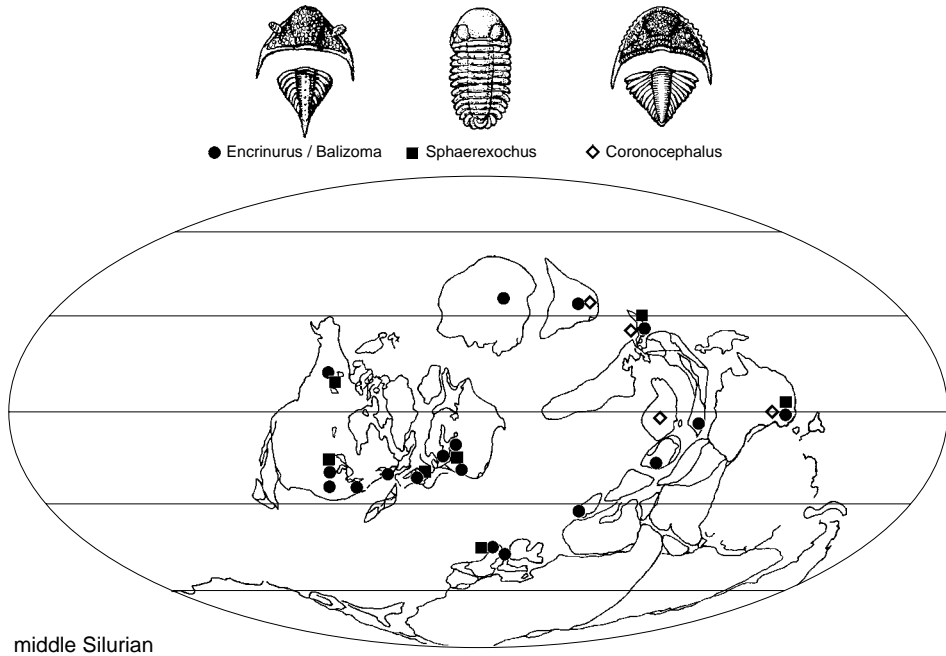
FIG. 208. Reconstruction of Early Cambrian global paleogeography (based on world maps of SCOTESE & MCKERROW, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents. Note primary division into Redlichiina and Olenellina (*Olenellus, Holmia, Callavia, Fallotaspis*) realms and local development of endemic eodiscoids (adapted from Fortey & Owens, 1990b, fig. 7.2).

presumably restricted to specific facies. *Coronocephalus* is a distinctive encrinurid that is restricted to eastern Gondwana: South China, Pamirs, Japan, and eastern Australia (Fig. 211).

Three contrasting provinces mark the earlier part of the Devonian (Fig. 212). The southern, polar Malvinokaffric Province had a taxonomically restricted fauna dominated by calmoniids (ELDREDGE & ORMISTON, 1979; ELDREDGE, 1980; ELDREDGE & BRANIŠA, 1980), some of which developed remarkable homeomorphy with phacopids. The remainder of the world was dominated by the Old World Province, with an Appalachian Province developed more locally in eastern North America. In the former, many taxa are widely distributed. Subspecies of *Warburgella rugulosa* occur almost worldwide at the base of the Lochkovian (G. ALBERTI, 1975) in the Hercynian magnafacies along with the conodont *Icriodus woschmidti* and

the graptolite *Monograptus uniformis,* while species of *Acastella* occur at the same level in the Rhenish magnafacies. The common occurrence of species of *Warburgella* and *Acastella* in parts of Europe and North Africa permits correlation of widespread, lowermost Devonian strata. Old World Province faunas in some areas include locally distinctive features along with widespread taxa: arctic Canada and arctic Russia lack phacopids (ORMISTON, 1967), while there are endemic phacopids in faunas from Inner Mongolia and northeastern Japan (Zhigiang ZHOU & CAMPBELL, 1990).

The Appalachian Province of eastern North America was a marine gulf opening to the south for at least some of its history. Heterogeneous local facies, which are dominated by clastics and nearshore deposits, with more limited calcareous and reef deposits, influence the kind of trilobites that are found, which include proetids, phacopids,
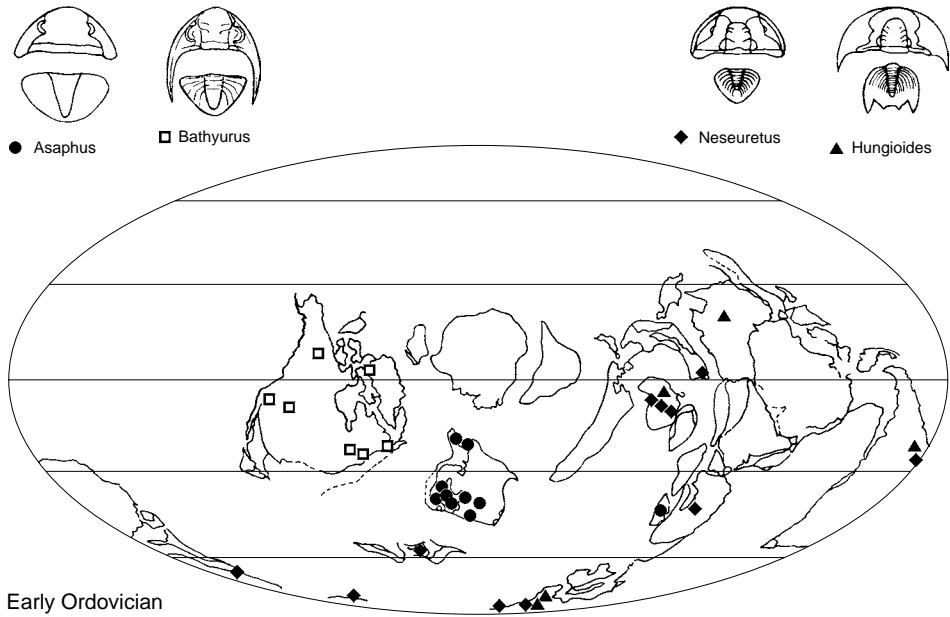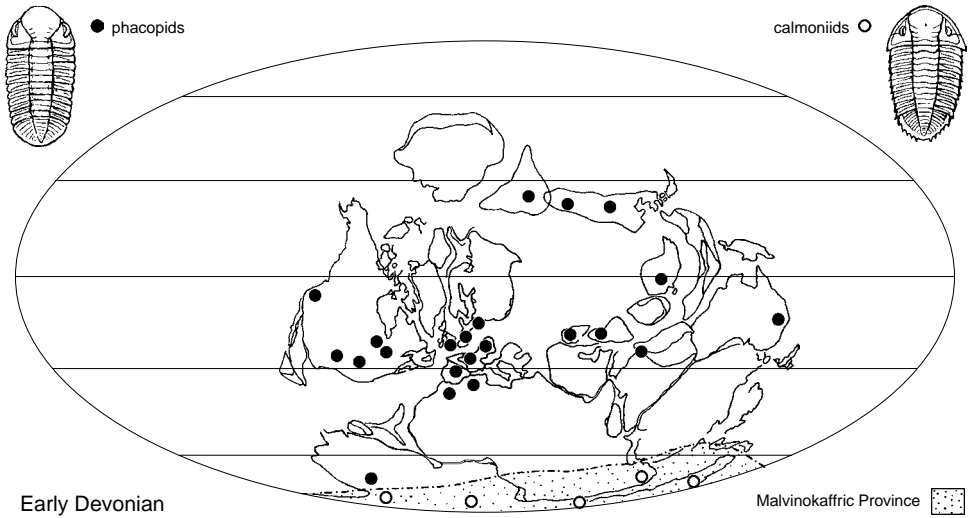
Fig. 209. Reconstruction of Early Ordovician global paleogeography (based on world maps of Scotese & McKerrow, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents, with differentiation of Gondwana (*Neseuretus, Hungioides*) from Baltica (*Asaphus*) and Laurentia (*Bathyurus*) (new).

and lichids belonging to genera distinct from those of the Old World Province. Some elements of the Appalachian Province fauna, however, are also known from central Kazakhstan (Maximova, 1968) and Xinjiang Province, China, which is an indication that there is an element of facies control over the occurrence of these trilobites (House, 1971).

In the Late Devonian, pelagic sediments with an atheloptic fauna were widespread over Europe, southern Urals, southeastern Asia, South China, and northwestern Australia. At the very end of the Devonian, *Phacops (Omegops) accipitrinus* was widespread in Europe, northern Africa, Afghanistan, central Asia, and China.

In Carboniferous rocks, Owens and Hahn (1993) distinguished three broad faunal tracts in the Tournaisian and Viséan: in the former, *Breviphillipsia-Thigriffides* (North America), *Cummingella-Phillipsia* (Europe to the Urals), and *Conophillipsia* (central Asia, Japan, and eastern Australia)

and in the latter, occupying the same three regions, faunas characterized by *Paladin-Griffithides, Cummingella,* and *Palaeophillipsia,* respectively (Fig. 213).

From the Namurian onwards, two major realms are recognized (Fig. 214). The North American-Andean area maintained its distinctness from Paleotethys, which embraced Eurasia, North Africa, and Australia. Typical trilobite faunas have been named after some of their characteristic constituents: for the North American-Andean area, *Paladin-Sevillia* (Namurian), *Ameura* (Westphalina-Stephanian), *Anisopyge* (Permian); and for Paleotethys, *Paladin-Cummingella* (Namurian), *Pseudophillipsia-Cummingella* (Westphalian-Stephanian), and *Pseudophillipsia* (Permian). The distinctive features of these realms can be explained in part by the separation of the landmasses of North America and Paleotethys after the Viséan (and before that time possibly by differences in local habitats, water temperature,
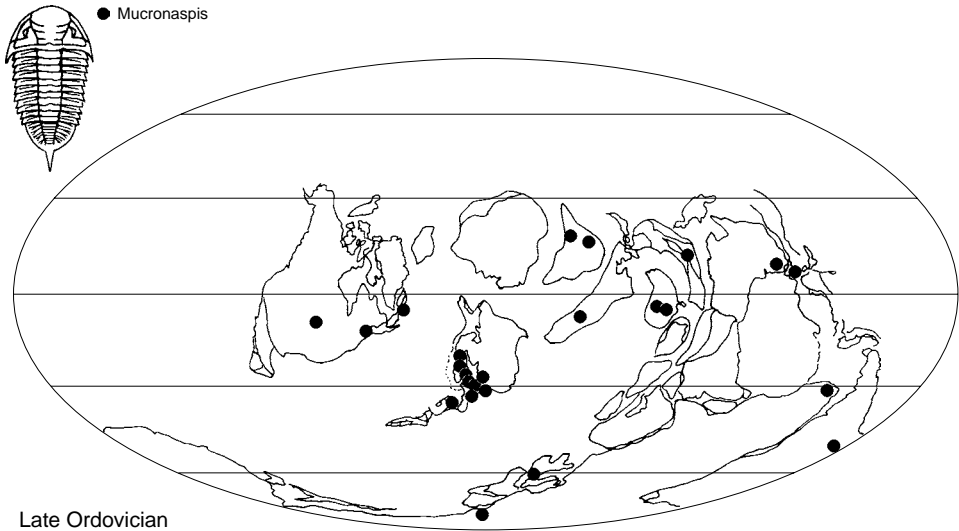
FIG. 210. Reconstruction of Late Ordovician global paleogeography (based on world maps of SCOTESE & MCKERROW, 1990) showing the wide distribution of *Mucronaspis* accompanying glaciation (new).

and depth). Some genera, however, were cosmopolitan—for example, *Pudoproetus* in the Early Carboniferous, *Brachymetopus* throughout the Carboniferous, and *Ditomopyge* in the Late Carboniferous and Permian.

TIMES OF MAJOR CHANGE IN TRILOBITE HISTORY

During some periods in the history of the Trilobita, faunal composition changed rapidly, either through extinction or through the appearance of new clades. These periods usually corresponded with similar events affecting other organisms and provide the most important extrinsic control on the history of the trilobite.

LOWER CAMBRIAN

As with many groups of marine organisms, some trilobite clades that were to last for tens of millions of years began in the Early Cambrian. In many stratigraphic sections the trilobite-bearing beds are underlain by beds containing the remains of Tommotian small shelly faunas. Most complete sections of this kind have a relatively species-poor fauna at the base, and more spe-

cies appear upwards in the section (BRASIER, 1989, fig. 7.16–7.19). The appearance of new supraspecific taxa is generally quite sudden, and, with the possible exception of the Olenellina, stratigraphically based species-to-species lineages of the early trilobites are not obvious. Nor do first appearances of new clades coincide in the various sections (BRIGGS & FORTEY, 1992), so it seems likely that much of the early history of cladogenesis is not recorded in known fossils. As was discussed previously, there is also marked provincialism in these early faunas. Within the span of the Lower Cambrian, Olenellina and Redlichiina had diversified, and Corynexochida, Agnostida, and libristomate Ptychopariina had appeared. In that some of these are probably paraphyletic groups, they may well include sister groups of other higher taxa, and the so-called extinction of the Redlichiina at the top of the Lower Cambrian may have resulted primarily from their continuation within more advanced clades.

UPPER CAMBRIAN

The biomeres of the Upper Cambrian described by North American authors (PALMER, 1965a; STITT, 1975) have been de-

● Encrinurus / Balizoma   ■ Sphaerexochus   ◇ Coronocephalus
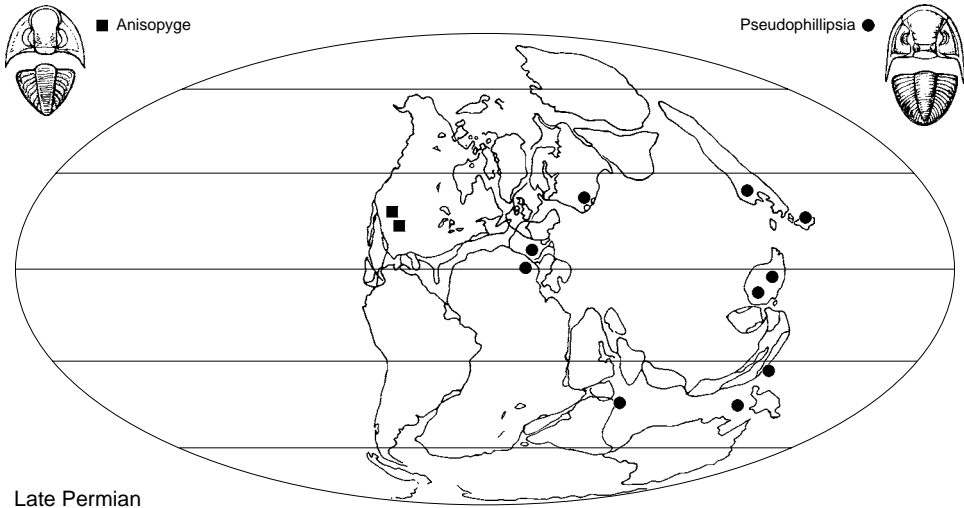
middle Silurian

FIG. 211. Reconstruction of middle Silurian global paleogeography (based on world maps of SCOTESE & MCKERROW, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents. The wide distribution of *Sphaerexochus, Encrinurus, and Balizoma* is typical of many taxa, but *Coronocephalus* is an example of more restricted distribution (new).

scribed as packages of rapid evolution, eventually followed by widespread extinction events affecting especially shelf faunas. They have a cyclical pattern, which some authors maintain also applies to the Early Ordovician hystricurid or symphysurinid biomere. It is not clear, however, that biomeres were global phenomena; nor is there agreement about how fundamental was their influence on the taxonomic composition of faunas (FORTEY, 1983). Deeper-water faunas were supposedly relatively unaffected by the biomere phenomenon. LUDVIGSEN (1982) and WESTROP and LUDVIGSEN (1987) related biomeres to sedimentary cycles and the shift in biofacies disposition; the extinction events have also been related to cool water incursions onto the platform. Although platform endemics no doubt evolved and were extinguished in Cambrian epeiric seas, it is uncertain whether the biomere events were the equal of the other events listed here.

LOWER ORDOVICIAN

Many of the clades that dominated Ordovician and later trilobite faunas have their first known occurrence in the Lower Ordovician. The Cambrian-Ordovician boundary marks a period of faunal turnover, but although extinction was undoubtedly involved in this change in faunas, it is as a time of origination of clearly differentiated clades that the Early Ordovician is remarkable. Cambrian sister groups of some of these taxa are now being recognized. Insofar as they are known, the new clades do not all appear suddenly at the base of the Tremadoc, but their first occurrences lie in an interval spanning the Upper Cambrian and the lowest two Series of the Ordovician: Proetidae (Arenig); Cheiruridae (lower Tremadoc); Cyclopygoidea (uppermost Cambrian–basal Tremadoc); Dalmanitoidea (Arenig); Dimeropygidae (upper Tremadoc); Trinucleoidea (Upper

Fɪɢ. 212. Reconstruction of Early Devonian global paleogeography (based on world maps of Sᴄᴏᴛᴇsᴇ & MᴄKᴇʀʀᴏᴡ, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents. Note primary division of Malvinokaffric (cool-water) faunas from phacopid-bearing areas at lower paleolatitudes (new).

Cambrian); Illaenidae (basal Arenig); Harpina (uppermost Cambrian). The combination of these new families and superfamilies with those of longer pedigree (Asaphidae, Agnostina, Remopleurididae, Olenidae) lend the Ordovician faunas their distinctive characteristics.

UPPER ORDOVICIAN

The extinction event at the end of the Ordovician was one of the most important in the history of the biosphere, and the trilobites were affected drastically by it. Many families with Cambrian origins and those listed as typically Ordovician were either greatly reduced or extirpated at the end of the Hirnantian. Many families (Asaphidae, Cyclopygidae, Nileidae, and the Trinucleoidea) belong to the Asaphida, which has led some authors to conclude that the planktonic asaphoid protaspis was especially vulnerable (Sᴘᴇʏᴇʀ & Cʜᴀᴛᴛᴇʀᴛᴏɴ, 1990). There was a reduction in diversity before the Hirnantian (Bʀᴇɴᴄʜʟᴇʏ, 1984, 1989), but many Ordovician families persisted into this short time period (Oᴡᴇɴ, 1986), and had they survived it is possible that they would

readily have recovered to their former diversity. The fact that they did not argues for an exceptional crisis at the Ordovician-Silurian boundary. This has been associated with widespread anoxia in the oceans during the postglacial rebound. It seems to be true that the families of trilobites eliminated were especially those that were oceanic (all pelagics), deeper water (olenids, agnostids), or those having pelagic larvae (Asaphida). Some of the shelf-dwellers (Lichida, Dalmanitoidea, Cheiruridae, Calymenidae, Illaenidae, Harpetidae) were survivors. It is also clear that there were some Lazarus taxa (e.g., *Scharyia*) that must have existed in refugia during the crisis as they are found in strata below the uppermost Ordovician and they reappear (or a close relative does) in strata well above the base of the Silurian. There is no doubt, however, about the profound effect of the end-Ordovician extinction. The lowest Silurian (Llandovery) has faunas of relatively low diversity, but more diverse faunas are present by the late Llandovery, and cladogenesis builds continuously into the Devonian. The general composition of trilobite faunas in terms of families present remained essentially
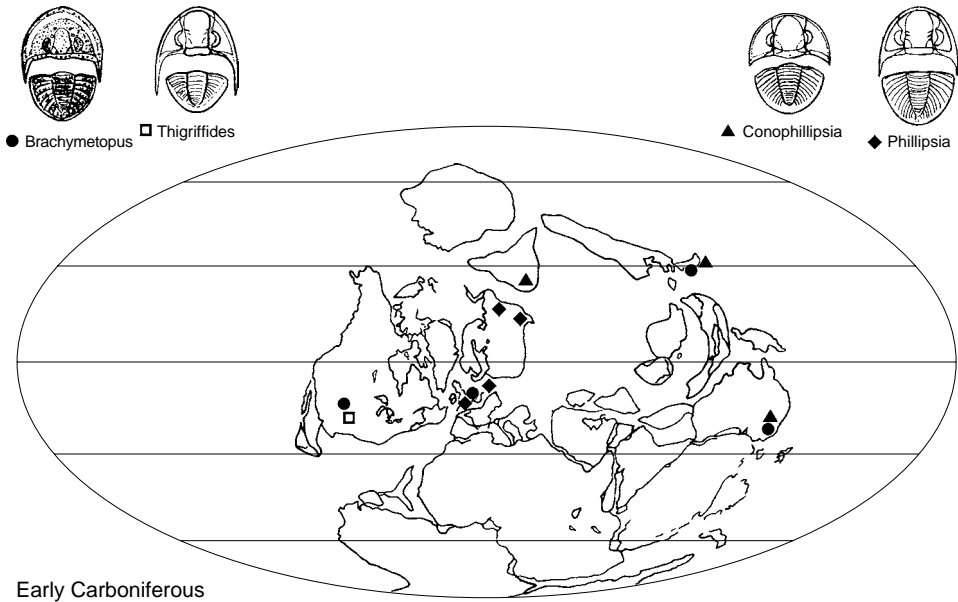
FIG. 213. Reconstruction of Early Carboniferous global paleogeography (based on world maps of SCOTESE & MCKERROW, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents. *Thigriffides* (North America), *Phillipsia* (Europe), and *Conophillipsia* (Australasia) are endemics; *Brachymetopus* is more widespread (adapted from Owens & Hahn, 1993).

similar from the late Llandovery to mid-Givetian, except that the Encrinuridae became extinct in the early Lochkovian (STRUSZ, 1980), and the related Staurocephalidae, together with the Raphiophoridae (the last Asaphida), did not survive the Ludlow.

MIDDLE TO UPPER DEVONIAN

A drastic series of extinctions, brought about by global eustatic perturbations, affected the Trilobita in the Middle to Late Devonian (BRIGGS, FORTEY, & CLARKSON, 1988; FEIST, 1991; FEIST & SCHINDLER, 1994) (Fig. 215). In the late Eifelian, a change from well-oxygenated to oxygen-deficient conditions in the outer shelf (the Kačák-*otomari* event) resulted in a depletion in the number of species and the extinction of the synphoriids and rorringtoniids. A regression associated with expansion of the cool-water, Malvinokaffric, calmoniid faunas at or about this time has been interpreted as a result of a sudden lowering of global climatic gradient (BOUCOT, 1988, 1990). The mid-Givetian Taghanic or *Pharciceras* event was a marine transgression that resulted in the loss of trilobite clades adapted to life in shallow-water habitats. Lichids and cheirurids disappeared from the record at this time; in total, five families and one order became extinct. The end-Frasnian Kellwasser event (and the subsequent end-Famennian Hangenberg event) involved sudden changes of sea level leading to a break in the redox equilibrium, which has been invoked as the cause of extinction of a large number of specialized lineages (FEIST, 1991). The Kellwasser event was one of the most dramatic extinctions in the history of the Trilobita—three orders and all but five families were terminated. This event has been claimed to coincide with a major meteorite impact, but may better be accounted for by the loss of specialized groups through an influx of oxygen-depleted water (FEIST & SCHINDLER, 1994). Of the survivors, the Phacopidae disappeared with the Hangenberg event, and only Proetida

Fig. 214. Reconstruction of Late Permian global paleogeography (based on world maps of Scotese & McKerrow, 1990) showing the provincial distribution of shelf trilobites related to continent distribution and paleolatitudes. *Pseudophillipsia* and *Anisopyge* are examples of mutually exclusive distribution in Paleotethys and western North America, respectively (adapted from Owens & Hahn, 1993).

crossed into the Carboniferous. The restriction of aulacopleurids, brachymetopids, and proetids in the Late Devonian was probably an example of pseudoextinction (Owens, 1994) because several of these taxa reappeared in the Carboniferous when appropriate habitats were reestablished.

PERMIAN

No deeper-water, atheloptic trilobite faunas are known from strata younger than Namurian, although they were varied in earlier Carboniferous offshore basinal environments. The youngest trilobites are all in shallower-water, shelf habitats. Comparatively diverse faunas of Proetida remained in such habitats until the late Kazanian or Guadalupian, from which rocks seventeen genera are known belonging to five phillipsiid subfamilies, together with one proetid and one brachymetopid. However, only two genera, the ditomopyginids *Pseudophillipsia* and *Acropyge,* seem to have survived into the latest Permian. The major extinction seems to have accompanied a drastic regression that particularly affected reef and perireef habitats. The decline of the trilobites, therefore, seems to have happened shortly before the coup de grace at the end of the Paleozoic.

Taxa	Middle Devonian		Upper Devonian		Carboniferous
	Eifelian	Givetian	Frasnian	Famennian	Tournaisian
Proetida					
Proetidae					
Tropidocoryphidae					
Aulacopleuridae					
Brachymetopidae					
Rorringtoniidae					
Phillipsiidae					
Ptychopariida					
Harpetidae					
Corynexochida					
Styginidae					
Phacopida					
Cheiruridae					
Homalonotidae					
Calymenidae					
Calmoniidae					
Synphoriidae					
Dalmanitidae					
Phacopidae					
Lichida					
Lichidae					
Odontopleurida					
Odontopleuridae					
"Extinction Events"	Kačák- *otomari*	Taghanic- *Pharciceras*	Kellwasser	Hangenberg	

FIG. 215. Fossil record of important trilobite groups through a series of Late Devonian extinctions (recognized in Europe, but also elsewhere), showing staggered last appearances of orders (*stippled arrows*) and families. The names given to the extinction events are those currently in use (adapted from Feist, 1991).

CLASSIFICATION

Richard A. Fortey

A group as large and as complex as the trilobites poses particular problems in classification. Systems of classification seek to achieve a measure of stability, but changes in taxonomic methods as well as new discoveries mean that such stability has remained elusive. Harrington (in Moore, 1959, p. 145) remarked that a "wholly satisfactory, natural classification of the trilobites is beyond possibility at the present moment." This is still true a quarter of a century later.

Harrington was inclined to ascribe the difficulties in developing a higher classification to our incomplete knowledge of trilobite morphology and ontogeny. Many more ontogenies have been described in the last two decades, and these have contributed to improvements in classification. It is still true that we know the appendages of very few trilobite species, and, because appendages are among the most important criteria for classifying living arthropods, it would certainly be desirable to know more. With the exception of those of the highly specialized *Agnostus* (Müller & Walossek, 1987), trilobite appendages appear to be rather similar along the length of the animal. The extremes of specialization of appendages found among living crustaceans may not have generally obtained in the trilobites. On the other hand, there are many striking modifications of the dorsal and ventral exoskeletons that have no counterparts among the living arthropods, and it was the exploitation of the possibilities of a tough, calcareous cuticle that contributed to the success and adaptive range of the group. The inevitable limitations on our knowledge of trilobite limbs does not necessarily imply that a natural classification is impossible.

The history of trilobite classification shows that some groups that would still be accepted as natural—that is, monophyletic—were recognized very early by the more perceptive, early students of the group. Salter (1864a), for example, classified trilobites into the following families: Phacopidae, Cheiruridae, Proetidae, Acidaspidae (=Odontopleuridae), Lichidae, Bronteidae (=Styginidae), Calymenidae, Cyphaspidae (=Aulacopleuridae), Asaphidae, Harpedidae (=Harpetidae), Olenidae, Trinucleidae, Agnostidae, and Conocephalidae. Of these, only the Conocephalidae is not in use today; all the others refer to good clades of trilobites, even though Salter included more genera than are in the taxa of the same name today. More families were introduced in the latter part of the nineteenth (e.g., by Beecher, 1897) and the first four decades of the twentieth century (Gürich, 1907; Kobayashi, 1935), and, for the most part, these are also used today. Figure 216 shows the enduring status of many of these families, which have been been passed on from one classification system to the next, with more and more families being added with the passage of time and the discovery of more fossils. The last comprehensive treatment before the 1959 edition of the *Treatise on Invertebrate Paleontology* was that of Hupé (1954, 1955a), who recognized some 170 families, nearly all of which are accepted today.

The recognition of a family implies that several genera share some well-characterized features that permit their inclusion in a higher taxon. The Asaphidae, for example, are isopygous or subisopygous trilobites with effaced glabellar furrows having eight thoracic segments with petaloid facets and a ventral median suture; many have hypostomes with a posteromedian fork. The identification of Asaphidae implies that this combination of characters did not arise more than once—and, indeed, no students of the group have claimed asaphids as polyphyletic, even though there have been many opinions on how further to subdivide them. Most trilobite families can be characterized by features that allow confidence in the monophyly of the group concerned. This is true in

Legend: ░ = shaded gray, ▨ = diagonal shading, blank = unshaded

	Salter 1864a	Beecher 1897	Gürich 1907	Swinnerton 1915	Poulsen 1927	Richter 1932
Agnostidae	░	░	░	▨	░	░
Anomocaridae	░	░	░	░	░	░
Asaphidae	░	░	░	░	░	░
Aulacopleuridae	░	░	▨	░	░	░
Bathyuridae	░	░	░	░	░	░
Bathyuriscidae	░	░	░	░	░	░
Burlingiidae	░	░	░	░	░	░
Calymenidae	░	░	░	░	░	░
Ceratopygidae	░	░	░	░	░	░
Cheiruridae	░	░	░	░	░	░
Conocoryphidae	░	░	░	░	░	░
Corynexochidae	░	░	░	░	░	░
Cyclopygidae	░	░	▨	▨	▨	░
Dikelocephalidae	░	░	░	░	░	░
Dionididae	░	░	░	░	░	░
Ellipsocephalidae	░	░	░	▨	░	░
Encrinuridae	░	░	░	░	░	░
Eodiscidae	░	░	▨	░	░	░
Harpetidae	░	░	░	░	░	░
Homalonotidae	░	░	░	░	░	░
Illaenidae	░	░	░	░	░	░
Lichidae	░	░	░	░	░	░
Menomoniidae	░	░	░	░	▨	░
Nileidae	░	░	░	░	▨	▨
Norwoodiidae	░	░	░	░	░	░
Odontopleuridae	▨	▨	▨	░	░	░
Olenellidae	░	░	░	▨	░	░
Olenidae	░	░	░	░	░	░
Oryctocephalidae	░	░	░	░	░	░
Otarionidae	▨	░	▨	░	▨	░
Paradoxididae	░	░	░	░	░	░
Phacopidae	░	░	░	░	░	░
Proetidae	░	░	░	░	░	░
Ptychopariidae	░	░	░	░	░	░
Raphiophoridae	░	░	▨	░	░	░
Redlichiidae	░	░	░	░	░	░
Remopleurididae	░	░	░	░	░	░
Styginidae	▨	▨	▨	▨	▨	░
Shumardiidae	░	░	░	▨	▨	░
Solenopleuridae	░	░	░	░	░	░
Trinucleidae	░	░	░	░	░	▨
Zacanthoididae	░	░	░	░	░	░

Fig. 216. Trilobite families in some of the principal classification systems developed through the mid-nineteenth to mid-twentieth centuries. Family-level taxa are the most enduring concepts, which, once proposed, survive into modern classification, but the list of families has been progressively augmented. Families that have always been known by the name listed in the lefthand column are *shaded gray*. Families that, while encompassing a similar concept, have undergone one or more nomenclatural changes over the period under consideration are indicated by the *diagonal shading*. For example, the family Cyclopygidae was known as Aeglinidae by some early authorities but embodies a similar suite of genera (new).

particular of families younger than Cambrian in age, because morphological gaps between clades were apparently wider then. Where problems of defining families occur (such as in Ptychopariina), they seem to come about because of problems in discriminating convincing morphological characters to define the clades. Particular Cambrian families have been discriminated on the basis of features that would not merit familial status in younger trilobites, such as details of the shape of the glabella or the size of the eyes. The traditional importance accorded to trilobites in Cambrian biostratigraphy may have contributed to these problems because the families often appear to be stratigraphically rather than morphologically bounded. Thus, there are few families found in the Ordovician that have a stratigraphic range of a span less than that of the whole system, and many that extend into the systems above or below; by contrast, there are only two families, Agnostidae and Ptychopariidae, that extend throughout the Cambrian, and the Ptychopariidae is not regarded as a satisfactory taxon. Many trilobite families regarded as typically Cambrian do not extend through more than a few biozones. Because the morphological range encompassed by Cambrian trilobites is, as a whole, less than that of Ordovician and later forms (FOOTE, 1991) and the Cambrian is also known to represent a shorter timespan than the Ordovician, it seems probable that both the short geological ranges and the difficulties with definition of some Cambrian trilobite families are to some extent a result of taxonomic practice, with the Cambrian groups being the more finely split.

More contentious problems, however, appear with classification above the family level. Whereas the families are generally diagnosable entities, the arrangement and status of superfamilies and orders have changed repeatedly, as opinions on the importance of one morphological character or another have been altered. HARRINGTON (in MOORE, 1959) ably summarized the main contributions to the higher classification made prior to the 1959 *Treatise,* and no particular purpose is served by repeating his discussion in detail here. The *Treatise* (MOORE, 1959) classification has remained the general reference for the last thirty-five years. Since 1959, LU and others (1965) published a compendium of the Chinese trilobite fauna; BERGSTRÖM (1973a) attempted a new comprehensive classification; FORTEY and OWENS (1975) proposed a new order Proetida; and a start has been made on phylogenetic analysis using cladistic methods (FORTEY & CHATTERTON, 1988; FORTEY, 1990a). In these, as in the earlier works, it is the higher taxonomic categories that have differed from one publication to another.

A few higher taxa have been stable. For example, the Phacopida has been consistently recognized as including phacopids and dalmanitids since the last century, although there have been differences of opinion as to whether the Calymenina should be classified with the Phacopida; and the status of the group has varied from superfamily to order. There are several readily recognizable morphological features that obviously unite the suborder Phacopina (Phacopoidea and Dalmanitoidea): the schizochroal eye; forwardly expanded glabella with long S3; proparian sutures combined with yoked cheeks; and typical pygidial form. These are all advanced characters, connecting what are otherwise rather disparate morphologies.

HIGH-LEVEL TAXA THAT ARE REDUNDANT

The problems with stability of other high-level taxa have stemmed from the difficulties in recognizing suites of characters appropriate for the discrimination of major natural groups. There are few groups as neatly defined as the Phacopida.

In the course of the debate about high-level classifications, some characters have come to assume particular importance. Prime among these are the patterns of cephalic sutures, which were emphasized in classical papers by BEECHER (1897) and

STUBBLEFIELD (1936). Suture patterns continue to be of importance in trilobite classification at ordinal level, although they are no longer accorded the primacy that they once had. HARRINGTON (in MOORE, 1959) sketched the voluminous history of the debate about which suture patterns were to be regarded as primitive for the group as a whole. The division of most trilobites into the two orders Proparia and Opisthoparia (or their several synonyms) on the basis of proparian and opisthoparian sutural patterns, respectively, enjoyed a widespread currency in the first half of this century (RICHTER, 1932; STØRMER, 1942). Consideration of the total morphology, however, showed that the inclusion of such proparian families as Eodiscidae, Norwoodiidae, and Phacopidae in the same higher taxon was entirely arbitrary, and the Proparia as construed was polyphyletic. The demonstration that proparian sutures could appear within the monophyletic family Olenidae (HENNINGSMOEN, 1957a)—most genera of which were opisthoparian—administered the coup de grace to the indiscriminate use of this suture pattern in classification. Nonetheless, it remains a useful character, among others, in the definition of clades; proparian suture pattern is a genuine derived character, and no example is known of a proparian trilobite that is ancestral to an opisthoparian one. It is abundantly clear, however, that proparian sutures in adult trilobites evolved more than once.

While it remains true that the Agnostida include the greatest number of trilobites with only two or three thoracic segments, it is no longer true that major ordinal divisions can be defined on the basis of thoracic segment number alone. This was the basis of the division of the Trilobita (JAEKEL, 1909) into the orders Miomera (with two to three segments) and Polymera (six or more segments). Indubitable corynexochoids (ROBISON & CAMPBELL, 1974) and trinucleoids (W. ZHANG, 1980), however, have now been described with numbers of segments that are typical of Miomera but which are otherwise clearly unrelated both to each other and to

any miomerid previously described. Also, a shumardiid trilobite, *Acanthopleurella,* is known that has four thoracic segments, forming a bridge between Miomera and Polymera (FORTEY & RUSHTON, 1980). Because it is now clear that the release of segments into the thorax is under developmental control, the generation of lineages with but a few thoracic segments does not seem to be a matter of great difficulty. All that is required is a process whereby release of segments from the front of the pygidium during ontogeny is inhibited and is accompanied by precocious sexual maturation. This is a neotenous process and is more strictly described as progenesis (MCNAMARA, 1983). As with suture patterns, the number of thoracic segments remains a useful taxonomic character, but it is not diagnostic in a simple way.

There have been various attempts to interpret the original cephalic segmentation (see discussion, p. 132), which have proved problematic with regard to the number of segments and their disposition in the preoral parts of the cephalic anatomy. Thus HUPÉ (1951) regarded the rostral plate, hypostome, and free cheek as comprising a single, ocular segment. Because the larval hypostome takes up much more of the venter, at which size it also shows paired, marginal spines, another interpretation might include more than one segment in the hypostome alone. None of these interpretations has contributed significantly to high-level classification, and the resolution of cephalic segmentation is still far from clear; it is probably preferable that untested and possibly untestable assumptions about homology not be built into systems of classification.

SYSTEMATIC POSITION OF OLENELLINA

Olenellus, Fallotaspis, and allied genera have occupied a special place in discussions of trilobite phylogeny and classification (STØRMER, 1942; HUPÉ, 1954). In many stratigraphic sections spanning the Precambrian-Cambrian transition, they are the first trilobites to appear near the base of

the Lower Cambrian. They have several features that have been regarded as primitive—most conspicuously, a lack of facial sutures—and this has invited speculation about how they relate to other early or primitive arthropods.

Lauterbach (1980, 1983) suggested that Olenellina are not trilobites at all. This interpretation of their morphology stresses alleged homologies between the tagmatization of merostome chelicerates and some of the species of Olenellina. This view has been repeated in some textbooks (Ax, 1987). Størmer (1933) had pointed out earlier the similarities between trilobites and merostomes. Cladistic analyses of the arthropods as a whole (Briggs, Fortey, & Wills, 1992) also place trilobites into a larger clade that includes *Limulus* and its allies. It seems likely that trilobites and merostomes shared a common ancestor shortly before the Cambrian radiation. However, consideration of those characters shared between undoubted trilobites and Olenellina (Fortey & Whittington, 1989) shows that there are more features that support trilobite relationships of these Early Cambrian forms than support merostome affinities (also Edgecombe & Ramsköld, 1991). The features shared by Olenellina and higher trilobites include the pygidium, the calcified cuticle, the structure of the hypostome, and the eye ridges; also once the cuticle was calcified, a perrostral suture facilitated molting, and the calcitic corneal surface of the eye (also unique to trilobites) was molted separately by means of a circumocular suture.

Hence it is probable that Olenellina and all other trilobites comprise a good clade, which descended from a common ancestor late in the Precambrian. The general resemblance between Olenellina and more generalized Redlichiina is striking, but the latter have functional facial sutures. This is a character unique to higher trilobites (although sutures are secondarily lost in several highly derived clades). The absence of such sutures in Olenellina is usually regarded as a primitive feature. Certainly, Olenellina retain other characters that are primitive: thin cuticle, no evidence of a calcified protaspis, nonfulcrate thoracic articulation, and minute pygidium. Moreover, some species have many additional thoracic segments grouped in a posterior opisthothorax.

The taxonomic status that should be accorded Olenellina and their close relatives is also a problem. The group as a whole is united by primitive (symplesiomorphic) characters. On the other hand, their position near the root of the trilobites has resulted in their being recognized as a higher taxon (e.g., order Olenellida in Bergström, 1973a). Both Olenellina and Redlichiina are probably paraphyletic groups. It is considered preferable, therefore, to unite these more or less primitive trilobites into a single order Redlichiida, while recognizing that future phylogenetic studies may well further limit its scope.

The recognition that the morphology of Olenellina is primitive for the Trilobita is important in determining which characters are advanced in other trilobites and hence in determining the diagnostic features of clades within the group.

STATUS OF NARAOIIDS

Naraoia and a number of other genera placed in the family Naraoiidae cannot be included within the diagnosis of Trilobita given here because they lack a calcified cuticle, evidence of sutures, and other important features of the group. On the other hand, naraoiids have a large pygidium, a trilobite-like arrangement of cephalic limbs, and, where known in *Tarricoia* (Hammann, Laske, & Pillola, 1990), nonfulcrate thoracic segments. *Naraoia* has been described from the Lower Cambrian of China (W. Zhang & Hou, 1985); hence its stratigraphic occurrence is not relevant in determining its relationships other than being consistent with its being primitive.

Naraoiids have an obvious if superficial resemblance to Agnostida by virtue of their enormous pygidia. They differ, however, in that the cephalic shield is shorter than the

pygidium, a condition that is otherwise known only in a few, advanced trilobites belonging to the Asaphidae and Styginidae. Furthermore, naraoiids are not progenetic (as are Agnostida) because they reach normal—even large—trilobite size. Instead, they may have arisen by a different neotenous process known as hypermorphosis. *Naraoia* resembles a giant, degree 0 meraspis in lacking a thorax and in having a relatively large pygidium.

The likely relationship of naraoiids to other calcified trilobites is that they form an uncalcified sister group of the larger, more diverse clade (WHITTINGTON, 1977; BRIGGS, FORTEY, & WILLS, 1992). They comprise a clade that, while having several peculiarities (autapomorphies) of their own, had not acquired some of the other, typical trilobite characters (e.g., calcite cuticle, sutures). In a formal classification system they might be recognized as a higher taxon commensurate with their inferred phylogenetic position, and the name Nektaspida RAYMOND (used as an order by MOORE, 1959) is available to accomodate the group. But it does not seem appropriate to use a class to encompass this handful of fossils, as would be required formally to recognize its sister group status to the class Trilobita. Instead, it is proposed to treat the family Naraoiidae as Trilobita order uncertain (essentially as a plesion in relation to the higher and diverse clade of calcified trilobites, see RAMSKÖLD & EDGECOMBE, 1991). The inclusion of Naraoiidae in the class acknowledges their systematic position, but the open, higher taxon allows the formal definition of Trilobita to be based upon the characters of calcified forms.

TAXONOMIC POSITION OF AGNOSTINA

Agnostina are remarkably abundant in Cambrian rocks and exhibit a wide range of morphology within the constraints imposed by their small size. They are clearly highly specialized: diminutive, blind, and isopygous, with two thoracic segments and vari-

ous modifications of the axial segmentation. The distinctive limbs of *Agnostus pisiformis* have been described by MÜLLER and WALOSSEK (1987).

The systematic position of Agnostina has been much debated. Some maintain that the Agnostina are not trilobites, a view promulgated by C. E. RESSER in the 1930s ["This group of Crustacea . . . a subclass parallel to the Trilobita . . . " (1938, p. 47)] and espoused most recently by SHERGOLD (1991). This opinion lays emphasis upon the unique characters of Agnostina, as an indication that they must have had a phylogenetically separate arthropod origin. The same view also regards Eodiscina as not being closely related to Agnostina. No one doubts that Eodiscina are trilobites; for example, early members of the group have facial sutures, and all have typical trilobite thoracic structures. Under the view of Agnostina as nontrilobites, therefore, such similarities as there are between Agnostina and Eodiscina are a matter of convergence. Advanced Eodiscina, for example, include species that were blind and have only two thoracic segments.

The other view contends that Agnostina are trilobites, albeit of a very specialized kind. The similarities between them and Eodiscina are indicative of their shared common ancestry, with the Eodiscina representing the more primitive morphology. This is not to say that any particular species of Eodiscina is necessarily nominated as ancestor of the Agnostina. This opinion would regard the peculiar features (autapomorphies) uniquely possessed by Agnostina as not relevant to determining their systematic position, however interesting these may be in determining their life habits or evolution within the group; for example, Agnostina have a unique exoskeletal opening, the cephalothoracic aperture, between the occipital part of the cephalon and the axial part of the thorax, which is exposed during enrollment. Instead, emphasis is placed on those characters shared between Agnostina and Eodiscina (synapomorphies) as indicating common descent. Such a view on classi-

fication has been articulated recently by Jell (1975a), W. Zhang, Lu, and others (1980), and Fortey (1990a).

It is not possible completely to falsify a hypothesis invoking convergence between groups. Trilobite history has several examples of remarkable morphological convergence between groups that are not close phylogenetically. The evolution of phacopid-like Proetida late in the history of the group is one instance; and the resemblance between some early Cambrian Redlichiina and Ordovician remopleuridids is another. In these cases, the convergence is revealed by one of two methods: (1) a series of morphologically intermediate species is known connecting the homeomorph in question with its mother group, and (2) critical analysis of the homology of characters reveals fundamental similarities that betray the convergence. Thus, in the examples given, the inspection of ventral, hypostomal, or pygidial characters will reveal the origins of the phacopid-like Proetida, or the origins of the remopleuridids from Asaphina. There is, however, no final arbitration to say how far homeomorphy may proceed, and the usual procedure is to weigh up the characters to see which hypothesis of relationship is supported by the most derived (synapomorphic) characters.

For the Agnostina, a suite of species connecting the group with some other taxon is not yet known (which is perhaps not surprising, given that Agnostina go back to the Early Cambrian), and we are obliged to accept comparison of homologous characters to determine phylogenetic relationships.

In a comparison between the possible theories of the relationships of the Agnostina, Fortey (1990a) found that more shared characters supported Agnostina and Eodiscina having descended from a common ancestor than their having separate origins. In particular, the ventral surface of both groups has a narrow marginal selvage (not a wide doublure), which in one agnostid is backed by a calcified rostral plate like that of Olenellina (Hunt, 1966). In either case, the venter is certainly not like that of Redlichiina and all higher trilobites. The hypostome is not suturally attached. The long (sag.) cephalic shield, wide (tr.) occipital ring, reduction in number of thoracic segments, and features of cephalic and pygidial margin are also shared by the two groups. It seemed to Fortey (1990a) to be less parsimonious to assume that all these characters were acquired in parallel by Eodiscina and Agnostina, particularly in the absence of a plausible sister group for the latter. As discussed above, the naraoiids are not likely candidates. Shergold (1991) chose to put great emphasis on the discovery of an eodiscoid protaspis (of usual trilobite type) as an indication that this group is closer to other trilobites, especially ptychoparioids, and that the Agnostina were independently derived. No calcified protaspis of a species of Agnostina has yet been discovered. In this regard, Agnostina are like Olenellina. The simplest explanation, however, is that Agnostina have retained a primitive or plesiomorphic condition; since Olenellina are trilobites, there is nothing special in lacking a calcified protaspis. A less simple alternative would be for Agnostina to have descended from an Eodiscina-like ancestor, the loss of the calcified protaspis being secondary—a reversion to the primitive state—and another specialized character of Agnostina among many. Agnostina may well have been planktonic animals (Robison, 1972a), and both small size and accelerated development are not implausibly associated with planktonic habits. In any case there is nothing especially persuasive about the protaspis of Eodiscina as an indication of separate origins for the Agnostina and Eodiscina. In the classification below the two groups are included within a single clade, but it is noted that this opinion is not held by all specialists in Agnostida.

THE PROBLEM OF THE PTYCHOPARIINA

Beginning in the Lower Cambrian and extending into the Ordovician there occurs commonly a type of trilobite with a rather

uniform bauplan. It might be termed the ptychopariid morphology and has a tapering glabella, a preglabellar field, opisthoparian sutures, rimlike cephalic borders extending into genal spines, natant hypostome, usually more than 12 thoracic segments, and a small, transverse, well-furrowed pygidium without remarkable features. Such a morphology is often referred to as generalized, but it is quite far removed from the primitive Redlichiida design, and it might be better to refer to it as exceptionally durable by virtue of a successful specialization. Where taxa of Ptychopariina occur, they often do so in great profusion. A typical example, *Elrathia kingi* (Middle Cambrian), has been extracted from its type locality in Utah in tens of thousands, and abundant specimens remain. This abundance suggests that these trilobites may have occupied a place comparatively low in the food chain, possibly by directly ingesting the sediment or living by filter feeding.

Partly because of the success and persistence of the design, Ptychopariina pose peculiar taxonomic difficulties. These difficulties stem from three sources. First, these trilobites have a range of morphological variations within a basically conservative design, which intergrade in such a way as to make the recognition of discretely bounded taxa genuinely debatable. Many of the changes that occur, concerning the size of the eye, width of border or preglabellar field, or depth of furrows, are trivial ones. Even generic diagnoses are difficult to frame using such characters, let alone those of families. Second, many of the taxa are known only from cranidia and pygidia—often only the former. It is possible that thoracic or librigenal characters may have been important. Third, in the absence of distinctive morphological characters, stratigraphic and geographical criteria have come into play in the taxonomy, and the result has probably been excessive splitting. For example, generic names applied in the Cambrian of Siberia or China are different from those in North America without critical evaluation of their morphological justification. For this group

of trilobites in the Cambrian, generic stratigraphic ranges have tended to be artificially short, crossing neither stage nor biomere boundaries. The result has been a proliferation of taxa with imprecise morphological definitions.

Even the definition of Ptychopariina as a whole is problematic. So-called ptychoparioid ancestors have been invoked for several other higher trilobite taxa: Olenina, Proetida, Harpina, Asaphida, and, more doubtfully, Phacopida. These groups have distinctive characters, which unite them and ensure their discreteness, but their earliest and most primitive members have a more general resemblance to the typical Ptychopariina morphology. In the previous edition of the *Treatise* (MOORE, 1959), there was no consistency about classifying these orders and suborders together in a still higher taxon, as they should be if they were ultimately descended from a common ancestor. FORTEY (1990a) described the ventral sides of typical Ptychopariina and noted that in these the hypostome was natant. In many of the groups derived from Ptychopariina, the hypostome was secondarily attached to the doublure (WHITTINGTON, 1988b). FORTEY applied the name Libristoma to the huge monophyletic group that includes Ptychopariina together with all those groups descended from them that had a natant hypostome.

Ptychopariina represent the primitive morphology of the libristomate groups. A paraphyletic suborder Ptychopariina can be defined as including trilobites with a natant hypostome that do not belong to one or another of the derived groups, that is, which retain the primitive exoskeletal morphology. This is not entirely satisfactory, but it does provide a phylogenetic rationale for this most difficult group. The order Ptychopariida includes also those other suborders, Harpina and Olenina, in which the bulk of the species retain the natant condition, even though they are good clades from other morphological criteria. The definition of Ptychopariida is accordingly a more re-

stricted one than that used in the previous edition of the *Treatise* (MOORE, 1959).

It is not yet possible to resolve many of the problems within Ptychopariina at the family and generic levels. Many of the taxa will probably remain those of convenience rather than natural groups.

OUTLINE OF CLASSIFICATION

The growth in the number of trilobite genera described since the previous edition of the *Treatise on Invertebrate Paleontology* (MOORE, 1959) has made it necessary to publish the revised edition in several parts. An outline of classification is necessary to determine which families should be included in each part. This account accompanies the first part and naturally cannot anticipate what advances will be made as subsequent parts are compiled. Nor can numbers of genera within each family be given, as did HARRINGTON (in MOORE, 1959), because this will change as work proceeds. Nonetheless, it is of service briefly to describe the systematic arrangement and to note some of the changes that have occurred since 1959. Superfamily endings have been changed from -acea to -oidea following Recommendation 29A in the *International Code of Zoological Nomenclature* (1985).

Criteria relating to larval characters can now be incorporated into diagnoses of high-level taxa because many more ontogenies have been described. The descriptions of exquisitely preserved, silicified faunas over the last thirty years have probably added the most new morphological information. BERGSTRÖM (1973a) brought some features of thoracic construction to attention that are useful at a high taxonomic level, but his general system of classification has not been adopted. WHITTINGTON (1988a, 1988b) and FORTEY (1990a) have emphasized the characters of the hypostome and its attachment in high-level classification.

This first volume includes primitive trilobites that appeared early in the geological record: these are grouped together in the orders Agnostida and Redlichiida. The problems with the definition of these taxa and their status within the Trilobita have been discussed previously. The second volume will probably include the orders Corynexochida, Lichida, and Phacopida. Libristomate orders and problematica comprise a third volume.

The orders recognized at this stage are discussed below.

ORDER AGNOSTIDA

The order embraces suborders Agnostina and Eodiscina. The view that these should be classified separately was discussed previously. All Agnostina have distinctive articulating structures on their two thoracic segments and a cephalothoracic aperture between cephalic shield and thorax. Eodiscina have either two or three thoracic segments of normal trilobite form and a wide range of morphological characters (with or without eyes, different forms of pygidial segmentation, effacement) that are the basis of family divisions within the group. Classification of Agnostina is based particularly upon the work of ÖPIK (1979) and SHERGOLD, LAURIE, and SUN (1990). Advances in classification of Eodiscina were made by JELL (1975a) and W. ZHANG, LU, and others (1980).

ORDER AGNOSTIDA
 SUBORDER AGNOSTINA
  Superfamily Agnostoidea
   Family Agnostidae
   Family Ptychagnostidae
   Family Spinagnostidae
   Family Peronopsidae
   Family Diplagnostidae
   Family Clavagnostidae
   Family Metagnostidae
  Superfamily Uncertain
   Family Phalacromidae
   Family Sphaeragnostidae
  Superfamily Condylopygoidea
   Family Condylopygidae
 SUBORDER EODISCINA
  Superfamily Eodiscoidea
   Family Tsunydiscidae

Family Hebediscidae
Family Calodiscidae
Family Weymouthiidae
Family Yukoniidae
Family Eodiscidae

ORDER REDLICHIIDA

This order includes the suborders Olenellina (PALMER & REPINA, 1993) and Redlichiina (W. ZHANG, LU, & others, 1980). Olenellina lack facial sutures and a calcified protaspis and have a wide rostral plate and nonfulcrate thoracic articulation, all characters which can be regarded as primitive. Redlichiina have facial sutures, a rostral plate bounded by connective sutures, and, where known, a calcified protaspis, characters which may be regarded as derived relative to Olenellina.

ORDER REDLICHIIDA
 SUBORDER OLENELLINA
  Superfamily Olenelloidea
   Family Olenellidae
   Family Holmiidae
  Superfamily Fallotaspidoidea
   Family Fallotaspididae
   Family Archaeaspididae
   Family Judomiidae
   Family Neltneriidae
   Family Nevadiidae
 SUBORDER REDLICHIINA
  Superfamily Emuelloidea
   Family Emuellidae
  Superfamily Redlichioidea
   Family Redlichiidae
   Family Dolerolenidae
   Family Yinitidae
   Family Mayiellidae
   Family Gigantopygidae
   Family Saukiandidae
   Family Metadoxididae
   Family Abadiellidae
   Family Kueichowiidae
   Family Menneraspididae
   Family Redlichinidae
   Family Chengkouaspidae
  Superfamily Paradoxidoidea
   Family Paradoxididae
   Family Centropleuridae

ORDER CORYNEXOCHIDA

This order is more inclusive here than in the previous edition of the *Treatise* (MOORE, 1959). Three suborders are placed in this group: Corynexochina, Illaenina, and Leiostegiina. All have conterminant (or impendent, derived therefrom) hypostomal attachment, often ledgelike cranidial borders, and typically elongate and pestle-shaped glabella with splayed glabellar furrows (FORTEY, 1990a). This glabellar shape resembles that of protaspides and early meraspides of other trilobites, and its presence in the adult is therefore probably neotenous. As with Agnostida, there is the question whether such a neotenous transformation could occur more than once and thus whether the Corynexochida might be polyphyletic. At the present time the evidence for this is not conclusive. Advanced members of all groups included may become effaced, which conceals their diagnostic characters. The suborder Corynexochina characteristically has the hypostome fused with the rostral plate.

ORDER CORYNEXOCHIDA
 SUBORDER CORYNEXOCHINA
   Family Corynexochidae
   Family Cheiruroididae
   Family Chenghuiidae
   Family Dorypygidae
   Family Ogygopsidae
   Family Oryctocephalidae
   Family Dolichometopidae
   Family Edelsteinaspididae
   Family Jakutidae
   Family Longduiidae
   Family Zacanthoididae
   Family Dinesidae

The suborder Illaenina is part of the suborder Illaenina as used by MOORE (1959). Other members formerly placed in this group have now been assigned to the order Proetida (FORTEY & OWENS, 1975). The older name Illaenina is preferred to Scutelluina. That the Illaenidae and Styginidae together comprised a monophyletic group was suggested by FORTEY (1980b, p. 59) and

LANE and THOMAS (1983). An important synapomorphy of the group is the presence of an extra-axial cephalic muscle impression, the lunette. FORTEY (1990a) added the family Tsinaniidae to the group. The relationship of the families here incorporated into the suborder Leiostegiina to those in the Corynexochina or Illaenina has not yet been determined.

SUBORDER ILLAENINA
  Superfamily Illaenoidea
    Family Styginidae (=Scutelluidae)
    Family Phillipsinellidae
    Family Illaenidae
    Family Tsinaniidae
SUBORDER LEIOSTEGIINA
  Superfamily Leiostegioidea
    Family Leiostegiidae
    Family Pagodiidae
    Family Kaolishaniidae
    Family Cheilocephalidae
    Family Lecanopygidae (=Illaenuridae)
    ?Family Shirakellidae

ORDER LICHIDA

THOMAS and HOLLOWAY (1988) regarded Lichida and Odontopleurida (*sensu* MOORE, 1959) as comprising a monophyletic group. This view depends on interpreting the complex glabellar lobes of the former as being homologous with the generally simpler lobes of the latter, as well as accepting a fundamental similarity in the protaspides of the two groups. Another view relates the lichids instead to the Styginidae. The former view is adopted here. FORTEY (1990a) regarded the superfamily Dameselloidea as likely to represent the Cambrian sister group to Odontopleuridae. Accordingly, the order Lichida is considered to include three superfamilies: Lichoidea, Odontopleuroidea, and Dameselloidea. All three superfamilies are good clades. Lichoidea have a unique glabellar structure; in addition, the pygidial structure of most lichoids is distinctive, and many have a characteristic surface sculpture comprising two sizes of granules or tubercles. Odontopleuroids have pleural tips with two

kinds of spines, one of which is usually greatly extended; the short, transverse pygidium with tubular marginal spines is also characteristic. Their classification has been discussed by RAMSKÖLD (1991b). Dameselloids differ from odontopleuroids in their less specialized thoracic segments, longer pygidia with more axial segments, and thickset marginal spines.

ORDER LICHIDA
  Superfamily Lichoidea
    Family Lichidae
    Family Lichakephalidae
  Superfamily Odontopleuroidea
    Family Odontopleuridae
    Family Selenopeltidae
  Superfamily Dameselloidea
    Family Damesellidae

ORDER PHACOPIDA

The order Phacopida comprises three suborders: Calymenina, Cheirurina, and Phacopina. All three share a distinctive protaspis type; the latter two are proparian. Calymenoids and cheiruroids retain a rostral plate from their common ancestor, but in virtually all phacopoids the free cheeks are yoked as a single piece. All three groups have epifacetal pleural furrows. Phacopoids have schizochroal eyes and a typical glabellar structure. Cheiruroids have distinctive thoracic segments, and typically spinose pygidia. As WHITTINGTON (1988b) noted, the anterior wing of the hypostome of these superfamilies carries a prominent process. Granulate sculpture is very common and invariable among cheiruroids. The Calymenina include the most primitive morphology of the group, both with regard to the facial suture pattern and the presence of a circumocular suture. The coherence of this clade has been challenged by ELDREDGE (1977), who emphasized several of the ptychoparioid characters of Calymenina. More characters support its unity. It is possible that Phacopida was derived from a libristomate ancestor, but while several plausible ptychoparioids are known (eulomids and lonchocephalids among

them), none is linked to the Phacopida by unequivocal characters. For this reason Phacopida are not included with other libristomate trilobites.

ORDER PHACOPIDA
  SUBORDER CALYMENINA
    Superfamily Calymenoidea
      Family Calymenidae
      Family Homalonotidae
      Family Carmonidae
      Family Bathycheilidae
    SUBORDER PHACOPINA
    Superfamily Phacopoidea
      Family Phacopidae
      Family Pterygometopidae
    Superfamily Dalmanitoidea
      Family Dalmanitidae
      Family Prosopiscidae
      Family Diaphanometopidae
    Superfamily Acastoidea
      Family Acastidae
      Family Calmoniidae
    SUBORDER CHEIRURINA
    Superfamily Cheiruroidea
      Family Cheiruridae
      Family Pliomeridae
      Family Pilekiidae
      Family Encrinuridae
      Family Staurocephalidae
      Family Hammatocnemidae

LIBRISTOMATE TRILOBITES

Trilobites that either have a natant hypostomal condition or were derived from such trilobites by secondary joining of the hypostome to the cephalic doublure were included in a subclass Libristoma by FORTEY (1990a). This formal subdivison is not adopted here, partly because the analysis necessary to determine other clades at this highest taxonomic level has not yet been done. Nonetheless, the orders below probably comprise a major clade, and hence their diagnoses are interdependent.

Order Proetida

This order was introduced by FORTEY and OWENS (1975) to include families that had

been placed in the Illaenina in the previous edition of the *Treatise* (MOORE, 1959), an assignment that is not considered to reflect their true systematic affinities. After some debate (BERGSTRÖM, 1977; FORTEY & OWENS, 1979; CHATTERTON, 1980; LÜTKE, 1980), the order Proetida has achieved wider acceptance, although not invariably accorded ordinal status. The order includes those trilobites that were included by MOORE (1959) in the superfamilies Proetacea, Bathyuracea, Dimeropygacea, and Holotrachelacea, here combined into three superfamilies: Proetoidea, Aulacopleuroidea (see OWENS & HAMMANN, 1990), and Bathyuroidea. Much more is known of ontogenies of Proetida than in 1959, and these demonstrate a common likeness among protaspides (see section on ontogeny). FORTEY (1990a) suggested that the natant condition may have been initiated earlier in ontogeny in Proetida. Although the bulk of the group retains the natant condition in the adult, there are good examples of the secondarily conterminant hypostome in late Proetida and Bathyuridae.

ORDER PROETIDA
  Superfamily Proetoidea
    Family Proetidae
    Family Phillipsiidae
  Superfamily Aulacopleuroidea
    Family Aulacopleuridae
    Family Brachymetopidae
    Family Rorringtoniidae
  Superfamily Bathyuroidea
    Family Bathyuridae
    Family Dimeropygidae
    Family Celmidae
    Family Lecanopygidae
    Family Glaphuridae
    Family Holotrachelidae (downgraded from monotypic superfamily)
    Family Telephinidae

Order Asaphida

The classification of trilobites included in this group was discussed in detail by FORTEY and CHATTERTON (1988). By comparison

with Moore (1959), the Asaphidae and Ceratopygidae are united within the same superfamily, Asaphoidea, based on their glabellar structure, while the Cyclopygoidea includes other families (Nileidae, Taihungshaniidae) besides the highly specialized Cyclopygidae, again based on cephalic characters. The superfamily Remopleuridioidea includes Remopleurididae and some allied families. The superfamily Dikelocephaloidea is used as revised by Ludvigsen and Westrop (1983b) to include saukiids and ptychaspidids as well as Dikelocephalidae. Primitive Asaphida are united in the Anomocaroidea, which includes a number of families retaining the natant hypostomal condition. All the above taxa have a ventral median suture, at least in primitive species, and many of the more advanced members have an inflated, globular protaspis, termed asaphoid by Fortey and Chatterton (1988). The Trinucleoidea is also included within the Asaphida; it was one of the so-called ptychoparioid groups in previous classifications. The systematic position of this important and specialized group has always been difficult to decide. Numerous Ordovician species of raphiophorids and trinucleids have their free cheeks yoked together, but the protaspis invites comparison with the asaphoid protaspis. However, yoked cheeks also occur among Asaphidae and Cyclopygidae, which have a median suture in early species. Liostracinidae include Cambrian species with a probable median suture and that show other points of resemblance to advanced trinucleoids (for example, a pyriform glabella). Inclusion of Trinucleoidea in Asaphida seems to be the best hypothesis available (see Chatterton & others, 1994).

The median suture may have arisen by reduction and eventual loss of the rostral plate. An intermediate grade of organization is probably shown by those trilobites that have a small, triangular rostral remnant termed a rostellum by Öpik (1967). There is a possibility that this evolved more than once (Robison, 1964). While this is conceivable, there is no convincing evidence for it, and

the similarity of early Asaphida (together with the Cambrian age of the rostellum-bearing forms) argues against such polyphyly.

ORDER ASAPHIDA
  Superfamily Anomocaroidea
    Family Anomocaridae
    Family Pterocephaliidae (includes Housiinae)
    Family Parabolinoididae
    Family Dikelokephalinidae
  Superfamily Asaphoidea
    Family Asaphidae
    Family Ceratopygidae
  Superfamily Dikelokephaloidea
    Family Dikelokephalidae
    Family Saukiidae
    Family Ptychaspididae
    Family Eurekiidae
    Family Loganellidae
  Superfamily Remopleuridioidea
    Family Remopleurididae
    Family Kainellidae
    Family Opipeuteridae
    Family Bohemillidae
    Family Auritamiidae
    Family Idahoiidae
    Family Hungaiidae
  Superfamily Cyclopygoidea
    Family Cyclopygidae
    Family Taihungshaniidae
    Family Nileidae
  Superfamily Trinucleoidea
    Family Trinucleidae
    Family Dionididae (=?Tongxinaspididae)
    Family Orometopidae
    Family Raphiophoridae
    Family Alsataspididae
    Family Orometopidae (includes Myindidae, Hapalopleuridae, Jegorovaiidae)
    Family Liostracinidae
  Superfamily Uncertain
    Family Rhyssometopidae (includes Mapaniidae, Plectriferidae)
    Family Monkaspididae (=?Chelidonocephalidae)

Order Ptychopariida

The problem of defining the Ptychopariina was discussed above. In the current classification the Ptychopariida includes only libristomates in which the secondary conterminant condition of the hypostome is not far advanced. The most primitive (plesiomorphic) families are lumped into the suborder Ptychopariina, which is dominated by families having the typical morphology as exemplified by *Ptychoparia* itself or *Elrathia*. The families are not all readily definable on unequivocal characters. When more is known of their morphology, they may be assigned as sister groups to one or another of the more derived clades, but for the moment they are retained together.

Two other suborders are included in Ptychopariida: Olenina and Harpina. The former has been well studied from Cambrian and Ordovician stratigraphic sections; all except the very earliest olenids (which have rostral plates) have yoked free cheeks, connected by a vary narrow strip of cephalic doublure. Extremely thin cuticles are typical. Harpina were formerly classified with Trinucleina, but the resemblance between the two groups is probably merely one of convergence. The families Entomaspididae and Loganopeltidae from the Upper Cambrian to Lower Ordovician are considered to be related to Harpina.

ORDER PTYCHOPARIIDA
  SUBORDER PTYCHOPARIINA
    Superfamily Ellipsocephaloidea
      Family Ellipsocephalidae
      Family Protolenidae
      Family Agraulidae
    Superfamily Ptychoparioidea
      Family Ptychopariidae
      Family Marjumiidae
      Family Solenopleuridae
      Family Conocoryphidae
      Family Dokimokephalidae
      Family Onchonotopsidae
      Family Nepeiidae
      Family Crepicephalidae
      Family Lonchocephalidae
      Family Kingstoniidae
      Family Shumardiidae
      Family Asaphiscidae
      Family Cooosellidae
      Family Elviniidae (includes Komaspididae)
      Family Cedariidae
      Family Norwoodiidae
      Family Menomoniidae
      Family Bolaspididae
      Family Papyriaspididae
      Family Emmrichellidae
      Family Diceratocephalidae
      Family Tengfengiidae
      Family Lisaniidae
      Family Inouyiidae
      Family Wuaniidae
      Family Lorenzellidae
      Family Proasaphiscidae
      Family Ignotogregatidae
      Family Holanshaniidae
      Family Mapaniidae
      Family Acrocephalitidae
  SUBORDER OLENINA
    Family Olenidae
  SUBORDER HARPINA
    Family Harpetidae
    Family Harpididae
    Family Entomaspididae
  SUBORDER UNCERTAIN
    Family Ityophoridae
     Polyphyletic groups
    Family Catillicephalidae
    Family Raymondinidae
    Family Avoninidae
    Family Plethopeltidae

TRILOBITA ORDER UNCERTAIN

Here are included a number of distinctive taxa that are not accomodated into the broad classification given above. Burlingiidae and Bathynotidae are undoubtedly trilobites, but their place within the group is uncertain. As discussed above, Naraoiidae is regarded as the sister group of the calcified Trilobita.

Family Burlingiidae
Family Bathynotidae
Family Bestjubellidae
Family Naraoiidae

EXPLANATORY NOTES FOR THE CAMBRIAN CORRELATION CHART

By JOHN H. SHERGOLD

BACKGROUND

Biostratigraphic subdivision of the Cambrian probably began earlier in Scandinavia than elsewhere, particularly in Sweden and Norway where pioneering schemes for the Middle and Upper Cambrian, which foreshadowed the subdivisions shown in Table 1, were published between 1854 and 1883 (see MARTINSSON, 1974). Subsequently, a high-resolution biostratigraphy based on Agnostina was established for the Middle Cambrian by WESTERGÅRD (1946), who also made contributions to Upper Cambrian biostratigraphy (1922, 1947). An Upper Cambrian zonation based on olenid trilobites was worked out in great detail by HENNINGS-MOEN (1957a).

Biostratigraphic division of the Lower Cambrian of Scandinavia has developed at a slower pace than that of the Middle and Upper with the use of local zones. Because the lowest Cambrian lacks trilobites, zonations using trace fossils and small shelly fossils have been established for the Precambrian-Cambrian type area in southeastern Newfoundland (see Laurentia, Table 1.4, "Tommotian" and "Nemakit-Daldynian" faunas). That part of the Lower Cambrian zoned on the basis of trilobites in Scandinavia (Table 1.3) follows the latest correlations of MENS, BERGSTRÖM, and LENDZION (1990). Essentially this is the scheme of BERGSTRÖM and AHLBERG (1981), AHLBERG (1985), and SHERGOLD and BRASIER (1986) with the substitution of the Zone of *Holmia inusitata* for that of *Holmia* sp. nov. (see AHLBERG, BERGSTRÖM, & JOHANSSON, 1986).

In Scandinavia, biostratigraphers use stages based on groups of zones; these stages are named after characteristic trilobites, the stage being divided into zones that are defined at specific level.

An Iberian Cambrian biostratigraphy (Table 1.3) was first established by LOTZE (1961) in which thirty-two trilobite horizons were recognized and assigned to three informal series (A–C). SDZUY (1968) described Middle Cambrian stages, subsequently demoted to substages. He also introduced three Lower Cambrian stages (Ovetian–Bilbilian) (SDZUY, 1971a, 1971b, 1972). LIÑÁN and FERNÁNDEZ-CARRASCO (1984) added the Cordubian Stage. This stadial scheme has been reviewed recently by LIÑÁN, PEREJON, and SDZUY (1993), and the trilobites that define the Lower Cambrian Ovetian–Bilbilian interval were discussed. Previously, eleven informal archaeocyathan zones (I–XI) were determined by PEREJON (1986). No formal zonation by either trilobites or archaeocyathans has been published. The Cordubian Stage is defined on the basis of ichnofossils, which include *Phycodes pedum* (see LIÑÁN, PEREJON, and SDZUY, 1993, for ranges).

The stadial divisions shown here (Table 1.3) for the Lower and lowest Middle Cambrian of Morocco are based on the recent conclusions of GEYER (1990a, 1990b, 1993). These are based essentially on the pioneering work of HUPÉ (1952, 1953a, 1960) and on revisions by SDZUY (1971a, 1971b, 1972, 1978) and GEYER (1983). The two stages, Soussien and Issafénien, recognized by HUPÉ have been replaced by the three shown in Table 1.3. The Tissafinian Stage, the Aguilizien Substage of HUPÉ, is now regarded by GEYER (1990a) as lowermost Middle Cambrian following the discovery of a paradoxidoid and an Olenellina trilobite together in the *Cephalopyge notabilis* Zone. An independent archaeocyathan biostratigraphy calibrated to the HUPÉ (1960) trilobite zonation has been published by DEBRENNE (1990).

In the Cambrian of Laurentia, with the exception of the lowest Cambrian, the bio-

stratigraphy is based on a succession of trilobite genera (Fig. 254). Assemblages of species within such generic zones are regarded variously as subzones, faunizones, and biozones, among others, but these assemblages are the most highly resolved biostratigraphic units used for correlation. Zones based on genera are grouped into stages that have developed historically and often in multiplicity. Neither the stages of the Lower nor Middle Cambrian are satisfactorily defined. WALCOTT originally called the Lower Cambrian the Georgian Epoch, but, according to RESSER and HOWELL (1938), he subsequently (1912b) substituted the name Waucoban when it was realized that the Georgian contained rocks younger than Early Cambrian. Nevertheless, LOCHMAN-BALK and WILSON (1958) and ÖPIK (1975b) have continued to use the term Georgian. PALMER (1971) preferred to use neither. Waucoban, however, is favored here because it apparently refers to definite trilobite-bearing Lower Cambrian zones in North America: *"Fallotaspis," "Nevadella,"* and *Bonnia-Olenellus* (PALMER & REPINA, 1993).

A Lower Cambrian biochronology has been developed recently for the Avalonian part of North America as a result of the deliberations on the Precambrian-Cambrian boundary. There, the biochronological interval covered by the previously proposed Etcheminian (MATTHEW, 1899a) and Hanfordian (HAYES & HOWELL, 1937) Series has been revised by LANDING (1993) and LANDING and others (1989), who recognized the Placentian and Branchian Series, in ascending order.

As with the Lower Cambrian, two series names have long been available for the Middle Cambrian of Laurentian North America: Acadian and Albertan. Because Acadian, like Georgian, has several connotations, Albertan was used for the *Bathyuriscus-Elrathina* (=*Ehmaniella*) and *Bolaspidella* Zones. The Upper Cambrian Croixian Series (WINCHELL, 1873), originally Potsdamian or Saratogan (WALCOTT, 1912a), traditionally contains the Dresbachian (WIN-

CHELL, 1886), Franconian (HOWELL & others, 1944), and Trempealeauan (HOWELL & others, 1944) Stages defined from the Mississippi Valley and applied continent-wide.

An alternative stadial terminology for the upper Middle and Upper Cambrian of Laurentian North America has been applied by LUDVIGSEN and WESTROP (1985). The bases of their Marjuman, Steptoean, and Sunwaptan Stages are tied to well-defined and readily correlated trilobite assemblage-zones: *Acidusus atavus, Aphelaspis (Glyptagnostus reticulatus),* and *Irvingella major* Zones. They are shown here (Table 1.2, 1.4) as an alternative to the traditional stages. Although regarded by LUDVIGSEN and WESTROP (1985) as an initial Ordovician stage, the Ibexian is here regarded as terminal Cambrian, at least initially (see discussion below). Its base, at the first appearance of the conodont *Cordylodus proavus,* is widely correlatable.

The Lower Cambrian of the Siberian Platform, characterized by its succession of small shelly fossils and archaeocyathan biotas, has become a standard for the biostratigraphic subdivision of carbonate-platform sequences. Most of the stages shown on Table 1.3 are those recommended by SPIZHARSKI and others (1983) and SPIZHARSKI and others (1986) and are the official stage names currently recognized by the Interdepartmental Stratigraphic Committee of Russia. This committee has traditionally regarded the lowest Cambrian stage as the Tommotian. The newly defined base of the Cambrian in Newfoundland, however, now demands recognition of the Nemakit-Daldynian (KHOMENTOVSKY, 1976) as the initial Lower Cambrian stage of the Siberian Platform (ROZANOV & ZHURAVLEV, 1992).

The Middle Cambrian of the Siberian Platform, containing Agnostina, is readily correlatable, although the Lower-Middle Cambrian boundary is problematical (see below). That part of the Amgaian Stage containing *Triplagnostus gibbus* and the first appearance of *Hypagnostus parvifrons* at the base of the Mayaian Stage are significant da-

tum points. Upper Cambrian biostrati-
graphic division (Table 1.1) follows Ivshin
and Pokrovskaya (1968) in recognizing the
Tuorian Stage. Their Shidertan Stage and
those stages recommended by Spizharski
and others (1986) are based on Kazakh units
and are not used here for the Siberian Plat-
form.

In Kazakhstan (Table 1.2, 1.4), the Upper
Cambrian stadial scheme established by
Ergaliev (1980) and recommended by
Spizharski and others (1983, 1986) is de-
monstrably incomplete, as is that of
Astashkin and others (1991). In Lesser
Karatau sections, southern Kazakhstan, and
particularly at Batyrbai, Upper Cambrian
stages younger than Aksayan are recognized
on the basis of both trilobites and conodonts
(Apollonov, Chugaeva, & Dubinina, 1981;
Chugaeva & Apollonov, 1982; Apollonov
& Chugaeva, 1982; Dubinina, 1982). The
Batyrbaian and Ungarian stages, defined by
trilobites and conodonts, were proposed by
Apollonov (1991) and are accepted here,
even though their published correlations
may not be entirely correct.

Ergaliev (1990) introduced new stages
for the Kazakh Middle Cambrian sequences.
The Amgaian Stage of the Siberian Platform
is replaced by Tyesaian, Mayaian by Zhana-
rykian, and additionally the Ayusokkanian
extended downward to encompass the whole
of the range of *Lejopyge laevigata*. The last
goes some way to resolving the Mayaian-
Ayusokkanian boundary in the earlier
scheme. The Sakian remained unchanged in
concept, as did the Aksayan, but a new
Kazakhstanian stage was proposed to replace
Batyrbaian. This seems unnecessary since
nothing new is added. Accordingly, this
stage is not included on the chart.

Traditionally, Chinese Cambrian bio-
stratigraphy has been closely tied to
lithostratigraphic units. All the stage names
currently in use relate to formations and, by
inference, the faunas they contain diagnose
the stages. Facies changes are not accounted
for, and the units are assumed to be cor-
relatable across China. The Chinese column

in Table 1.2, 1.4 follows the systems pro-
posed by Xiang and others (1979, 1981) and
W. Chang (1980, 1988), which were in turn
derived from the zonal biostratigraphy out-
lined by Lu and others (1974). Following
current Chinese official preference, the stage
names are now given in Pinyin translitera-
tion.

The Lower Cambrian in southwestern
China has been exhaustively investigated in
connection with the search for the Precam-
brian-Cambrian boundary, and the place-
ment of stage boundaries and their correla-
tion, particularly with Siberia and
Kazakhstan, has fluctuated considerably
since their original definition. The correla-
tion suggested here is based on those made
by Shergold and Brasier (1986), Sher-
gold, Laurie, and Sun (1990), and Brasier
(in McKerrow, Scotese, & Brasier, 1992),
in preference to those of Landing (1992,
1993). In these correlations, the Toyonian
Stage of Siberia is considered to encompass
the interval from the mid-Canglangpuan to
the Maozhuangian of China and most of the
Proampyx linnarssoni Zone and *Acadopara-
doxides (Baltoparadoxides) oelandicus* Stage of
Scandinavia.

As elsewhere, the interval represented by
the Xuzhuangian Stage is closely confined by
the *Triplagnostus gibbus* and *Acidusus atavus*
Zones. The Middle-Upper Cambrian transi-
tion has been addressed by Dong (1990)
and Xiang (1991), who relied on the last
appearance of *Lejopyge laevigata* to indicate
the top of Middle Cambrian rocks (see also
Daily & Jago, 1975), but this is recognized
largely in the Chiangnan Belt (Lu, Zhu, &
others, 1974) and the northern marginal belt
of the North China Platform. Strata of the
Gushanian Stage show an endemized
Australo-Sinian trilobite biofacies, which
does not contain *L. laevigata.* The concepts
of its constituent zones, based on *Black-
welderia* and *Drepanura,* however, can be
supported by correlation with Australia
(Öpik, 1967; Daily & Jago, 1975). Zhang-
shanian and Fengshanian Stages are also
based on the faunas of carbonate-platform

environments representing Australo-Sinian Upper Cambrian biofacies (Shergold, 1988), and their intercontinental utility depends also on the precision with which they can be correlated with the faunas of the Chiangnan Belt.

The history of the development of the Cambrian time scale in Australia (Table 1.2, 1.4) has been discussed at length by Shergold (1989). Whitehouse (1927, 1930) was the first to erect a detailed subdivision of the Cambrian in Australia, and with subsequent additions and modifications (Whitehouse, 1931, 1936, 1939; Whitehouse in David, 1932; David & Browne, 1950) this scheme remained current until the research of Öpik. With the advantage of Westergård's (1946) conclusions in Scandinavia, Öpik was able to formulate a more highly resolved Middle and lower Upper Cambrian biostratigraphy. The uppermost Cambrian series has also been intensely investigated, and a complete zonation is available for the eastern Georgina basin (Shergold, 1989, 1993). A complete, local, stage nomenclature has been applied to both the Middle and Upper Cambrian in the same area. No local stage terminology has been established for the Lower Cambrian of Australia. The stage nomenclature of the Siberian Platform, however, has been applied to the archaeocyathan and small-shelly-fossil-bearing deposits of South Australia, the Amadeus basin and southwestern Georgina basin of central Australia. "Upper Atdabanian–Lower Botomian" (Qiongzhusian) trilobite zones have been proposed in South Australia (Jell in Bengtson & others, 1990).

In northern Australian basins, the Middle Cambrian has been zoned wholly on the basis of trilobites, particularly Agnostina. Original concepts relating to the Ordian and Templetonian stages have been reviewed by Southgate and Shergold (1991) with the result that the Ordian Stage (Öpik, 1967) has been merged with the lower Templetonian because the latter is so difficult to discriminate from it biostratigraphically. The upper Templetonian (the *Triplagnostus gibbus* Zone) logically belongs with the succeeding Floran Stage (Öpik, 1979), which contains the zones of *Acidusus atavus* and *Euagnostus opimus.* This is in turn was succeeded by the Undillan (Öpik, 1979) and Boomerangian (Öpik, 1979) stages, which cover the zones of *Ptychagnostus punctuosus* to *Lejopyge laevigata.* The Mindyallan Stage (Öpik, 1963) straddles the Middle-Upper Cambrian boundary, which was placed within the *Acmarhachis quasivespa* Zone by Daily and Jago (1975). Idamean (Öpik, 1963), Iverian (Shergold, 1993), Payntonian, and Datsonian stages (Jones, Shergold, & Druce, 1971) complete the Upper Cambrian stadial scheme, the last two subdivided by zones based on both trilobites and conodonts (Nicoll & Shergold, 1991; Shergold & Nicoll, 1992).

CONTENTIOUS LEVELS OF CORRELATION

Traditionally, Lower Cambrian rocks were thought to have been characterized by the occurrence of Olenellina, Redlichiina, and Protolenidae; the Middle Cambrian by Paradoxidoidea; and the Upper Cambrian by Olenidae. With increased biostratigraphic discrimination, these divisions are no longer so clear-cut.

In Spain and Morocco there is an apparent overlap of protolenid, holmiid, and ellipsocephalid with paradoxidoid trilobites (Sdzuy, 1972; Geyer, 1990a, 1990b, 1993), which has led Geyer (1990a, 1990b, 1993) to correlate the Moroccan Tissafinian Stage (Table 1.3) with the *Proampyx linnarssoni* and *Acadoparadoxides insularis* Zones (i.e., lower *Acadoparadoxides (Baltoparadoxides) oelandicus* Stage) of Scandinavia and the Toyonian Stage and lower part of the Amgaian Stage in Siberia. In China and Australia (Table 1.4), late species of *Redlichia* occur in the Longwangmiaoan and Ordian Stages. Since Walcott's work (1912c), Chinese authorities have regarded rocks containing *Redlichia* as Lower Cambrian, as have

Australian authorities until the mid-1950s. Öpik (1968) developed his Ordian Stage from an earlier concept of Whitehouse (1930, 1931, 1936). Characterized by the occurrence of *Redlichia,* the Ordian Stage also contains the first species of *Xystridura,* which Öpik (1975a) regarded as a possible affiliate of both Protolenidae and Paradoxididae. Hypostomal morphology suggests a relationship between *Xystridura* and *Paradoxides* (Whittington, 1988a). Thus, a relationship between Paradoxidoidea and Redlichiina is surmised. Jell (in Bengtson & others, 1990, p. 310) denied the relationship between Xystriduridae and Paradoxididae, believing that it is the result of contemporaneous homeomorphy. Accordingly, he considered the Xystriduridae to represent a family of Ellipsocephaloidea that should be classified alongside Ichangiidae, Protolenidae, and Ellipsocephalidae. The correlations suggested here favor a relationship between Xystriduridae and Paradoxididae and the conclusions of Geyer (1990a, 1990b). They are supported by the correlation of the succeeding sequences of the upper *Acadoparadoxides oelandicus* Stage (*Eccaparadoxides pinus* Zone) in Scandinavia with the Lower Templetonian of Australia and the Maozhuangian Stage of China, postdating the ranges of Olenellina, Redlichiina, and Protolenidae (see also W. Zhang & Jell, 1987; Kruse, 1990).

The placement of the Middle-Upper Cambrian boundary is debatable but less problematical than the Lower-Middle Cambrian boundary. There is a growing consensus of support for the observations of Daily and Jago (1975) that the disappearance of *Lejopyge laevigata* marks the end of Middle Cambrian time. This is indicated by current work in China (e.g., Dong, 1990; Xiang, 1991) and by the revision of the Ayusokkanian Stage by Ergaliev (1990) in Kazakhstan. The disappearance of *L. laevigata* is recorded primarily in outer-shelf environments. In carbonate-platform rocks, correlation must be made through intermediate steps via other Agnostina. Based on this criterion, the Ayusokkanian, Mindyallan, and Dresbachian stages straddle the Middle-Upper Cambrian boundary. Both the problems of this boundary and those of the Lower-Middle Cambrian boundary were avoided by Ludvigsen and Westrop (1985) and Pratt (1992), who recognized only Lower and Upper Cambrian, the boundary between them lying at the base of their Marjuman Stage, at the base of the *Bolaspidella* Zone (=*Acidusus atavus* Zone).

The exact position of the Cambrian-Ordovician boundary has yet to be agreed upon internationally. There is considerable support for defining the base of the Ordovician System at the base of the Tremadoc Series or its correlative, which in biostratigraphic terms means at the first appearance of the nematophorus graptoloids or at the conodont biostratigraphic datum closest to this event. Initial correlation of the base of the Tremadoc with the first appearance of *Cordylodus proavus* is incorrect by the magnitude of a stage. The Zone of *Cordylodus lindstromi* is regarded here as the closest correlate to that of *Dictyonema flabelliforme sociale.* Therefore, the upper *Peltura* and *Acerocare* Zones of Scandinavia, the Ungurian Stage of Kazakhstan, the Xinchangian Stage of China, the Datsonian Stage of Australia, and the basal Ibexian Stage are wholly or partly uppermost Cambrian.

TABLE 1.1. *Correlation Chart of the Cambrian (part 1).*

		Scandinavia	Iberia	Morocco	Siberia
Ordovician	Dictyonema	Dictyonema flabelliforme norvegicum			
		Dictyonema flabelliforme flabelliforme			
		Dictyonema flabelliforme sociale			
Upper Cambrian	Acerocare	Acerocare ecome			
		Westergaardia			
		Peltura costata			
		Peltura transiens			
	Peltura	Peltura scarabaeoides			
		Peltura minor			
		Protopeltura praecursor			
	Leptoplastus	Leptoplastus stenotus			
		Leptoplastus angustatus			
		Leptoplastus ovatus			
		Leptoplastus crassicornis			
		Leptoplastus raphidophorus			
		Leptoplastus paucisegmentus			
	Parabolina	Parabolina spinulosa			
		Parabolina brevispina			
	Olenus Zones	Olenus scanicus			Tuoriam
		Olenus dentatus			
		Olenus attenuatus			
		Olenus wahlenbergi			Glyptagnostus reticulatus
		Olenus truncatus			
		Olenus gibbosus			
	Agnostus pisiformis	Agnostus pisiformis			Glyptagnostus stolidotus Agnostus pisiformis-Proagnostus fecundus

Table 1.2. *Correlation Chart of the Cambrian (part 2).*

Kazakhstan			China			Australia		Laurentia		
Ungurian	*Cordylodus caseyi*	*Dikelocephalina*	**Xinchangian**	*Cordylodus angulatus*	*Wanliangtingia*	**Warendan**	*Chosonodina herfurthi-Cordylodus angulatus*	**Canadian**	*Symphysurina* (**Ibexian**)	*Symphysurina bulbosa*
	Cordylodus prion			*Cordylodus lindstromi*	*Yosimuraspis*		*Cordylodus lindstromi*			
	Cordylodus oklahomensis	*Euloma limitaris-Taoyuania*		*Cordylodus intermedius*	*Richardsonella-Platypeltoides*	**Datsonian**	*Cordylodus prolindstromi Hirsutodontus simplex*			*Symphysurina brevispicata*
	Cordylodus proavus			*Cordylodus proavus*	*Mictosaukia Fatocephalus* / *Missisquoia perpetis*		*Cordylodus proavus*		*Missisquoia*	*Missisquoia typicalis Missisquoia depressa*
					Mict. striata Mict. angusti					*Eurekia apopsis*
Batyrbaian	*Proconodontus muelleri-Eoconodontus notchpeakensis*	*Lotagn. hedini*	**Fengshanian**	*Cambrooistodus*	*Tsinania-Ptychaspis*	**Payntonian**	*Mictosaukia perplexa*	**Trempealeauan**	*Saukia*	*Saukiella serotina*
		Harpidoides					*Neoagnostus quasibilobus-Shergoldia nomas Sinosaukia impages*			
		Lophosaukia			*Kaolishania pustulosa*					*Saukiella junia*
Aksayan	*Westergaardodina-Furnishina*	*Trisulcagnostus trisulcus*		*Proconodontus muelleri*		**Iverian**	*Rhaptagnostus clarki maximus-Rhaptagnostus papilio*			
		Eolotagnostus scrobicularis					*Rhaptagnostus bifax-Neoagnostus denticulatus*			
		Neoagnostus quadratiformis					*Rhaptagnostus clarki prolatus-Caznaia sectatrix*			
				Proconodontus posterocostatus			*Rhaptagnostus clarki patulus-Caznaia squamosa*	**Sunwaptan**		*Saukiella pyrene-Rasettia magna*
				Proconodontus tenuiserratus			*Hapsidocare lilyensis*		*Ptychaspis-Prosaukia*	*Ellipsocephaloides*
	Oncagnostus ovaliformis						*Peichiashania tertia-Peichiashania quarta*			*Idahoia*
	Oncagnostus kazachstanicus							**Franconian**		
	Pseudagnostus pseudangustilobus						*Peichiashania secunda-Prochuangia glabella*			*Taenicephalus*
							Wentsuia iota-Rhaptagnostus apsis			
Sakian	*Ivshinagnostus ivshini*			*Maladioidella*			*Irvingella tropica*			*Elvinia*
	Pseudagnostus "curtare"					**Idamean**	*Stigmatoa diloma*	**Steptoean**		*Dunderbergia*
	Oncagnostus longiformis			*Changshania conica*			*Erixanium sentum*			
							Proceratopyge cryptica			*Aphelaspis*
	Glyptagnostus reticulatus			*Chuangia batia*			*Glyptagnostus reticulatus*			
Aryusokkanian	*Glyptagnostus stolidotus Agnostus pisiformis-Proagnostus fecundus*		**Gushanian**	*Drepanura*		**Mindyallan**	*Glyptagnostus stolidotus*			*Crepicephalus*
				Blackwelderia			*Acmarhachis quasivespa*	**Dresbachian** (**Marjuman**)		*Cedaria*
	Lejopyge laevigata						*Erediaspis eretes*			

TABLE 1.3. *Correlation Chart of the Cambrian (part 3).*

	Scandinavia		Iberia	Morocco	Siberia	
Middle Cambrian		*Agnostus pisiformis*			*Glyptagnostus stolidotus* / *Agnostus pisiformis-* / *Proagnostus fecundus*	**Mayaian**
	Paradoxides forchhammeri	*Lejopyge laevigata*	Solenopleuropsidae free		*Lejopyge laevigata-* / *Aldanaspis truncata*	
		Jincella brachymetopa			*Anomocarioides limbataeformis*	
		Goniagnostus nathorsti				
	Paradoxides paradoxissimus	*Ptychagnostus punctuosus*	*Solenopleuropsis*		*Anopolenus henrici-* / *Corynexochus perforatus*	
		Hypagnostus parvifrons	*Pardailhania*			**Amgaian**
		Tomagnostus fissus- / *Acidusus atavus*	*Badulesia*		*Tomagnostus fissus*	
		Triplagnostus gibbus			*Triplagnostus gibbus*	
	Acadoparadoxides (Baltoparadoxides) oelandicus	*Acadoparadoxides pinus*	**Leonian** *Acadolenus* / *Conocoryphe ovata* / *Eoparadoxides mureroensis*	*Ornamentaspis frequens*	*Kounamkites*	
		Acadoparadoxides insularis			*Oryctocara*	
Lower Cambrian	*Protolenus*	*Proampyx linnarssoni*	**Bilbilian** Archaeocyath Zone XI	**Tissafinian** *Cephalopyge notabilis* / *Hupeolenus*	*Anabaraspis splendens*	**Toyonian**
					Lermontovia grandis	
					Bergeroniellus ketemensis	
	Holmia	*Holmia kjerulfi*	**Mariarian** Archaeocyath Zones VIII–X	**Banian** *Sectigena*	*Bergeroniaspis ornata*	**Botomian**
					Bergeroniellus asiaticus	
				Antatlasia gutta-pluviae	*Bergeroniellus gurarii*	
					Bergeroniellus micmacciformis- / *Erbiella*	
		Holmia inusitata	**Ovetian** Archaeocyath Zones I–VII	*Antatlasia hollardi*	*Judomia-Uktaspis*	**Atdabanian**
					Pagetiellus anabarus	
		Schmidtiellus mickwitzi		**Issendalenian** *Daguinaspis* / *Choubertella* / *Fallotaspis tazemmourtensis* / *Eofallotaspis*	*Fallotaspis*	
					Profallotaspis jakutensis	
					Dokidocyathus lenaicus	**Tommotian**
		sub-*Holmia*	**Cordubian**		*Dokidocyathus regularis*	
					Aldanocyathus sunnaginicus	
					Nemakit-Daldynian faunas	

TABLE 1.4. *Correlation Chart of the Cambrian (part 4).*

Kazakhstan		China		Australia		Laurentia	
Ayusokkanian	*Glyptagnostus stolidotus* / *Agnostus pisiformis-* / *Proagnostus fecundus*	Gushanian	*Drepanura*	Mindyallan	*Glyptagnostus stolidotus*	Dresbachian	*Crepicephalus*
	Lejopyge laevigata		*Blackweldaria*		*Acmarhachis quasivespa*		*Cedaria*
		Zhangxian	*Damsella-Yabeia* / *Leiopeishania* / *Taitzuia-Poshania*		*Erediaspis eretes*	Marjuman	
				Boomerangian	*Lejopyge laevigata*		*Bolaspidella*
Zhanarykian	*Leiopyge armata*		*Amphoton*	Undillan	*Goniagnostus nathorsti*		
	Goniagnostus nathorsti				*Ptychagnostus punctuosus*		
	Ptychagnostus punctuosus		*Crepicephalina*	Upper Templetonian-Floran	*Euagnostus opimus*	Albertan	
Tyesaian	*Acidusus atavus*	Xuzhuangian	*Bailiella-Lioparia*		*Acidusus atavus*		
	Ptychagnostus intermedius		*Poriagraulos* / *Hsuchuangia-Ruichengella*		*Triplagnostus gibbus*		*Ehmaniella*
	Peronopsis ultimus	Maozhuangian	*Shantungaspis* / *Yaojiayuella*	Ordian-Lower Templetonian	*Xystridura templetonensis-* / *Redlichia chinensis*		*Glossopleura*
							Albertella
		Longwangmiaoan	*Redlichia nobilis* / *Redlichia chinensis*				*Plagiura-Poliella*
		Canglangpuan	*Megapalaeolenus* / *Palaeolenus* / *Drepanuroides*	Lower Cambrian	*Pararaia janeae*	Waucoban	*Bonnia-Olenellus*
			Yunnanaspis / *Yiliangella* / *Malungia*		*Pararaia bunyerooensis*		
					Pararaia tatei		
		Qiongzhusian	*Eoredlichia-Wutingaspis*		*Abadiella huoi*		
			Abadiella				"*Nevadella*"
		Meishucunian	"Tommotian" faunas				"*Fallotaspis*"
							"Tommotian" faunas
			"Nemakit-Daldynian" faunas				"Nemakit-Daldynian" faunas

MORPHOLOGICAL TERMS APPLIED TO TRILOBITA

H. B. Whittington and S. R. A. Kelly

This glossary is based on that of Harrington and others (in Moore, 1959) and terms proposed since that date. Earlier definitions have been modified to reflect the results of research over the past 30 years. For clarity, all paired structures are referred to in the singular. Terms considered to be of lesser or greater importance are not distinguished here by typeface, but those regarded as synonyms are thought to be less desirable alternatives. Many terms are discussed and illustrated in the introductory sections.

A compilation by S. R. A. Kelly was the starting point for this glossary, the terms included and their definitions having been changed by H. B. Whittington as the introductory sections were prepared. Comments from P. D. Lane and other contributing authors are gratefully acknowledged, as are the terminology for Agnostina prepared by J. H. Shergold and J. R. Laurie (Fig. 6, 11, 13) and the collaboration of W. H. Fritz and A. R. Palmer on terms applicable to Olenellina (Fig. 16).

abathochroal eye. Similar to schizochroal eye in that lenses were separated, but lacking scleral projections and intrascleral membranes. Each lens probably with a separate cornea fixed at the lens margin to the interlensar sclera.

abaxial. Away from axial line.

accessory furrow. A diagonal furrow in the pygidium of *Pseudagnostus* arising at the posterolateral corner of the second axial ring and directed abaxially and rearward (syn., pseudofurrow).

accessory upper horizontal row. Row of lenses in eye lying above upper horizontal row but consisting of few lenses and confined to posterior part of visual surface.

acrolobe. Portion of cephalon or pygidium enclosed within border furrow in Agnostina. Described as constricted when lateral margin curves slightly adaxially and unconstricted when lateral margin maintains constant curvature.

adaxial. Toward the axial line.

aggregate eye. See schizochroal eye.

ala (pl., alae). Smooth, depressed area adjoining posterolateral portion of glabella in Harpetidae (syn., alar lobe).

alar furrow. Curved furrow bounding ala.

alar lobe. See ala.

alimentary canal. Digestive tract extending from mouth to anus.

anaprotaspis (pl., anaprotaspides). Smallest protaspides in a size series in which protopygidium is supposedly unrecognizable. Inadequately defined and not recommended as a subdivision of protaspid period.

antenna (pl., antennae). Multijointed sensory appendage attached to front part of cephalon on ventral side.

antennal notch. Notch in the anterior cephalic border immediately outside of where the connective suture crosses the border in, for example, Odontopleuridae (syn., antennular notch).

antennary pit. See fossula.

antenniform cercus (pl., cerci). Uniramous, multijointed appendage immediately behind posterior limb, probably attached to the telson; known only in *Olenoides serratus* (syn., caudal ramus, cercus).

antennular notch. See antennal notch.

antennular pit. See fossula.

anterior accessory area. See anterior pleural band.

anterior accessory ridge. Ridge on anterior pleural band separated by a flattened area (the pleural furrow) from principal pleural ridge.

anterior arch. Formed by anterior border of cephalon, as seen in anterior view, rising dorsally to midline because of convexity of cephalon.

anterior area (of fixed cheek). See anterior area (of fixigena).

anterior area (of fixigena). Portion of fixigena in front of preglabellar furrow and eye ridge. If eye ridge is absent, posterior boundary of the area is marked off by imaginary transverse line passing through anterior extremity of palpebral lobe. This area is the left or right side of the frontal area (syn., anterior area of fixed cheek, anterior fixigena, anterior region of fixigena, preocular cheek).

anterior baccular ridge. Short, low ridge running anteriorly on floor of the axial furrow from the baccula to behind the anterior lateral glabellar lobe in Eodiscidae.

anterior band of pleura. See anterior pleural band.

anterior border (of cephalon). Portion of cephalic border between anterior branches of facial sutures, when anterior branches of suture cross border; otherwise term is ill defined.

anterior border (of hypostome). Extends between anterior wings in front of middle body; bounded by anterior border furrow.

anterior border furrow (of cephalon). Portion of border furrow bounding anterior border (syn., front furrow, frontal furrow).

anterior border of cranidium (in Encrinuridae). Extends between axial furrows and is bounded by preglabellar furrow and rostral and facial sutures (previously referred to as a portion of preglabellar field) (syn., false preglabellar field, pseudoglabellar area).

anterior boss. See fossular apodeme.

anterior branch (of facial suture). Portion of facial

suture lying anterior to eye [syn., anterior section (of facial suture), preocular branch (of facial suture), preocular suture].

anterior field of fixigena. Portion of fixigena in front of eye ridge and glabella and inside anterior border furrow; this area is the left or right side of frontal field (syn., anterior fixigenal field).

anterior fixigena. See anterior area (of fixigena).

anterior fixigenal field. See anterior field of fixigena.

anterior fixigenal spine. Prominent anterior spine on protocranidium of protaspis; may be adjacent to either branch of facial suture.

anterior flange. See flange.

anterior fossula. See fossula.

anterior furrow. Furrow bounding laterally the preglabellar area in *Neseuretus.* Also used for false preglabellar furrow in Encrinuridae, and for transglabellar furrow in Agnostina.

anterior glabellar furrow. See lateral glabellar furrow.

anterior half rib. See articulating half rib.

anterior limb. See frontal area.

anterior lobe (of glabella). Portion of glabella anterior to transglabellar furrow in Agnostina (syn., anteroglabella). See also frontal lobe.

anterior lobe (of hypostome). Portion of middle body of hypostome in front of middle furrows.

anterior median process. See frontal process.

anterior node. Occurring in axial furrow in the position occupied by fossula in some trilobites as in *Dechenella (Pedinodechenella).* Also used for pit in visceral surface of cephalon, situated between fossula and cephalic margin; preserved as small node on internal mold in the illaenid *Cybantyx.*

anterior ocular line. Ridge in Olenellina that curves outward and backward from anterior end of visual surface of eye toward the genal angle.

anterior pit. See fossula.

anterior pleural band. Strip of thoracic or pygidial pleura bounded posteriorly by deepest part of pleural furrow (syn., anterior accessory area, anterior band of pleura, propleura, propleuron). See also articulating half rib.

anterior pleural spine. Extension of distal end of anterior pleural band.

anterior region (of fixigena). See anterior area (of fixigena).

anterior section (of facial suture). See anterior branch (of facial suture).

anterior wing (of hypostome). Extension of anterolateral angle of hypostome.

anterior wing process (of hypostome). Rounded boss or thornlike protuberance on interior (dorsal) surface of anterior wing.

anteroaxis. Anterior portion of axis of pygidium in Agnostina, including first two axial rings (referred to as M1 and M2, numbering backward from the anterior margin).

anteroglabella. Region in front of transglabellar furrows 1S, as in *Centropleura;* alternative term for anterior lobe of glabella in Agnostina.

anterolateral furrow. Lateral portion of transglabellar furrow in Agnostina, when transglabellar furrow is interrupted by the axial glabellar node.

anterolateral lobe of posterior lobe of glabella. In Agnostina a low inflation on external surface immediately behind transglabellar or anterolateral furrow; on internal mold it forms the anterolateral muscle scar impression.

anteromedian depression. Depression in sagittal line that may be in the preglabellar furrow or extend forward from it or may join the longitudinal median glabellar furrow.

antirostral hood. Low swelling of frontal area reflecting shape of rostral plate.

apodemal pit. Excavation in external surface of exoskeleton corresponding to apodeme on internal surface (syn., appendiferal pit).

apodemal sector. Anterior portion of axis of pygidium in which inter-ring furrows have lateral apodemal pit and apodeme on inner surfaces.

apodeme. Process presumably for attachment of muscles or ligaments, formed by inbending or thickening of dorsal exoskeleton on internal side of exoskeleton (syn., appendifer).

appendage. See biramous appendage (or limb).

appendifer. See apodeme.

appendiferal pit. See apodemal pit.

arc. Curving row of pits on trinucleid fringe (syn., concentric row).

articulated pleura. See inner portion of pleura.

articulating boss (and socket). Corresponding structures on margins of thoracic segment, posterior margin of cephalon, and anterior margin of pygidium. See also axial process, axial socket, fulcral process, fulcral socket, ring process, ring socket.

articulating furrow. Transverse groove on external surface formed by transverse fold in exoskeleton separating articulating half ring from axial ring.

articulating half rib. Term applied to anterior pleural band of pygidium (syn., anterior half rib).

articulating half ring. Extension of axial ring anterior to articulating furrow that passes under posterior doublure of next anterior axial ring (syn., axial articulating half ring, half ring).

articulating socket (and boss). See articulating boss (and socket).

asaphid suture. Cephalic suture in which two anterior branches (or sections) meet in the midline, either marginally or intramarginally on the dorsal side and are continued across the doublure by a median suture (syn., isoteliform suture, niobiform suture).

asaphoid protaspis. Spherical or ovoid in form; doublure semitubular in shape, extending far back; with marginal cephalic suture and median suture in later developmental stages; librigena lacks genal spine; hypostome is relatively large and spinose. The term asaphoid as used here does not imply that all species having such a protaspis are classified in the superfamily Asaphoidea (syn., nonadult-like protaspis).

asymmetric pygidial rib. Rib that slopes steeply to the pleural furrow posterior to it and slopes less steeply anteriorly.

attached (condition). See hypostome.

axial articulating half ring. See articulating half ring.

axial bar. Convex floor of the articulating furrow of the pygidium in Agnostina.

axial furrow. Groove on external surface formed by fold in exoskeleton that outlines axial region of cephalon, thorax, and pygidium (syn., circumaxial furrow, dorsal furrow, rachial furrow).

axial glabellar carina. A narrow, exsagittal ridge between the axial and terminal nodes of the glabella, situated immediately abaxial to the sagittal, axial glabellar sulcus in internal molds of Pseudagnostinae.

axial glabellar node. In Agnostina an elongate node lying near midlength of glabella, either between (condition known as papilionate) or behind (condition known as spectaculate) the anterolateral lobes of the posterior glabellar lobe. An axial glabellar carina may run back from the node to the terminal glabellar node (syn., axial node of glabella, median node). See also glabellar node.

axial line. See sagittal line.

axial lobe. See axis.

axial node. Median (or paired) tubercle on external surface of axial ring of thorax or pygidium.

axial node of glabella. See axial glabellar node.

axial process. Projection from anterior edge of thoracic segment at axial furrow.

axial region. See axis.

axial ridge. Triangular projection of axis over posterior border of pygidium as in Proetoidea.

axial ring. Central portion of thoracic segment or of a segment of pygidium, bounded laterally by axial furrow (syn., rachial ring, ring). May be subdivided by intra-annular furrow into preannulus and postannulus.

axial shield. Articulated exoskeleton lacking librigenae, rostral plate, and hypostome (i.e., consists of articulated cranidium and thoracopygon).

axial socket. Indentation on posterior edge of axial furrow of thoracic pleura into which axial process fits.

axial spine. Median (or paired) pointed structure projecting from external surface of axial ring.

axiolobate. Referring to Agnostina with basic unmodified pygidial axial lobe.

axis (pl., axes). Median region of dorsal exoskeleton, bordered by axial furrow including preglabellar furrow (syn., axial lobe, axial region, rachis, rhachis).

axis (of pygidium). Median region of pygidium, bordered by axial furrow (syn., pygorachis). May be subdivided into apodemal and post-apodemal sectors.

axis (of thorax). Median region of thorax, outlined by axial furrow.

baccula (pl., bacculae). Swelling flanking posterior portion of glabella, which may be separated from glabella by axial furrow or may merge with anterolateral corner of occipital ring and which may be separated from fixigena by baccular furrow or may merge into fixigena.

baccular furrow. Furrow separating baccula from fixigena; may be considered the lateral part of the axial furrow if the baccula is within the axial furrow as in Eodiscidae.

band furrow. Furrow delimiting posterior band of occipital and axial thoracic rings in asaphids.

basal glabellar furrow. See lateral glabellar furrow.

basal lobe (of glabella). See lateral glabellar lobe. In Agnostina, triangular or pear-shaped in outline, situated at posterolateral corner of glabella and separated from it by curved or sinuous basal furrow; may be effaced.

beak. See frontal process.

Bertillon pattern. Pattern of anastomosing, subconcentrically arranged, symmetrical ridges (lirae) on external surface resembling a fingerprint (syn., fingerprint pattern). See also hapsidium.

bicomposite glabellar lobe. See bullar lobe.

bigeniculate (glabellar furrow). Glabellar furrow having two marked changes in direction.

biramous appendage (or limb). Ventral appendage having an outer branch (ramus) and an inner branch (syn., appendage).

border. Outer dorsal portion of cephalon and pygidium and outer ventral portion of hypostome, usually bounded by border furrow (has been referred to as rim, marginal rim, or marginal limb, but the term rim is restricted here to narrow peripheral ridge of fringe of Trinucleidae, etc.).

border furrow. Furrow defining adaxially border of cephalon, pygidium, and hypostome (syn., marginal furrow).

border pit. One of a row of pits along anterior border furrow of cephalon as in *Angelina;* may occur also in lateral border furrow as in *Euloma* (syn., marginal pit).

border roll. Tubular border of cephalon formed by convex border and doublure that is convex ventrally.

border sector. Outer, anterior portion of rostral plate separated by sharp flexure from the inner, doublure sector.

border spine. Spine (other than genal, fixigenal, librigenal) on anterolateral border of cephalon and to pleural spine of pygidium when border is present.

brim. Peripheral portion of fringe, bounded on inward side by girder or corresponding inflexion of upper lamella as in Harpetidae, Harpididae, and Trinucleidae (formerly used for frontal field).

brim prolongation. Peripheral portion of fringe prolongation, bounded by girder; represents posterior extension of brim as in Harpetidae and Harpididae.

bulla (pl., bullae). Rudimentary swelling in early lichid growth stage (situated inside the axial furrow and opposite L2), which grew rapidly in subsequent stages to form bullar lobe or composite lobe.

bullar lobe. Lateral glabellar lobe in lichid trilobite in position of L2 and L3 and formed by growth of bulla. This term replaces bicomposite or tricomposite glabellar lobe.

burlingiiform sutures. Proparian sutures in which the anterior and posterior sections are subparallel, diverging outward and forward at an angle of about 45° to axial line of cephalon as in *Burlingia*.

buttress. Projection from abaxial wall of axial furrow of cephalon, opposing a papilla of glabellar lobe. See also papilla, papillate-buttress structure.

caecal node. Point at which diverticulum or major caecum branches.

caesura (pl., caesurae). Line of separation between two differently oriented blocks of rows of lenses in a schizochroal eye.

carapace. Term applied to Crustacea; incorrectly used for trilobite exoskeleton.

cast. A replica of an original, made from a mold.

caudal ramus (pl., rami). See antenniform cercus.

caudal shield. See pygidium.

caudal spine. See posterior spine.

cedariiform suture. Opisthoparian suture in which the posterior section runs outward (abaxially) and onto or across the lateral border before curving backward and then turning adaxially to the posterior margin (syn., pseudoproparian suture).

central area (of glabella). Middle portion of glabella between frontal lobe and occipital furrow, bounded laterally by adaxial ends of lateral glabellar furrows [syn., central region (of glabella), median cervical lobe, median lobe (of glabella)].

central body (of hypostome). See middle body (of hypostome).

central region (of glabella). See central area (of glabella).

cephalic axis. See glabella.

cephalic beak. Median anterior protuberance from doublure of cephalon that on enrollment interlocks with a depression on the median posterior doublure of the pygidium.

cephalic recess. Upwardly arched recess below occipital band, visible in posterior view of cephalon in Agnostina. See cephalothoracic aperture.

cephalic region. See cephalon.

cephalic sutures. General term for all the sutures (circumocular, connective, facial, hypostomal, perrostral, rostral) of the cephalon.

cephalon (pl., cephala). Anterior tagma composed in trilobites of a number of fused somites, applied by authors to anterior portion of exoskeleton separated from remainder of exoskeleton by an articulation (syn., cephalic region, head, head shield).

cephalothoracic aperture. An elliptical gap in the exoskeleton in Agnostina, in the median portion of the axial region, between the cephalic recess and the thoracic recess. The gap was open in the enrolled exoskeleton (Fig. 48).

cercus (pl., cerci). See antenniform cercus.

cheek. See gena.

cheek area. See gena.

cheek field. See genal field.

cheek lobe. See gena.

cheek region. See gena.

cheek roll. See genal roll.

cheek roll prolongation. See genal roll prolongation.

circumaxial furrow. See axial furrow.

circumocular suture. Suture surrounding the visual surface; in trilobites having a facial suture, it is composed of an upper section, the palpebral suture, and a lower section, the ocular suture.

coaptation (coaptative, adj.). Fitting together of two independent parts of the same animal. In trilobites coaptative structures are morphological devices that interlocked when the exoskeleton was fully enrolled.

composite internal mold. Mold of internal surface of dorsal exoskeleton and impression of external surface of ventral exoskeleton (i.e., of hypostome, rostral plate, and doublure).

composite lobe. Lobe formed by partial or complete fusion of bullar lobe with L1 in lichid trilobites.

concentric row. See arc.

connecting doublure. Bridging piece that unites the doublures of the librigenae medially where connective sutures are lacking.

connective band: Vertical to horizontal band (depending on convexity) immediately behind the pygidial axis and anterior to the border furrow and that may connect the pleural fields of pygidium. This term has been used as a synonym for occipital band.

connective suture. One of paired longitudinal sutures transecting border or doublure in front of hypostome and defining rostral plate laterally.

constricted. See acrolobe.

conterminant (condition of hypostome). Hypostome underlies anterior portion of glabella and is attached at a suture to the anterior cephalic doublure.

cornea (corneal membrane). A thin external covering on the surface of the lens of the eye, continuous in the holochroal eye, discrete in the schizochroal and abathochroal eye.

corner angle. Angle between outer lateral and posterior margins of librigena.

corner furrow. Groove extending obliquely outward from axial furrow at anterolateral corner of glabella as in *Strenuella.*

coxa. Proximal podomere of biramous appendage, attached directly to ventral surface of body (syn., coxite, coxopodite).

coxite. See coxa.

coxopodite. See coxa.

cranidial spine. Strong occipital spine in Eodiscidae at posterior of glabella and occipital ring. Swelling of the axis obscures original site.

cranidium (pl., cranidia). Central portion of exoskeleton of cephalon, bounded laterally by facial suture.

crenal tongue. Tongue of librigena between ocular suture and retrodivergent anterior facial suture as in *Centropleura.*

cuticle. Mineralized portion of the integument, which constitutes the exoskeleton.

dalmanitidiform suture. Proparian suture in which anterior sections meet on dorsal side of cephalon near anterior margin as in *Dalmanites.*

degree of meraspid period. Stage in development characterized by number of articulated thoracic segments. Degree 0 has none, degree 1 has one freely articulating segment, etc. Meraspid degrees may be abbreviated as M0, M1, etc.

deliquiate. Condition in which border furrow in Agnostina is deep and channel-like, rather than a change in convexity.

deltoid area. Triangular depression in Agnostina, lying between oblique lateral ridge and axial glabellar carina.

deltoid depression. Triangular depression in Agnostina, formed by expansion of anterior border furrow at its junction with the median preglabellar furrow.

detached (condition). See hypostome, natant (condition) of hypostome.

deuterolobate. Agnostina in which the deuterolobe is well defined by tumidity and accessory furrow.

deuterolobe. Composite pygidial lobe of confluent pleural and axial regions, which lies between anterior lobe of axis defined by axial furrow and posterior border furrow. Laterally it is defined by the accessory furrow (syn., endlobe, pseudolobe).

distal. Portion of body away from the point of origin or sagittal line.

distal portion of pleura. See outer portion of pleura.

dome. Area of cuticle that bulges above the general level, thinning markedly at the apex of the bulge.

dorsal exoskeleton. See exoskeleton.

dorsal furrow. See axial furrow.

dorsal shield. See exoskeleton.

doublural plate. See lower lamella.

doublure. Reflexed continuation of dorsal exoskeleton onto ventral surface.

doublure sector. Inner part of rostral plate separated from border sector by sharp flexure.

E. See external.

ecdysis. Processes of preparing to cast off and casting off (exuviation) old exoskeleton.

effaced. Condition in which furrows and lobes are obliterated to give smooth or almost smooth surface. The term therefore implies that ancestral forms were not effaced, i.e., were en grande tenue.

elliptical ring. See intranotular axis.

endite. Inwardly directed lobe of podomere of inner branch.

endlobe. See deuterolobe.

endopod. See inner branch (of biramous appendage).

endopodite. See inner branch (of biramous appendage).

en grande tenue. Condition in Agnostina in which furrows and lobes are distinct (syn., non-effaced).

entomaspidiform suture. Opisthoparian facial suture in which anterior branch is retrodivergent, running outward and backward from eye to lateral margin as in *Entomaspis.*

epiborder furrow. Furrow or change in slope between the convex inner, and flattened outer portions of the cephalic border in dalmanitinids; associated with a doublure that has a flat outer portion and a steeply upturned inner portion, the latter being beneath the inner portion of the border. In eodiscoids a furrow on the cephalic border in which the distal ends of the scrobiculae lie.

epifacetal (type of pleural furrow). Outer portion of pleural furrow that crosses posterior margin of articulating facet and continues as a narrow, distinct furrow on articulating facet. See postfacetal pleural furrow.

epipalpebral furrow. See ocular furrow.

epistoma. See hypostome, rostral plate.

epistomal plate. See rostral plate.

epistome. See rostral plate.

euptychopariid rostral suture. Connective suture marginal to a broad (tr.) rostral plate (contrast with stenoptychopariid). See ptychopariid suture.

exite. See outer branch (of biramous appendage).

exopod. See outer branch (of biramous appendage).

exopodite. See outer branch (of biramous appendage).

exoskeleton. Mineralized dorsal cuticle extended onto ventral side as doublure and hypostome (syn., dorsal exoskeleton, dorsal shield, shield, test).

exsagittal. Direction parallel to, but outside sagittal (median) line (abbreviation, exs.).

external (E). Used in referring to pits in the trinucleid fringe outside girder, to arcs of pits, to individual or to irregular pits.

external mold. Mold of outer surface of exoskeleton.

external rim. Outer, raised smooth border of fringe along anterior and lateral edges extending back to posterior tip of prolongation as in Harpetidae, Harpididae, and Trinucleidae.

extranotular axis. Longitudinal portion of axis of pygidium situated between axial furrow and notular line. If axial furrow is effaced, extranotular part of axis may be mistaken for part of pleural field and the notular line regarded as the axial furrow.

extraocular area. Area of the genal field outside and behind the ocular lobe in Olenellina.

exuviae. Any or all portions of molted trilobite exoskeleton, mineralized or nonmineralized. This term for the remains of a trilobite is plural; it has no singular form.

exuviation. The active phase of ecdysis, the withdrawal of the animal from its old exoskeleton.

eye. Visual organ on external side of gena, bearing eye lenses.

eye field. See librigenal field.

eye lappet. See visual surface (of eye).

eye list. See eye ridge.

eye lobe. Ensemble of palpebral lobe and visual surface of eye.

eye platform. See librigenal field.

eye ridge. Raised band extending from anterior end of eye lobe to, or just behind, anterolateral angle of glabella; may be subdivided by ocular furrow (syn., eye list, ocular band, ocular ridge, paired eye ridge).

eye ridge fossula. See fossula.

eye socle. Rim directly below visual surface of eye and separated from the librigenal field by break in slope or furrow, the eye socle furrow.

eye socle furrow. Furrow separating eye socle from librigenal field.

eye tubercle. Raised knob bearing simple eye as in Trinucleidae.

F. In Agnostina only, used to denote lateral glabellar furrow (numbered forward from the posterior margin of the glabella) and inter-ring furrow of pygidium (numbered backward from the anterior margin).

facet. Triangular area that bevels anterolateral area of outer portion of pleura of a fulcrate thoracic segment and the corresponding area of the anterior pleural segment of the pygidium. See also epifacetal and postfacetal types of pleural furrow, petaloid facet.

facial line. Ridge in Redlichiina extending from the palpebro-ocular ridge to the border furrow of the cranidium, subparallel to, or at a slight angle to, the

anterior section of the facial suture (syn., preocular facial line).

facial suture. Suture bounding adaxial margin of eye surface, which has anterior and posterior branches (sections), each of which may extend over the border and on to the doublure; suture separates librigena from fixigena. Posterior branch extends to inner margin of doublure, anterior branches may meet medially on dorsal or ventral surface of exoskeleton or may join extremity of rostral suture. Facial suture may be present when eye is absent. Particular points on the dorsal suture are denoted by Greek letters in Figure 3.

false eye ridge. See sutural ridge.

false preglabellar area. See precranidial lobe.

false preglabellar field. See anterior border of cranidium (in Encrinuridae).

false preglabellar furrow. Furrow separating precranidial lobe from border of cephalon in Encrinuridae (syn., anterior furrow).

fenestra (pl., fenestrae). An opening in the postcephalic pleural region of the dorsal exoskeleton, situated intersegmentally.

fibular furrow. Furrow separating outer flat and inner projecting portion of doublure of pygidium in Agnostina; at enrollment, inner edge of cephalic doublure lies in this furrow.

field of free cheek. See librigenal field.

fingerprint pattern. See Bertillon pattern.

fixed cheek. See fixigena.

fixigena (pl., fixigenae). Portion of cranidium abaxial to axial and preglabellar furrows and imaginary sagittal line bisecting frontal area (syn., fixed cheek).

fixigenal boss. Fixigenal protuberance at level of L1 as in *Neoredlichia*.

fixigenal eye stem. Supposed ridge separated from palpebral lobe by palpebral furrow and running posteriorly from it in Phacopida.

fixigenal field. Portion of fixigena between axial and border furrows.

fixigenal spine. A spine borne by the border of the fixigena. Anterior, mid-, and posterior fixigenal spines are recognized in certain protaspides.

flange. Inner posterior portion of lower lamella that may be expanded posteriorly in Trinucleidae [syn., inner margin (of lower lamella), integument attachment]. Also used for projecting strip along anterior edge of thoracic pleura or pleural field of pygidium, which fits below posterior flange of adjacent segment or posterior border of cephalon (syn., anterior flange).

flange furrow. Furrow defining inner edge of flange of thoracic segment.

flank. See pleural field (of pygidium).

flip. Angled edge of librigena between posterior section of facial suture and posterior margin.

fossette. One of several pits on eye socle.

fossula (pl., fossulae). Small, circular or oval depression that may occur in axial furrow at or near anterolateral edge of glabella and that lies at junction with anterior edge of eye ridge (when present) (syn., antennary pit, antennular pit, anterior fossula, anterior pit, eye ridge fossula, hypostomal pit, pore, pseudoantennary pit).

fossular apodeme. Projection from parietal surface formed by inbending of exoskeleton corresponding to fossula on external side (syn., anterior boss).

free cheek. See librigena.

free pleura. See outer portion of pleura.

fringe. External pitted portion of cephalon in Harpetidae, Harpididae, and Trinucleidae.

front furrow. See anterior border furrow (of cephalon).

frontal area. Portion of cranidium lying between anterior branches of facial suture (and rostral suture, if developed), preglabellar furrow, and eye ridge. If eye ridge is absent, posterolateral boundary of this area is marked off by imaginary line connecting anterior extremity of palpebral lobe with end of preglabellar furrow (syn., anterior limb, limb). See also frontal field.

frontal boss. See preglabellar boss.

frontal field. Portion of frontal area posterior to border furrow (syn., brim of HOWELL & others, 1947).

frontal furrow. See anterior border furrow (of cephalon).

frontal glabellar spine. Median or paired spine projecting forward from frontal part of glabella.

frontal lobe (of glabella). Lobe of glabella between preglabellar furrow and most anterior lateral glabellar furrows; may be referred to as LA. See also anterior lobe of glabella.

frontal process. Projection of anterior border and doublure of cephalon; may bifurcate or trifurcate anteriorly as in *Neoprobolium* (syn., anterior median process, beak).

frontal spine. Projection of anterior border and doublure of cephalon ending anteriorly in point (syn., median anterior border spine).

frontal sulcus. Continuation of median preglabellar furrow on to frontal glabellar lobe in Agnostina.

fronto-median lobe. Frontal lobe and central area of glabella.

fulcral joint. Pivot joint between adjoining tergites, situated at the fulcrum.

fulcral line. Imaginary exsagittal line joining the fulcra.

fulcral notch. See fulcral socket.

fulcral process. Projection from anterior edge of thoracic pleura or pygidium at fulcrum (syn., fulcral prong). See also prong.

fulcral prong. See fulcral process.

fulcral socket. Indentation on posterior edge of thoracic pleura or border of cephalon at fulcrum, into which fulcral process fits (syn., fulcral notch).

fulcral spine. Larger projection than fulcral prong in Agnostina.

fulcral swelling. Thickening of ridge at fulcrum of pleura connecting principal pleural ridge and posterior (principal) pleural spine.

fulcrate. Describes thoracic segment that has the fulcrum.

fulcrum (pl., fulcra). Geniculation of pleural region separating horizontal inner portion from inclined outer portion (syn., geniculation).

furrow process and socket. Ball and socket articulating device in the axial furrow.

gena (pl., genae). Lateral portion of dorsal exoskeleton of cephalon, abaxial to imaginary sagittal line bisecting frontal area, and to axial furrow (syn.,

cheek, cheek area, cheek lobe, cheek region, genal lobe, genal region).

genal angle. Posterolateral corner of cephalon.

genal artery. See genal ridge.

genal bar. Longitudinal ridge on fixigena, close to axial furrow as in *Centropleura.*

genal caecum (pl., caeca). Pattern of raised ridges on external surface (grooves on parietal surface) radiating and distally anastomosing on frontal area and genal field of cephalon; arising from the eye ridge, eye lobe, axial or preglabellar furrow. The ridges are much narrower in relation to the cephalon than the rugae of Agnostina.

genal diverticulum. See genal ridge.

genal field. Area of gena enclosed within border furrows (syn., cheek field). May be divided into librigenal field and fixigenal field.

genal flange. Area of genal roll of fringe opposite posterior margin of genal region, commonly occupied by irregularly distributed pits in Trinucleidae.

genal lobe. See gena.

genal prolongation. Portion of fringe posterior to genal region in Trinucleidae, Harpetidae, and Harpididae.

genal region. See gena.

genal ridge. Raised, narrow band running outward and backward from outer side of eye lobe, visual surface of ocular lobe in Olenellina, or eye tubercle (or axial furrow if no eye lobe or eye tubercle) toward genal angle (syn., genal artery, genal diverticulum, paraocular facial line, principal genal vein).

genal roll. Inner portion of fringe bounded on outer side by girder or corresponding inflection of upper lamella and on inner side by genal region as in Harpetidae and Trinucleidae (syn., cheek roll).

genal roll prolongation. Inner portion of genal prolongation, bounded outwardly by girder; represents extension of genal roll as in Harpetidae and Harpididae (syn., cheek roll prolongation).

genal spine. General term for hollow, posteriorly directed extension of border and doublure at genal angle, forming pointed projection. See fixigenal spine, librigenal spine.

generative zone (ocular). Narrow strip at base of visual surface of eye from which new lenses are added at exuviation.

genicranidium (pl., genicranidia). See genicranium.

genicranium (pl., genicrania). Dorsal cephalic shield of hypoparian forms and Olenellina, separated by marginal (or supramarginal in conocoryphids) suture from ventral doublural plate (syn., genicranidium).

geniculate (glabellar furrow). Glabellar furrow having single angular change in direction.

geniculation. See fulcrum.

gill branch. See outer branch (of biramous appendage).

girder. Thickening or ventrally raised flexure of lower lamella parallel to cephalic margin, found at some distance within external rim at angulation of lamella as in Harpetidae, Harpididae, and Trinucleidae.

girder list. Ridge on upper lamella of fringe in Trinucleidae corresponding in position to girder of lower lamella.

glabella (pl., glabellae). Axial portion of cephalon, bounded by axial and preglabellar furrows (syn., cephalic axis); only in Agnostina is basal lobe and occipital band excluded from the glabella.

glabellar carina. See glabellar keel.

glabellar culmination. Rounded or angulate posterior extremity of the posterior glabellar lobe (posteroglabella) in Agnostina.

glabellar furrow. See lateral glabellar furrow; transglabellar furrow.

glabellar impression. See muscle scar.

glabellar keel. Sagittal ridge on parietal surface of glabella, preserved as a groove, the axial glabellar sulcus, in internal molds of Agnostina (syn., glabellar carina).

glabellar lobe. See lateral glabellar lobe.

glabellar node. Median (or paired) tubercle developed in some part of fronto-median lobe of glabella (syn., glabellar tubercle, median glabellar tubercle). See also median sensory organ.

glabellar spine. Median (or paired) spine arising from glabella. See also cranidial spine, frontal glabellar spine, median glabellar spine, occipital spine.

glabellar tongue. Subparallel-sided axial part of cranidium anterior to eye lobes, bounded by confluent anterior sections of facial suture, and continuous with posterior portion of glabella (which occupies axial region between eye lobes as in Remopleurididae).

glabellar tubercle. See glabellar node.

glyptagnostoid articulating device. Modification in Agnostina in which articulating half ring is a narrow, raised rim and articulating furrow is a wide, elliptical depression with exsagittal pair of notulae.

gonatoparian suture. Facial suture with posterior section reaching cephalic margin at genal angle.

granule. Minute protuberance from exterior surface of exoskeleton, smaller than tubercle or pustule.

groove. Groove or recess below posterior margin of inner portion of pleura or posterior border of cephalon, into which flange fits.

half ring. See articulating half ring.

hapsidium (pl., hapsidia). Concentric cluster of closed ridges of sculpture or of loops of ridges (cf. Bertillon pattern).

head. See cephalon.

head shield. See cephalon.

hinge. Line of articulation between adjoining tergites (syn., hinge line).

hinge line. See hinge.

holaspid period. Period of growth after specific number of thoracic segments had been attained.

holaspis (pl., holaspides). Exoskeleton at any particular stage of development during holaspid period.

holcos. Concave zone parallel to and near the lateral and posterior margins of the pygidium as in some Illaenina.

holochroal eye. Compound eye consisting of numerous adjoining lenses covered by a continuous cornea.

horn. See prolongation.

hyperglabella. Term introduced for immature glabella of *Daguinaspis* because S5 is said to be present in addition to S1–S4.

hypoparian. Condition in which facial suture traverses margin of cephalon.

hypostoma. See hypostome.

hypostomal pit. See fossula.

hypostomal suture. Line of junction between posterior margin of anterior doublure, rostral or perrostral plate, and anterior margin of hypostome.

hypostome (pl., hypostomes). Ventral sclerite situated beneath anterior portion of glabella, described as conterminant (attached) when in sutural contact with rostral plate and/or doublure of librigenae and described as natant (detached) when not in such contact [syn., epistoma (partim), hypostoma].

I. Abbreviation for internal.

impendent (condition of hypostome). A modified conterminant condition of the hypostome, in which the glabella is extended forward so that the most anterior portion is underlain by the cephalic doublure.

ingluvial sac. See ingluvie.

ingluvie. Expansion of the alimentary canal; in trilobites may be bilaterally arranged sacs or an axial boss (syn., ingluvial sac).

inner branch (of biramous appendage). Inner branch (ramus) of appendage arising from coxa, composed of a number of podomeres connected to each other and the coxa by movable articulations (syn., endopod, endopodite, leg branch, telopod, telopodite, walking leg).

inner margin (of fringe). Line separating genal region and preglabellar field (if present) from pitted area and running into posterior border as in Harpetidae [syn., lateral line (of fringe)].

inner margin (of lower lamella). See flange.

inner margin (of upper lamella). Boundary between genal region and fringe on dorsal side of cephalon; coincides with inner margin of fringe as in Harpetidae and Trinucleidae.

inner portion of pleura. Portion of pleura adaxial to fulcrum (syn., articulated pleura, proximal portion of pleura).

inner spine angle. Angle between median line of genal spine and margin of posterior border of cephalon.

insloping. Situation in genal or pleural region of exoskeleton of cephalon or pygidium in which exterior surfaces face upwards or inwards toward axial surfaces.

integument. The epidermal cell layer of the body and the overlying cuticle that it has secreted.

integument attachment. See flange.

intercalary lobe. See median preoccipital lobe.

intercalating furrow. Transverse furrow at anterior margin of intercalating ring.

intercalating ring. Ring anterior to occipital ring formed by fusion of L1 lobes across glabella as in phacopids (syn., preoccipital ring).

intercheek suture. See median suture.

intergenal angle. The angle in the posterior cephalic border where it may be flexed forward, so that the base of the genal spine lies in a transverse line well in advance of the occipital ring as in certain Olenellina and Redlichiina.

intergenal ridge. Ridge in Olenellina extending from interocular area of gena opposite L1, along or across border furrow to base of intergenal spine; prominent in early growth stages (syn., metagenal ridge, posterior genal ridge).

intergenal spine. Spine projecting posteriorly from cephalic border adaxial to genal angle (syn., interocular spine, metacranidial spine, metafixigenal spine, metagenal spine).

intergenal swelling. Inflation of posterior border of cephalon at base of intergenal spine; may be present when spine is absent in holaspis.

interlamellar suture. Suture through the pillars that connect the dorsal and ventral pits in upper and lower lamellae of fringe in harpetids and trinucleids.

interlensar sclera. That part of visual surface that lies between schizochroal lenses and is not covered by cornea.

intermediate lobe. Small lobe on median glabellar lobe at anterior, adaxial end of S1 in some calymenids (syn., supplementary lobe).

internal (I). Used in referring to arcs of pits, to individual pits, or to irregularly arranged pits in trinucleid fringe adaxial to girder.

internal axial septum. Septum located on the parietal surface at the posterior end of pygidial axis in *Pseudophillipsia.*

internal mold of exoskeleton. Mold of interior (parietal) surface of dorsal exoskeleton; may be combined with mold of external surface of doublure or hypostome. See composite internal mold.

internal rim. Smooth inner border of fringe, adjacent to thorax and extending from posterior margin of genal region to posterior tip of prolongation as in Harpetidae.

interocular area. Used in Olenellina for area adaxial to ocular lobe. See also palpebral area (of fixigena).

interocular channel. Transverse channel lying immediately behind eye ridge, extending between palpebral lobe and axial furrow in *Aulacodigma.*

interocular cheek. See palpebral area (of fixigena).

interocular fixigena. See palpebral area (of fixigena).

interocular spine. See intergenal spine.

interocular swelling. Inflation by which palpebral area is swollen and repeats form of palpebral lobe.

interpleural furrow. Transverse groove extending from axial furrow across pleural region of pygidium, indicating boundary of fused pleurae (syn., interpleural groove, rib furrow).

interpleural groove. See interpleural furrow.

inter-radial plate (or ridge). Plate or ridge that separates adjacent radial rows of pits in trinucleid cephalic fringe on both upper and lower lamellae; particularly evident when radial rows of pits lie in sulci.

inter-ring furrow. Groove bounding successive axial rings of pygidium (syn., ring furrow, transaxial furrow). In Agnostina referred to as F1, F2, F3, numbering from the anterior backward.

intersulcal field. Area between outer and inner border furrows in Proetidae.

intervening furrow. Lateral glabellar furrow intervening between LO and L1, recognized in olenids and an oryctocephalid.

intervening glabellar lobe. Lateral glabellar lobe isolated by intervening furrow curving back to meet occipital furrow, considered to intervene between occipital ring and L1.

intra-annular furrow. Furrow separating anterior part of thoracic axial ring (preannulus) from posterior part (postannulus), visible on exterior but not parietal surface of exoskeleton.

intra-axial furrow. Furrow between median and lateral lobe of thoracic axial ring of Agnostina.

intralensar bowl. Differentiated lower part of compound lens in the schizochroal eye of Phacopina.

intramarginal suture. Suture running along border of cephalon, close to margin. See also marginal suture, submarginal suture.

intranotular axis. Main median part of pygidial axial lobe between notular lines or between the two lines of notulae (syn., elliptical ring, lancetoid field).

intranotular ridge. Paired ridge flanking the intranotular sulcus, anteriorly merging with axial node of pygidium.

intranotular sulcus. Sagittal groove between axial and terminal nodes of pygidial axis in Agnostina; may be impressed into axial node posteriorly.

intraoccipital furrow. Furrow on lateral portion of occipital ring defining lateral occipital lobe.

intrapalpebral ridge. Ridge on fixigena adjacent to and parallel to palpebral lobe in *Carolinites*.

intrascleral membrane. Membrane holding lenses in position in schizochroal eye.

isopygous. Having a pygidium of about the same width (tr.) and length (sag. and exs.) as the cephalon.

isoteliform suture. See asaphid suture.

kainelliform suture. Opisthoparian suture in which anterior sections first diverge strongly outward and then bend sharply inward and frontward, meeting anterior cephalic margin at its median point as in *Kainella*.

L. Abbreviation for lateral glabellar lobe or transverse division; numbered forward from posterior, LO (occipital ring), L1, L2, L3, etc.

LA. Abbreviation for frontal lobe of glabella.

lancetoid field. See intranotular axis.

larval notch. See posterior indentation.

larval ridge. Supposed combination in a single ridge of frontal glabellar lobe, ocular lobe, and intergenal ridge in such Olenellina as *Elliptocephala*.

lateral axial lobe. Lobe at lateral margin of axial ring.

lateral band. Lower half of lateral side of pygidial axis, which joins upper half at change in slope. Axial rings and inter-ring furrows are indistinct. Used for Proetoidea.

lateral border (of cephalon). Portion of cephalic border between anterior section (branch) of facial suture and genal angle.

lateral border (of hypostome). Extends from anterior wing to posterolateral corner of hypostome, bounded by lateral border furrow.

lateral border furrow (of cephalon). Portion of border furrow bounding lateral border.

lateral border furrow (of pygidium). Portion of border furrow bounding lateral border in pygidium.

lateral glabellar furrow. Bilaterally symmetrical pairs of narrow grooves on external surface formed by fold in exoskeleton, extending partway across glabella from (or near) axial furrow. Furrows vary in length, depth, and direction; they may be short (tr.), limited to pits in or close to axial furrow, or isolated from axial furrow (syn., glabellar furrow). When three pairs are present, they have been referred to as anterior, median, and basal (syn., posterior glabellar furrow, preoccipital glabellar furrow). Numbering from the back forward is preferred: occipital as SO, preoccipital as S1, and continued forward as S2, S3, etc.

lateral glabellar lobe. Portion of glabella outlined and more or less separated by successive lateral glabellar furrows, may or may not be inflated. Numbering is from posterior end forward: L1, L2, etc. (syn., glabellar lobe). In lichids it is considered that L1 is subdivided into the posterior L1a and anterior L1b, and similar subdivisions are recognized in odontopleurids. When three pairs are present they have been referred to as anterior, median, and basal lobes (syn., preoccipital glabellar lobe). See also posterior lobe (of glabella).

lateral line (of fringe). See inner margin of fringe.

lateral margin (of cephalon). Margin between anterior branch of facial suture and genal angle (if former is absent, anterior limit of lateral margin is obscure).

lateral notch (of hypostome). Deep groove crossing border and doublure between shoulder and anterior wing of hypostome.

lateral occipital lobe. Lateral or anterolateral portion of occipital ring, if differentiated; referred to as LO (syn., occipital lobe, occipital lobula).

lateral pit. See posterior fossula.

lateral preoccipital lobe. Lobe L1; lateral portion of glabellar region directly in front of occipital ring, where differentiated, as in *Otarion, Ditomopyge* (syn., pre-occipital glabellar lobe). See also posterior lobe (of glabella), lateral glabellar lobe.

lateral projection of hypostome. See shoulder (of hypostome).

lateral tongue furrow. Portion of axial furrow bounding side of glabellar tongue as in *Remopleurides*.

leg branch. See inner branch.

levisellid-type suture. See nileiform suture.

librigena (pl., librigenae). Portion of cephalon abaxial to facial suture (syn., free cheek, movable cheek, paria).

librigenal field. Portion of librigena within border furrow (syn., eye field, eye platform, field of free cheek, ocular platform).

librigenal plate. The librigenae, united by connecting doublure, not separated by connective or median suture.

librigenal spine. Spine borne by border of librigena (syn., parial spine).

libristomate. Adjective derived from Libristoma, the group of trilobites in which the hypostome was conterminant in the protaspis but became natant during the meraspid and holaspid periods.

limb. See biramous appendage, frontal area, posterior area of fixigena.

lira (pl., lirae). Symmetrical raised ridge on external surface of exoskeleton.

list. A concentric ridge on the upper lamella occurring between arcs in trinucleids.

longitudinal furrow. Posteriorly directed extension of anterior lateral glabellar furrow as in Lichidae and Odontopleuridae.

longitudinal median glabellar furrow. Furrow commencing in preglabellar furrow and extending sagittally back.

lower lamella. Ventral exoskeleton of fringe as in Harpetidae, Harpididae, and Trinucleidae (syn., doublural plate).

lower rim (external or internal). Smooth, may be raised or thickened peripheral portion of lower lamella of fringe as in Harpetidae, Harpididae, and Trinucleidae.

lunette. Raised crescentic area on inner (parietal) surface of exoskeleton at abaxial margin of axial furrow, where glabella is narrowest (tr.) and approximately in transverse line with eye lobe; characteristic of Illaenidae.

M. Used in Agnostina only to denote transverse divisions of axis of glabella (where it is equivalent to L and numbered 1 to 3 from the posterior forward) or axis of pygidium (where it is equivalent to axial ring and numbered posteriorly from anterior margin of pygidium). Also used as abbreviation for meraspid period, in numbering degrees as M0, M1, etc.

macropleura (pl., macropleurae). Pleura in which the inner portion becomes longer (exs.) abaxially and the outer portion is a long, stout spine, or in which only the pleural spine is markedly longer than those adjacent (syn., macropleural segment).

macropleural segment. See macropleura.

macropleural spine. Pleural spine of macropleura.

macropleural unit. Macropleural sixth thoracic segment that is fused to fifth as in Emuellidae.

macropygous. Having a pygidium exceeding in maximum width (tr.) that of the cephalon.

macrospine. Axial spine, much larger than those adjacent.

macula (pl., maculae). Small area lying laterally in, or on posterior side of middle furrow of hypostome; it may be sunken, flat, or elevated, smooth or with lenslike structures on the surface.

major posterior (muscle) scar of posterior glabellar lobe (posteroglabella). In Agnostina a paired, circular, depressed area situated at the maximum width of the posterior glabellar lobe.

margin. Distal edge of portion of exoskeleton.

marginal band. Narrow vertical band uniting upper and lower edges of rim as in Harpetidae and Trinucleidae.

marginal connective device. Device for articulation between adjacent pleurae at base of pleural spine.

marginal furrow. See border furrow.

marginal gutter. Broad, overdeepened border furrow of either cephalon or pygidium in Agnostina.

marginal limb. See border.

marginal pit. See border pit.

marginal rim. See border.

marginal spine. Pleural spine of pygidium when border is not defined.

marginal suture. Suture traversing marginal band of cephalon, as in Harpetidae.

median anterior border spine. See frontal spine.

median axial lobe. Median portion of axial ring between lateral axial lobes.

median body (of hypostome). See middle body (of hypostome).

median border spine. See posterior spine.

median cervical lobe. See central area (of glabella).

median gap. See pygidial collar.

median glabellar spine. Median spine arising from central area of glabella (syn., preoccipital glabellar spine).

median glabellar tubercle. See glabellar node.

median lateral glabellar furrow. Furrow S2 when three pairs are present (see lateral glabellar furrow).

median lateral glabellar lobe. Lobe L2 when three pairs are present. See lateral glabellar lobe.

median lobe (of glabella). See central area (of glabella).

median node. See axial glabellar node.

median preglabellar furrow. Furrow along sagittal line in front of glabella as in Agnostina and Dimeropygidae (syn., preglabellar median furrow).

median preglabellar ridge. Ridge along sagittal line in front of glabella.

median preoccipital lobe. Median portion of glabellar region between L1 lobes as in *Ditomopyge* (syn., intercalary lobe).

median sensory organ. Median glabellar node in which either the exoskeleton is thinner or there are symmetrically arranged pits.

median suture. Median longitudinal suture transecting doublure in front of hypostome (syn., intercheek suture).

meraspid period. Period of development from appearance of first transverse articulation in exoskeleton until specific number of thoracic segments less one had been attained (see degree of meraspid period).

meraspis (pl., meraspides). Exoskeleton at any particular degree of development during meraspid period.

mesentery. Membrane attached to inner (parietal) surface of skeleton serving as a partition between and a support for organs.

metacranidial spine. See intergenal spine.

metafixigenal spine. See intergenal spine.

metagenal ridge. See intergenal ridge.

metagenal spine. See intergenal spine.

metamere. See somite.

metaparian suture. Sutural pattern in Olenellina in which the two branches of the facial suture are supposed to have been secondarily fused.

metaprotaspis (pl., metaprotaspides). Next largest protaspides to anaprotaspides in a size series, in which protopygidium is recognizable. Not recommended as a subdivision of protaspid period.

metastoma. See metastome.

metastome. Supposed small plate lying posterior to mouth opening on ventral side of body (syn., metastoma, postoral plate).

micropygous. Having a pygidium considerably shorter (sag. and exs.) and narrower (tr.) than the cephalon.

midcheek furrow. Furrow in Agnostina extending ob-

liquely from axial furrow adjacent to anterior portion of posteroglabella to border furrow.

middle body (of hypostome). Swollen middle portion of hypostome inside border, divided by middle furrows into anterior and posterior lobes [syn., central body (of hypostome), median body (of hypostome)].

middle furrow. Inward and backwardly directed furrow dividing middle body of hypostome into anterior and posterior lobes.

mid-fixigenal spine. Prominent spine on lateral border of protocranidium of protaspis.

midmost glabella. See posterior lobe (of glabella).

miomerid. Term originally proposed for trilobites having two or three thoracic segments (i.e., Agnostina and eodiscoids) and used as a convenient abbreviation to refer to them.

mold. See composite internal mold, external mold, internal mold of exoskeleton.

molting. The entire sequence of events, including ecdysis and postecdysis, between one shedding of the exoskeleton and the next.

movable cheek. See librigena.

mucro. Median, pointed posterior projection from posterior border of pygidium in dalmanitids and encrinurids. See posterior spine.

muscle scar (or impression). Smooth, may be slightly depressed, paired area in external surface of axial region of exoskeleton, interpreted as area of muscle attachment; may be darker in color than surrounding regions. Paired muscle impressions on glabella may be numbered from posterior forward as 1g, 2g, etc. (in Scutelluidae) or, in same manner as lateral glabellar furrows, as S1, S2, etc. In Agnostina they are preserved as shallow depressions on internal mold, reflecting raised rim of scar on parietal surface (syn., glabellar impression).

natant (condition of hypostome). Hypostome lies below anterior portion of glabella, but is not attached to the cephalic doublure.

neck furrow. See occipital furrow.

neck node. See occipital node.

neck ring. See occipital ring.

neck spine. See occipital spine.

nileiform suture. Cephalic suture in which two anterior branches (or sections) meet marginally in the midline; there is no median suture across the doublure (syn., levisellid-type suture).

niobiform suture. See asaphid suture.

node. Small subcircular or suboval swelling on exterior surface of exoskeleton.

nonadult-like protaspis. See asaphoid protaspis.

non-effaced. See en grande tenue.

nonfulcrate. Describes a thoracic segment that lacks the fulcrum (i.e., has no inner horizontal portion) but curves downward and outward from the axial furrow.

notula (pl., notulae). Small pit in internal mold of exoskeleton that may be included in an area occupied by a muscle scar.

notular furrow. Longitudinal furrow developed between notulae.

notular line. A longitudinal line of notulae converging

on terminal node of the pygidial axis.

nuchal furrow. See occipital furrow.

nuchal node. See occipital node.

nuchal ring. See occipital ring.

nuchal spine. See occipital spine.

O. Abbreviation for occipital ring.

oblique lateral muscle scars of posteroglabella. Grooves in Agnostina arranged in an arc running from the axial glabellar node to the basal glabellar lobe. The oblique lateral ridge flanks these grooves adaxially.

occipital band. Narrow (sag. and exsag.), depressed posterior band of occipital ring in odontopleurids; in Agnostina a narrow band that connects the basal lobes behind the posteroglabella. See also connective band.

occipital furrow. Transverse furrow (SO) that isolates occipital ring from remainder of glabella (syn., neck furrow, nuchal furrow).

occipital lobe. See lateral occipital lobe.

occipital lobula (pl., lobulae). See lateral occipital lobe.

occipital node. Median (or paired) tubercle developed on exterior of occipital ring (syn., neck node, nuchal node, occipital tubercle).

occipital ring. Axial region of most posterior segment of cephalon, bounded at sides by axial furrows, at front by occipital furrow, and at back by posterior margin. Considered part of glabella in all trilobites (syn., neck ring, nuchal ring).

occipital spine. Median (or paired) pointed structure projecting from exterior of occipital ring (syn., neck spine, nuchal spine). See also cranidial spine.

occipital tubercle. See occipital node.

occipitogenal diverticulum. Low ridge in eodiscoids that runs between occipital ring and inner, posterior corner of genal field.

occiput. Independently convex portion of glabella, bounded anteriorly by S1, lateral glabellar furrows, and posteriorly by the occipital furrow. Used in describing Trinucleidae, whereas intercalating ring is used for the similar structure in phacopids.

ocular band. See eye ridge.

ocular furrow. Furrow dividing the ocular lobe of Olenellina along its length into inner and outer bands (syn., epipalpebral furrow, ocular striga, striga).

ocular incisure. The abaxially convex curve of the margin between the eye lobe and the librigena.

ocular lobe. The ridge on the gena of Olenellina that curves outward and backward from the glabella immediately in front of S3 and bears on its outer, distal portion the curved visual surface of the eye.

ocular platform. See librigenal field.

ocular ridge. See eye ridge.

ocular striga. See ocular furrow.

ocular suture. Lower section of circumocular suture separating visual surface from librigena.

opisthoparian suture. Facial suture with posterior section cutting posterior margin of cephalon adaxial to genal angle, which is carried by librigena. See also cedariiform suture.

opisthothorax. Posterior portion of thorax when it is

divisible into a wider (tr.) anterior portion (the pro-thorax) and narrower posterior portion (syn., post-thorax).

opistopleura (pl., opistopleurae). See posterior pleural band.

orle furrow. Furrow near anterior margin of frontal glabellar lobe in *Chasmops* close to, and parallel with, preglabellar furrow.

ornament. See sculpture.

outer branch (of biramous appendage). Outer branch (ramus) of appendage arising from coxa (syn., exite, exopod, exopodite, gill branch).

outer glabellar region. See posterior lobe (of glabella).

outer portion of pleura. Portion of pleura outside fulcrum, which slopes downward and outward, may bear a facet, and has a doublure (syn., distal portion of pleura, free pleura).

outer spine angle. Angle between lateral border of cephalon and median line of genal spine.

paired eye ridge. See eye ridge.

palpebral area of fixigena. Portion of fixigena lying between eye ridge and imaginary transverse line connecting posterior corner of palpebral lobe with axial furrow (syn., interocular area, interocular cheek, interocular fixigena, palpebral region of fixigena).

palpebral furrow. Usually curved groove separating palpebral lobe from palpebral area of fixigena.

palpebral ledge. A marked ledge or groove situated on the palpebral lobe between the palpebral suture and the palpebral furrow as in *Lophosaukia.*

palpebral lobe. Protruding subsemicircular flange of fixigena bounded distally by palpebral suture. See eye lobe.

palpebral region of fixigena. See palpebral area of fixigena.

palpebral rim. Raised or thickened portion of palpebral lobe bordering palpebral suture.

palpebral suture. Portion of facial suture bounding distal edge of palpebral lobe.

palpebral view of cranidium. View normal to plane passing through palpebral lobes.

palpebro-ocular ridge. Curved ridge formed by confluence of eye ridge and palpebral lobe. The ridge may be subdivided by a longitudinal furrow into an outer (anterior) band and an inner (posterior) band.

pander organ. See panderian organ.

panderian notch. Notch in inner margin of cephalic or pleural doublure, assumed to have partially surrounded a panderian opening.

panderian opening. Small, rounded or elliptical opening in posterior genal and thoracic pleural doublure.

panderian organ. Supposed organ associated with panderian opening (syn., pander organ).

panderian protuberance. Small and rounded, elliptical, or elongate protuberance immediately adjacent to panderian opening; term also applied to raised anterior edge of panderian notch.

papilionate. See axial glabellar node.

papilla (pl., papillae). In calymenids refers to projections over axial furrow from lateral glabellar lobe or frontal lobe. See also buttress, papillate-buttress structure.

papillate-buttress structure. Projection bridging axial furrow of cephalon in calymenids, consisting of papilla and opposing buttress. See also papilla.

paradoublural line. Furrow, flexure, or ridge on dorsal exoskeleton of cephalon and pygidium, which is conformable with inner edge of doublure.

parafrontal band. Narrow, raised band following anterior border of frontal lobe of glabella and forming continuation of outer, anterior band of palpebro-ocular ridge as in protoleninids.

paraglabellar area. Arcuate, slightly depressed area at inner, posterior corner of fixigena; may be gently convex and outlined by furrow or change in slope as in homalonotids.

para-ocular facial line. See genal ridge.

para-postaxial ridge. Postaxial ridge on pygidium in which sagittal crest is prolonged into spine as in *Odontochile* and *Dalmanites.*

paraprotaspis (pl., paraprotaspides). Late protaspid stage, not precisely defined. Not recommended as a subdivision of protaspid period.

parathoracic segment. Region of transitory pygidium having the form of a thoracic segment, but still fused into pygidial exoskeleton.

paria. See librigena.

parial spine. See librigenal spine.

parietal surface. Inner surface of exoskeleton. See also visceral features.

pelturoid. Describes outline of gena when lateral and posterior margins form even curve.

pergenal spine. See procranidial spine.

peripheral pleural lobe. That part of the pygidial pleural region flanking or even enclosing deuterolobe in Agnostina.

perrostral suture. Ventral intramarginal cephalic suture crossing doublure at genal angle below spine as in Olenellina (syn., ventromarginal suture).

petaloid facet. Facet of thoracic segment crossed by subparallel terrace ridges, which are directed obliquely, the scarp slope facing downward and backward.

phaselus. Minute, oval body, deeply vaulted and widest anteriorly; narrow doublure flexed sharply, with marginal rim separating it from dorsal exoskeleton; reticulate sculpture. Thought to be a preprotaspid stage in development.

plectrum. Rearward projection of a median portion of anterior cranidial border; it may interrupt course of border furrow and may extend to front of glabella.

plethoid. Situation in *Pseudagnostus* in which accessory furrow defining deuterolobe continues to posterior border furrow.

pleura (pl., pleurae). Lateral portion of thoracic segment (syn., pleuron).

pleural band. Anterior or posterior strip resulting from transverse or oblique division of thoracic or pygidial pleura by pleural furrow.

pleural field (of pygidium). Lateral portion of pygidium bounded adaxially by axial furrow and abaxially by border furrow (syn., flank, pleural platform, pleural zone, pygopleura).

pleural furrow. Groove in external surface of thoracic pleura or pleural region of pygidium, formed by fold in exoskeleton. See epifacetal and postfacetal types.

pleural lobe. See pleural region.

pleural node. Inflated triangular area on adaxial part of thoracic pleura in Olenidae.

pleural platform. See pleural field.

pleural region. Lateral portion of thorax or pygidium abaxial to axial furrow (syn., pleural lobe, pleurothorax, side lobe).

pleural rib. See rib.

pleural ridge. Ridge along either anterior or posterior pleural band, latter commonly prominent as principal pleural ridge.

pleural spine. Hollow, pointed extension of distal end of a pleura or of either band of the pleura, of thorax or pygidium. See also border spine, marginal spine.

pleural stop. Ridge separating facet from pleural furrow in outer portion of second thoracic segment in certain Agnostina; morphologically equivalent to the anterior pleural band.

pleural zone. See pleural field.

pleuroccipital border. See posterior border (of cephalon).

pleuroccipital furrow. See posterior border furrow (of cephalon).

pleuron. See pleura.

pleurothorax. See pleural region.

podomere. Individual component of inner branch of biramous appendage, connected by movable articulation to coxa and adjoining podomeres (syn., segment).

polymerid. Term originally proposed for trilobites having six or more thoracic segments; commonly used as a convenient abbreviation to refer to all trilobites other than Agnostina and eodiscoids. This distinction cannot be made solely on numbers of thoracic segments, and the term should not be used formally as an order to include all trilobites other than Agnostina and eodiscoids.

pore. See fossula.

postannulus. Posterior part of thoracic axial ring separated by intra-annular furrow from preannulus.

post-apodemal sector. Posterior portion of axis of pygidium in which inter-ring furrows lack lateral apodeme but may show muscle scar on external surface.

postaxial furrow. Longitudinal groove bounding postaxial ridge of pygidium.

postaxial keel. See postaxial ridge.

postaxial median furrow. The pygidial median furrow behind the axis in eodiscoids and Agnostina.

postaxial region. Area on pygidium between posterior end of axis and posterior margin.

postaxial ridge. Sagittal ridge that extends back from tip of pygidial axis; latter indicated by change of slope (syn., postaxial keel, postrachial ridge).

posterior area of fixed cheek. See posterior area of fixigena.

posterior area of fixigena. Portion of fixigena lying behind imaginary transverse line connecting poste-rior corner of palpebral lobe with axial furrow [syn., limb, posterior area of fixed cheek, posterior fixigena, posterior limb, posterior region (of fixigena), posterolateral limb, postocular cheek, postocular fixigena].

posterior band of occipital ring. Narrow (sag. and exsag.) band, widest in midline, situated below and behind main part of occipital ring.

posterior band of pleura. See posterior pleural band.

posterior border (of cephalon). Portion of cephalic border between genal angle and occipital ring (syn., pleuroccipital border).

posterior border (of hypostome). Extends between posterolateral angles and is bounded by posterior border furrow.

posterior border furrow (of cephalon). Portion of border furrow bounding posterior border (syn., pleuroccipital furrow, posterolateral furrow).

posterior branch (of facial suture). Portion of facial suture lying behind eye [syn., posterior section (of facial suture), postocular branch, postocular suture].

posterior field (of fixigena). Portion of posterior area of fixigena lying anterior to posterior border furrow.

posterior fixigena. See posterior area of fixigena.

posterior fixigenal spine. Prominent spine at posterolateral corner of protocranidium in protaspis.

posterior flange. Narrow border extending along posterior edge of inner portion of pleura.

posterior fossula. Pit at lateral extremity of posterior border furrow opposed by a pit on flange of lower lamella in Trinucleidae (syn., lateral pit).

posterior genal ridge. See intergenal ridge.

posterior glabellar furrow. See lateral glabellar furrow.

posterior indentation. Small indentation in posterior margin of transitory pygidium in asaphids and immature proetoid pygidia (syn., larval notch).

posterior limb. See posterior area (of fixigena); see also posterolateral projection (of fixigena).

posterior lobe (of glabella). Lateral glabellar lobe L1. In Agnostina used for posterior portion of glabella (posteroglabella) lying behind transglabellar furrow. In some Agnostina a change in slope or faint exsagittal furrow divides this lobe into midmost glabella and outer glabellar regions.

posterior lobe (of hypostome). Portion of middle body of hypostome behind middle furrow.

posterior margin (of cephalon). Edge of cephalon between genal angles.

posterior median lobe of pygidium. See terminal axial piece.

posterior notch (of hypostome). Median notch in posterior border between posterolateral spines.

posterior ocular line. Ridge in Olenellina outside intergenal ridge, directed backward and outward from posterior end of ocular lobe.

posterior pleural band. Strip of thoracic or pygidial pleura bounded anteriorly by deepest part of pleural furrow (syn., opisthopleura, posterior band of pleura, postpleura).

posterior pleural spine. Pointed extension of distal end of posterior pleural band (syn., principal pleural spine).

posterior region (of fixigena). See posterior area of fixigena.

posterior section (of facial suture). See posterior branch (of facial suture).

posterior spine. Posterior extension of border and doublure of pygidium (syn., caudal spine, median border spine, mucro).

posterior wing (of hypostome). Extension of doublure of lateral border of hypostome.

posteroaxis. In Agnostina that portion of the pygidial axis lying behind the posterior inter-ring furrow (F2).

posteroglabella. Posterior portion of glabella as in *Centropleura*, formed by occipital ring plus ring formed by fusion of L1 and S1. In Agnostina synonymous with posterior lobe of glabella.

posterolateral furrow. See posterior border furrow (of cephalon).

posterolateral limb. See posterior area of fixigena.

posterolateral projection (of fixigena). Portion of fixigena lying abaxial to imaginary exsagittal line from posterior end of palpebral suture to posterior margin of cranidium (syn., posterior limb as used by some authors, but not as defined by Howell & others, 1947).

posterolateral spine (in Agnostina). Spine arising from posterolateral border of cephalon or pygidium.

posterolateral spine (of hypostome). Spine on posterolateral border of hypostome.

postfacetal pleural furrow. Outer portion of pleural furrow that runs behind facet in transverse direction until it becomes obsolete (in asaphids, bathyurids, etc.).

postocular area (of fixigena). Portion of posterior area of fixigena between axial furrow and imaginary exsagittal line from posterior end of palpebral suture [syn., postocular region (of fixigena)].

postocular branch. See posterior branch (of facial suture).

postocular cheek. See posterior area of fixigena.

postocular fixigena. See posterior area of fixigena.

postocular glabella. That part of the glabella behind adaxial end of eye ridge.

postocular margin. Margin of librigena defined by posterior branch of facial suture.

postocular region (of fixigena). See postocular area (of fixigena).

postocular suture. See posterior branch (of facial suture).

postocular tubercle. Tubercle at rear of field of fixigena in exsagittal line with or adaxial to palpebral lobe.

postoral plate. See metastome.

post-palpebral furrow. A furrow running from posterior end of palpebral lobe and crossing fixigena to meet posterior border furrow inside posterolateral angle of cranidium.

postpleura. See posterior pleural band.

postrachial ridge. See postaxial ridge.

post-thorax. See opisthothorax.

preannulus. Anterior portion of thoracic axial ring separated from postannulus by intra-annular furrow.

precranidial lobe. Area of librigena between facial suture, connective suture, and anterior border of cephalon in Encrinuridae (syn., false preglabellar area, pseudoglabellar area).

prefrontal furrow. Lateral portion of preglabellar furrow in *Pliomerina*.

prefrontal lobe. Lobe separated from rest of glabella by shallow furrow; it is lateral part of anterior border of cranidium in *Pliomerina*.

preglabellar area. Portion of cranidium between imaginary exsagittal lines running anteriorly from each end of preglabellar furrow, including preglabellar field if developed and median portion of anterior border.

preglabellar boss. Subcircular swelling of preglabellar field (syn., frontal boss).

preglabellar field. Portion of cranidium lying between front of glabella and anterior border furrow.

preglabellar furrow. Portion of axial furrow outlining front of glabella.

preglabellar keel. See preglabellar ridge.

preglabellar median furrow. See median preglabellar furrow.

preglabellar pit. Pit in preglabellar furrow as in Dimeropygidae.

preglabellar ridge. Sagittal ridge or fold in preglabellar field (syn., preglabellar keel). Contrast with transverse preglabellar ridge.

preoccipital glabellar furrow. See lateral glabellar furrow S1.

preoccipital glabellar lobe. See lateral glabellar lobe L1.

preoccipital glabellar spine. See median glabellar spine.

preoccipital ring. See intercalating ring.

preocular area (of fixigena). Portion of fixigena anterior to eye and eye ridge and abaxial to preglabellar area and including border.

preocular branch (of facial suture). See anterior branch (of facial suture).

preocular cheek. See anterior area (of fixigena).

preocular facial line. See facial line.

preocular field (of fixigena). Portion of preocular area inside border furrow.

preocular glabella. That part of the glabella in front of adaxial end of eye ridge; not coincident with the frontal glabellar lobe.

preocular suture. See anterior branch (of facial suture).

presulcal depression. Sagittally expanded part of outer anterior border furrow in Proetidae.

principal genal vein. See genal ridge.

principal pleural ridge. Refers to ridge of posterior pleural band when it is more prominent than ridge on anterior band; see also pleural ridge.

principal pleural spine. See posterior pleural spine.

procranidial spine. Spine on anterolateral border of cephalic shield, directed horizontally, in early developmental stages of Olenellina (syn., pergenal spine).

profixigenal spine. Spine projecting from border and doublure of fixigena in front of genal spine, as in *Sphaerocoryphe*.

prolibrigenal spine. Spine projecting from border and doublure of librigena.

prolongation. Extension of fringe beyond posterior margin of genal regions as in Harpetidae and Harpididae (syn., horn).

prong. Short projection at fulcrum at anterior margin of thoracic segment or pygidium in Agnostina. See fulcral process.

proparian suture. Facial suture with posterior branch cutting lateral margin of cephalon in front of genal angle.

propleura (pl., propleurae). See anterior pleural band.

propleuron. See anterior pleural band.

prosopon. See sculpture.

protaspid period. Period of development during which there is no transverse articulation in exoskeleton.

protaspis (pl., protaspides). Smallest known exoskeletons, subhemispherical to spherical in form; may exhibit size series, but lacking transverse articulation.

prothorax. Anterior portion of thorax when it is divisible into a wider (tr.) anterior and a narrower posterior, portion (opisthothorax).

protocephalon. Cephalic portion of protaspid exoskeleton.

protocranidium. Cranidial portion of protaspid exoskeleton.

protopygidium. Postcephalic portion of protaspis.

protothoracic segment. Segment in protopygidium or transitory pygidium destined to become thoracic segment.

proximal. End of part or organ that is nearest to point of origin or sagittal line of body.

proximal portion of pleura. See inner portion of pleura.

pseudoantennary pit. See fossula.

pseudo-articulating half ring. Lenticular or subrectangular median depression between anterior pygidial axial rings, resulting from embayment in posterior edge of ring and consequent widening of inter-ring furrow.

pseudofrontal lobe. Composite structure forming anterior part of glabella characteristically in Trinucleinae, bounded posteriorly by S2 and incorporating much reduced or absent S3.

pseudofurrow. See accessory furrow.

pseudogirder. Any concentric ridge occurring between E or I arcs on lower lamella in trinucleids.

pseudoglabellar area. See anterior border of cranidium (in Encrinuridae), precranidial lobe.

pseudolobe. See deuterolobe.

pseudopalpebral furrow. Furrow running obliquely across palpebro-ocular ridge at anterior end of palpebral rim as in *Resserops*.

pseudopostaxial ridge. A short (sag.) and narrow postaxial ridge that does not reach the posterior margin of the pygidium.

pseudoproparian suture. See cedariiform suture.

pseudotropidium. A ridge in the same position as the tropidium, but not reflected as groove on inner surface of exoskeleton.

ptychopariid suture. Opisthoparian suture in which anterior branches are directed forward and inward, librigenae are separated by connective sutures from rostral plate, and rostral plate is not suturally connected to hypostome; see euptychopariid and stenoptychopariid rostral sutures.

pulvinar furrow. Longitudinal furrow bounding pulvinus abaxially.

pulvinus. Swollen longitudinal lobe bounded adaxially by axial furrow and abaxially by pulvinar furrow in encrinurid *Cybeloides*.

pustule. Small, rounded elevation on any part of external surface of exoskeleton. See tubercle.

pygidial collar. Curved ridge on inner side of posterior border of pygidium of Agnostina; may be continuous or have a median gap.

pygidium (pl., pygidia). Posterior tagma in trilobites, composed of fused somites, applied by authors to posterior portion of exoskeleton separated from thorax by articulation (syn., caudal shield, tail, tail shield).

pygopleura (pl., pygopleurae). See pleural field (of pygidium).

pygorachis. See axis (of pygidium).

pygothorax. See thoracopygon.

rachial furrow. See axial furrow.

rachial ring. See axial ring.

rachis (pl., rachises). See axis.

rear eye ridge. Lateral continuation parallel to posterior cephalic margin of fixigenal eye stem in Phacopida. It is bounded distally by facial suture. Rear eye ridge is not a synonym of intergenal ridge.

retrodivergent suture. Anterior branch of suture that curves from eye lobe to be directed outward and backward before curving forward to margin of cephalon.

rhachis (pl., rhachises). Alternative spelling of rachis. See axis.

rhaptoid. Descriptive of Agnostina when notular line is present on pygidial axis.

rhynchos. Swollen anteromedian protuberance on anterior lobe of middle body of hypostome (as in encrinurids or calymenids).

rib. Portion of pygidial pleural region bounded by two successive pleural furrows (syn., pleural rib).

rib furrow. See interpleural furrow.

rim. Narrow peripheral ridge on either upper or lower lamella of fringe in Trinucleidae and Harpetidae; rims united at external edge by a flat, vertical marginal band. In Harpetidae rim present on external and internal edges of prolongation.

ring. See axial ring.

ring furrow. See inter-ring furrow.

ring process. Projection backward from posterolateral corner of axial ring, fitting into socket in next posterior ring.

ring socket. Hollow at extremity of articulating furrow and articulating half-ring for reception of ring process of next anterior ring.

rosette. Axial node in flared depression separating posteroaxis of pygidium in Agnostina into two parts.

rostellum. Small subtriangular plate enclosed between

rostal suture and connective sutures, the latter joining as median suture posterior to rostellum.

rostral flange. Hindmost part of rostral plate when it is strongly curved in anterior or dorsal direction so as to form fold, as in *Bumastus.*

rostral-hypostomal plate. Fused rostral plate and hypostome.

rostral plate. Median cephalic ventral portion of doublure (and rarely adjacent border) of variable size and relations; may be bounded anteriorly and laterally by the perrostral suture (Olenellina) or bounded anteriorly by the rostral suture and laterally by paired connective sutures, and in Homalonotidae it is partly dorsal [syn., epistoma (partim), epistomal plate, epistome, rostrum, rostral shield)]. See also rostellum. May be subdivided into border and doublure sectors.

rostral shield. See rostral plate.

rostral suture. Suture bounding anterior edge of unpaired, median rostral plate and separating it from the cranidium.

rostrum. See rostral plate.

ruga (pl., rugae). Ramifying, relatively broad, radiating ridges on the acrolobe of Agnostina.

S. Abbreviation for occipital or lateral glabellar furrow (sulcus), numbered forward from posterior, SO (occipital), S1, S2, S3, etc.

sagittal. Direction along axial line of body (abbreviation, sag.).

sagittal band. Smooth zone along pygidial axis, level with and joining tops of axial rings, interrupting inter-ring furrows.

sagittal groove. Smooth zone along pygidial axis, depressed below axial rings, which it interrupts partly or completely.

sagittal line. Median line of body (syn., axial line).

schizochroal eye. Eye with visual surface consisting of number of biconvex lenses, rounded or polygonal in outline, each lens covered by individual cornea and separated from others by sclerotic walls (syn., aggregate eye).

sclerite. Portion of exoskeleton into which it is divided either by an articulation or (during exuviation) by a suture.

scrobicula (pl., scrobiculae). Radiating furrows between rugae in Agnostina; groove or row of pits between border and epiborder furrows in eodiscoids.

scrobiculate. Refers to presence of scrobiculae in Agnostina.

sculpture. Refers to the features of the external surface of the exoskeleton, whether it is smooth or bears lirae, terrace ridges, tubercles, granules, pits, etc. (syn., ornament, prosopon).

segment. Exoskeleton of individual thoracic somite, divided into axial ring and pleura with doublure. Also used as a synonym of podomere.

semi-ankylosed segment. Posterior thoracic segment that may or may not be fused to the pygidium as in certain Redlichiina and paradoxidids.

shield. See exoskeleton.

shoulder (of hypostome). Anterolateral part of lateral border of hypostome, separated from anterior wing by lateral notch, generally the widest and most inflated part of lateral border; ridge crosses doublure of hypostome below shoulder (syn., lateral projection of hypostome).

shoulder (of pygidium in Agnostina). Ridge on anterior edge of pleural lobe, borders facet on inner side.

shoulder furrow (of pygidium in Agnostina). Separates shoulder from acrolobe; may be continuous with border furrow or cross border to margin.

side lobe. See pleural region.

simplimarginate. Pygidium of Agnostina in which border is not modified by pygidial collar.

socle. See eye socle.

somite. Transverse division of arthropod body (syn., metamere).

spectaculate. See axial glabellar node.

spine furrow. Longitudinal furrow on genal spine, a continuation of the lateral or posterior border furrow, or of both furrows.

stenoptychopariid rostral suture. Connective suture marginal to narrow (tr.) rostral plate (contrast with euptychopariid). See ptychopariid suture.

sternite. Sclerite of ventral portion of a somite.

striga. See ocular furrow.

subcephalic furrow. See vincular structure.

subcranial furrow. See vincular structure.

subgenal notch. Notch in posterior margin of cephalon immediately inside base of genal spine.

submarginal suture. Suture following margin of cephalon, slightly inside and below distal edge.

subocular area. Small, smooth area of librigena adjoining posterior portion of eye.

subocular groove. Smooth, bandlike depression of librigena surrounding visual surface of eye.

subocular ridge. Narrow ridge confining adaxially the subocular groove.

supplementary lobe. See intermediate lobe.

sutural ridge. Narrow ridge upon (or beside) which either branch of facial suture may be present on exterior surface of dorsal exoskeleton (syn., false eye ridge).

suture. Line along which portions of cephalic exoskeleton separated at exuviation. See cephalic, circumocular, connective, facial, hypostomal, marginal, perrostral, and rostral sutures.

tail. See pygidium.

tail shield. See pygidium.

telopod. See inner branch.

telopodite. See inner branch.

telson. Postsegmental part of arthropod body, bearing anus and commonly caudal furca or pair of cerci. Postcephalic somites form successively at the anterior margin of the telson during ontogeny.

tergite. Sclerite of dorsal portion of a somite. Not precisely equivalent to thoracic segment, because latter includes doublure.

terminal area (of pygidium). That part of pleural field or pleural region (in species having a ribbed field) that lies posterior to last rib.

terminal axial piece (or ring). Portion of axis of pygidium behind last inter-ring furrow (syn., posterior median lobe of pygidium, terminal axial segment).

terminal axial segment. See terminal axial piece.

terminal axial spine. Projection of median dorsal surface of terminal portion of axis of pygidium.

terminal node (of glabella). Small node at rear of glabella in Agnostina.

terminal node (of pygidial axis). In Agnostina, node at rear extremity of posteroaxis or intranotular axis.

terminal septum. Internal septum produced by median thickening of exoskeleton at steep termination of the axis in Proetoidea.

terrace ridges. Asymmetrical ridges on external surface of exoskeleton, having a steep scarp and gentle dip slope, may be parallel, subparallel, or anastomosing.

test. See exoskeleton.

thoracic recess. Median indentation in anterior margin of first thoracic segment (which lacks the articulating half ring) in Agnostina. See cephalothoracic aperture.

thoracic segment. See segment.

thoracopygon (pl., thoracopyga). Exoskeleton of thorax and pygidium (syn., pygothorax).

thorax. Region of trilobite body between cephalon and pygidium in which successive somites are articulated; also used to refer to exoskeleton of region, the segments of thorax. The thorax may show a division into prothorax and opisthothorax.

torular tubercle. Surmounts torulus and may persist in similar position after torulus has disappeared.

torulus. Rounded swelling beside glabella (typically opposite S2) on fixigena in early growth stages of encrinurids.

transaxial furrow. See inter-ring furrow.

transglabellar furrow. Continuous furrow across glabella resulting from meeting of adaxial ends of a pair of lateral glabellar furrows. In Agnostina furrow (F3) that separates the anterior and posterior glabellar lobes, anteroglabella and posteroglabella (syn., anterior furrow).

transitory pygidium. Fused segments of posterior region of exoskeleton during meraspid period.

transmarginal genal spine. Genal spine that arises from genal field, not from border.

transverse. Term used to designate the direction at right angles to sagittal line (abbreviation, tr.).

transverse preglabellar ridge. Transverse ridge crossing preglabellar field a short distance behind anterior border furrow. Contrast with preglabellar ridge.

tricomposite glabellar lobe. See bullar lobe.

tropidial ridges. Short, discontinuous, raised ridges that occupy similar position to tropidium.

tropidium (pl., tropidia). Concentric ridge that traverses preglabellar field and librigena a short distance inside and parallel with anterior border. Not coincident with inner margin of doublure.

tubercle. Small, knoblike prominence on external surface of exoskeleton. See pustule.

unconstricted. See acrolobe.

upper lamella. Upper or dorsal plate of fringe, as in Harpetidae, Harpididae, and Trinucleidae.

upper rim (external or internal). Smooth, raised portion of upper lamella of fringe as in Harpetidae, Harpididae, and Trinucleidae.

ventromarginal suture. See perrostral suture.

vincular structure. Furrow (subcephalic, subcranial), depression (or series of depressions), protuberance, ridge, or other structure associated with enrollment. See coaptation.

visceral features. Features of inner surface of exoskeleton.

visual surface (of eye). External surface of eye that bears lenses and is bounded above by palpebral portion of facial suture (syn., eye lappet). The visual surface may be bounded below by an ocular suture, so that there is a circumocular suture.

walking leg. See inner branch.

wing (of hypostome). See anterior wing, anterior wing process, posterior wing.

zonate. Situation in pygidium of Agnostina in which border is duplicated by pygidial collar between marginal spines.

SYSTEMATIC DESCRIPTIONS OF THE CLASS TRILOBITA

H. B. Whittington, W. T. Chang, W. T. Dean, R. A. Fortey, P. A. Jell, J. R. Laurie, A. R. Palmer, L. N. Repina, A. W. A. Rushton, and J. H. Shergold

[Diagnoses of ordinal and higher taxa by R. A. Fortey and H. B. Whittington; authorship of other diagnoses indicated within.]

Class TRILOBITA Walch, 1771

[*nom. correct. ex* Trilobiten Walch, 1771, p. 120] [This name, as "Trilobiten," was published by Walch (1771, p. 120) in his volume III of Knorr and Walch (1768–1774). Walch's work was rejected for nomenclatorial purposes by the International Commission on Zoological Nomenclature (Opinion 529, 1958). However, the Commission's remit extends only to the family-group level (Article 1b(4), *International Code of Zoological Nomenclature,* 1985), hence the name, emended to "Trilobita," remains available. The designation of the genus *Dalmanites* Barrande as type (Henningsmoen & Moore in Moore, 1959, p. 172) is invalid.]

Extinct marine arthropods, body divided by furrows longitudinally into median (axial) and lateral (pleural) regions, transversely into cephalon of fused segments, thorax of articulated segments, and pygidium of few to many fused segments. Length of mature individuals ranges from a little over 1 mm to about 700 mm.

Dorsal exoskeleton and periphery of venter (doublure) calcified (but see comments on Naraoiidae); calcified plate (hypostome) anterior to mouth and below anterior axial region. Anterior wing of hypostome extending dorsally to a fossula in the axial furrow. Facial suture characteristic, absent in Olenellina, but may be secondarily lost or modified. Rostral plate or median suture present, or cheeks conjoined. Cephalon with one pair of eyes (which may be lost), each eye lobe connected to axial region by raised ridge; eye lenses of crystalline calcite. Slightly oblique-transverse pleural furrows at posterior of cephalon, on each thoracic segment, and on pygidial segments. Growth of exoskeleton proceeded by molting from calcified protaspis about 1 mm long to adult, and by sequential release of segments into thorax. Protaspides of Olenellina and Agnostina not known. Limbs (where known) include one pair of antennae, followed postorally by series of generally similar biramous limbs, of which three (possibly four in one species) are

cephalic. *Lower Cambrian (Atdabanian)–Upper Permian.*

Order AGNOSTIDA Salter, 1864

[*nom. correct.* Shergold, Laurie, & Sun, 1990, p. 32, *pro* Agnostini Salter, 1864a, p. 2] [=Miomera Jaekel, 1909, p. 394; Agnostida Kobayashi, 1935, p. 81; see discussion in Robison & Campbell, 1974, p. 281]

Diminutive, isopygous, 2 or 3 fulcrate thoracic segments. Cephalic shield with deeply parabolic outline and maximum width (tr.) usually anterior to genal angle; border convex; glabella commonly fusiform, widest at base (except in Condylopygidae). Hypostome natant; rostral plate lacking or uncalcified. Outline of pygidium closely matching that of cephalon. *Lower Cambrian–Upper Ordovician.*

Suborder AGNOSTINA Salter, 1864

[*nom. correct.* Shergold, Laurie, & Sun, 1990, p. 32, *pro* Agnostini Salter, 1864a, p. 2]

No eye or facial suture; 2 thoracic segments; cephalothoracic aperture present; pygidium generally with wide axis, margin commonly bearing posterolateral spine. Cuticle thin. Calcified protaspis not known. *Lower Cambrian–Upper Ordovician.*

INTRODUCTION TO THE SUBORDER AGNOSTINA

John H. Shergold and John R. Laurie

The historical background to the classification of this suborder has recently been discussed in detail (Shergold, Laurie, & Sun, 1990, p. 1–3). The classification presented here is as developed in that paper and essentially follows ideas on relationships that have

been generated mainly in Australia, through the work of A. A. Öpik, and North America, particularly by R. A. Robison, during the past three decades.

Öpik (1967, p. 65) arrived at the general conclusion that due to the "combinative nature" of most taxa, "all agnostoids within their suborder are relatively close to each other, constituting a single superfamily, Agnostacea, with a restricted number of interrelated families." Öpik's classifications rely heavily on basic objective characteristics that allow intergrading morphologies to be independently diagnosed (e.g., Öpik, 1979). Although we do not follow his classifications here implicitly, we do agree that only characteristics in combination can be used for sophisticated taxonomic discrimination. Accordingly, we have made use of extended diagnoses particularly at family rank to facilitate assessment of the fullest range of permutations. In general, fewer, more succinctly diagnostic characteristics link genera at subfamilial level, as indicated in the review below. The approach has been adopted because Agnostina reiterate morphological conditions at different times in different familial groups, e.g., varyingly effacing or emphasizing external morphology, constricting acrolobes, developing zonate borders, effacing the anterior glabellar lobe or sagittally splitting it, or modifying the posterior pygidial axial lobe. We have in general made use of axial criteria to define broad groups at the familial and subfamilial level and degrees of effacement or scrobiculation at the generic and subgeneric level. As a result we emphasize morphological continuity.

Compared to treatment of Agnostina in the previous *Treatise,* we have also given more extended geographic and stratigraphic ranges. The former are given to state or province regions and the latter to local biochronological stage and zone. This is an acknowledgment of the stratigraphic and biofacies importance of these trilobites on a global scale, particularly during the Cambrian. First and last occurrences of taxa may not be the same in different zoogeographical provinces with different biofacies relationships and biochronologic schemes.

In addition, because the Linnean system of classification relies on the concept of the type specimen, we have included what is currently known about the status of the type material, its repository, and numbers assigned. Several old collections remain unlocated; several taxa are based on syntype material requiring the designation of lectotypes; and in some instances types are known to be lost, necessitating the search for topotype material and justification of neotypes.

In almost all instances the extant type material has been illustrated, frequently supplemented by more complete material to better illustrate the generic concepts. Where type material is not identified, suitable topotypes or other subjectively selected specimens are figured.

Suborder Agnostina, as used here, is based on concepts traditionally attributed to Salter (1864a), who recognized a Section Agnostini. This is the suborder Agnostina of Moore (1959), Rushton (1966), and Öpik (1961b, 1967, 1975b, 1979), and the order Agnostida of Rasetti (1945a, 1948b, 1952a), Shergold, Laurie, and Sun (1990), and Shergold (1991). Robison (1984) has also diagnosed an order Agnostida but attributed it to Kobayashi (1935) rather than Salter (1864a).

A total of 190 generic and subgeneric taxa assignable to the Agnostina have been assessed. Of these, four taxa are rejected from Agnostina, and a further six are *nomina nuda.* About thirty percent of the rest are synonyms, leaving for classification 123 valid taxa. These are assigned to the superfamilies Condylopygoidea and Agnostoidea and two families of uncertain affinity, Phalacromidae and Sphaeragnostidae.

Although Condylopygoidea is based on the single family Condylopygidae Raymond, 1913a, itself containing only two genera, *Condylopyge* and *Pleuroctenium,* its concept is stable and goes back to the first attempted generic subdivision of *Agnostus* by Hawle and Corda (1847). At one taxonomic rank

or another, the constituent genera of Condylopygidae have retained independent status in all classifications. We follow KOBAYASHI (1962) in recognizing them at the superfamilial level, but the familial concept remains that advocated by RAYMOND (1913a). The characteristic expansion of the anterior glabellar lobe, the apparent presence of occipital structures instead of the basal lobes, the possible retention of a cephalothoracic aperture (if RUSHTON, 1979, p. 45 is correct), and the presence always of three anterior segments in an otherwise axiolobate pygidium differentiate Condylopygoidea from Agnostoidea. Condylopygoids are also prone to spinosity: an occipital spine may be developed, and the elongate axial cephalic node may be an aggregation of small spines (see RUSHTON, 1979, p. 47, fig. 2a). *Pleuroctenium* also displays spines developing from the axial nodes of the thoracic and anterior three pairs of pygidial segments. Fringing spines or crenulations occur on the pygidia of both genera. There is also a tendency, well illustrated by WESTERGÅRD (1946, pl. 2), for both cephalic and pygidial acrolobes to become transversely divided. Division occurs adjacent to the anterior glabellar furrow of the cephalon and the third, posteriormost (F3), transverse furrow of the pygidial axis. It is only among the Pseudagnostinae that such features are displayed among Agnostoidea. Condylopygoidea are therefore most distinctive members of the Agnostina.

The great bulk of agnostoid genera and subgenera are assigned to the superfamily Agnostoidea and distributed among seven families and ten subfamilies. A significant number of genera cannot be classified with confidence at the familial level, either because they are inadequately preserved or are not diagnosable. Many of these genera are highly effaced, and most are in need of thorough revision. Agnostoid families recognized include Agnostidae, Ptychagnostidae, Spinagnostidae, Peronopsidae, Diplagnostidae, Clavagnostidae, and Metagnostidae.

Micragnostidae (HOWELL, 1935b), Glyptagnostidae (WHITEHOUSE, 1936), Hastagnostidae (HOWELL, 1937), and Rudagnostidae (LERMONTOVA, 1951a) are all considered synonyms of Agnostidae. Agnostidae, the largest family of Agnostina, is presently considered to embrace three subfamilies: Agnostinae with fourteen genera and subgenera; Ammagnostinae with seven genera and subgenera; and Glyptagnostinae with two genera. A further five genera cannot be placed in subfamilies. Agnostid genera can be divided in several ways, but the axial characteristics, particularly of the pygidium, have been primarily used in the present classification. In Agnostinae the pygidium is simple and axiolobate; in Ammagnostinae the posterior lobe of the pygidial axis is invariably expanded and lengthened and contains a well-developed secondary axial node; in Glyptagnostinae, although the simple axiolobate situation is commonly obscured by scrobiculation, a secondary axial node is developed in association with a well-defined transverse depression that occurs in the rear of the posterior lobe.

Use of the subgeneric rank is made within Agnostinae to express end members of gradational morphological series. Hence, *Homagnostus* is reinstated as a subgenus of *Agnostus,* representing morphs with a laterally expanded and extended pygidial axis. *Lotagnostus (Lotagnostus), L. (Eolotagnostus),* and *L. (Distagnostus)* represent recognizable degrees of effacement. In the revived genus *Oncagnostus* (WHITEHOUSE, 1936), the subgenus *Strictagnostus* is made available for morphs with short axes that have characteristically flared or tapered acrolobes, and the subgenus *Kymagnostus* is used for those with long axes without **deliquiate** border furrows. LUDVIGSEN, WESTROP, and KINDLE (1989) have shown that *Trilobagnostus* should not be referred to *Lotagnostus.* It is here given generic status but could also be interpreted as a subgenus of *Oncagnostus.* The species referred to the genera and subgenera *Oncagnostus, Strictagnostus, Kymagnostus,* and *Trilobagnostus* seemingly form a continuum in great need of revision. *Innitagnostus* and *Acutatagnostus* could also be regarded as

subgenerically related. *Micragnostus,* following the suggestions of FORTEY (1980b, p. 20), is restricted in specific composition but decidedly separated from *Geragnostus* (Metagnostidae) with which it has long been associated.

Glyptagnostinae is here regarded as a subfamily of Agnostidae rather than a family in its own right (KOBAYASHI, 1938, 1939a; WESTERGÅRD, 1947; HENNINGSMOEN, 1958; ÖPIK, 1961b; SHERGOLD, 1982). It is restricted here to the genera *Glyptagnostus* and *Agnostardis,* as envisaged by ÖPIK (1963, p. 38). The previously recognized subgenus *Lispagnostus* is considered here to be synonymous with *Ammagnostus*. The highly **scrobiculate** and deuterolobate *Pseudoglyptagnostus*, which has been associated with Glyptagnostinae, is referred to Pseudagnostinae (family Diplagnostidae) and regarded as an **en grande tenue** subgenus of *Agnostotes*. We prefer to regard Glyptagnostinae here as a subfamily of Agnostidae, rather than of Diplagnostidae as proposed by ÖPIK (1967), on the basis of cephalic axial similarity with such genera as *Innitagnostus* and pygidial axial similiarity with *Agnostus* itself.

Genera of the Ammagnostinae form a cohesive group with the exception perhaps of the diminutive *Kormagnostella* as recognized by ÖPIK (1967). *Tentagnostus* is considered to be an en grande tenue subgenus of *Ammagnostus*. *Proagnostus* is revived following ROBISON's (1988) designation of a lectotype for *P. bulbus*. *Agnostascus* and *Agnostascus (Paragnostascus)* must now be regarded as synonyms of *Proagnostus.*

Of uncertain subfamilial classification, *Aistagnostus* is partially effaced, the pygidium of Agnostinae type. The cephalon, however, is not like that of members of this subfamily. The remaining unclassified genera have long or long and expanded, posterior axial pygidial lobes. *Idolagnostus* is diminutive, could be deuterolobate, and may represent a genus of Pseudagnostinae. *Acmarhachis* has been similarly classified (PALMER, 1960, 1962a), and *Connagnostus* has been regarded by ÖPIK (1967) as a Diplagnostinae. Until investi-

gated in greater detail, however, we prefer to give these genera an undefined status among Agnostidae.

The family Ptychagnostidae is here considered to represent an independent family (*fide* ROBISON, 1984, p. 10), rather than a subfamily of the Agnostidae as originally established (KOBAYASHI, 1939a, p. 151) and often considered (ÖPIK, 1967, p. 90; 1979, p. 86; ERGALIEV, 1980, p. 67; PENG, 1992, p. 82; LAURIE, 1988, p. 171). The members of this family, although sharing some features with members of the Agnostidae, do not seem to be closely related to that family. Although there has been recent debate about the validity of many of the genera belonging to Ptychagnostidae (ÖPIK, 1979; ROBISON, 1982, 1984; LAURIE, 1988), there has been general agreement with regard to the association of species in the family. Genera belonging to the Ptychagnostidae usually have a median preglabellar furrow, a relatively elongate anterior glabellar lobe, elongate basal lobes, a basic articulating device, well-developed pygidial axial F1 and F2, an acuminate posterior pygidial axial lobe, and a tendency toward spinosity. Included in this family is *Tomagnostus,* the early species of which seem to be closely related to *Onymagnostus.* Using the principle of first reviser, SHERGOLD, LAURIE, and SUN (1990) selected Ptychagnostidae (KOBAYASHI, 1939a) as the family name. It may be possible to recognize several subfamilies using some of the synonymous familial names (Triplagnostinae, Lejopyginae), but this has not been attempted herein.

The family Spinagnostidae was established by HOWELL (1935a, p. 218) to accommodate the subfamilies Spinagnostinae and Quadragnostinae, both of which were founded on only one genus, each containing one species. The types of these species are very poorly preserved. For some time now the genus *Spinagnostus* has commonly been considered synonymous with *Hypagnostus* (see WESTERGÅRD, 1946, p. 44), despite ÖPIK's (1979, p. 66) belief that it should be considered a separate genus. This synonymy is upheld herein but does not invalidate the

family name. The types of the eponymous genus of the subfamily Quadragnostinae are very poorly preserved and are largely uninterpretable. *Quadragnostus* is therefore restricted to its type material.

As understood herein, the family Spinagnostidae contains two subfamilies: Spinagnostinae and Doryagnostinae. All members of this family have nondeliquiate border furrows; a nonspinose cephalon; small, triangular basal lobes; usually broadly rounded glabellar culmination; and usually effaced pygidial axial F1 and F2. While the Spinagnostinae may be polyphyletic, all of its members have a tendency to efface the anterior glabellar lobe, usually lack the median preglabellar furrow, have the glabellar node near the F2 furrows, and lack a secondary axial node on the posterior lobe of the pygidial axis. The subfamily Doryagnostinae consists of only three genera, which form a closely related, monophyletic group. All possess a well-developed anterior glabellar lobe, have the glabellar node located from level with F1 to midway between F1 and F2 furrows, and have a small secondary axial node located on the posterior pygidial axial lobe.

One genus assigned to Spinagnostidae, *Pseudoperonopsis* (Harrington, 1938), cannot be placed in a subfamily. This is because the types have never been satisfactorily illustrated and were not availbable to us for study. Subsequent interpretations vary considerably.

There are probably well over a hundred species that have been assigned to *Peronopsis,* and these remain there despite refinement in agnostoid taxonomy over the last few decades. This genus has for a long time been the receptacle for almost any Early to Late Cambrian agnostoid having an axiolobate, **simplimarginate** pygidium with effaced pygidial axial F1 and F2 and a cephalon with a bilobate glabella lacking a median preglabellar furrow. This has led to *Peronopsis* being, as it presently stands, probably the most morphologically diverse genus of the Agnostina. Herein, the genus is restricted to its type species and is associated with the reha-

bilitated genus *Diplorrhina* and with *Peronopsella* and *Gratagnostus* in the family Peronopsidae (Westergård, 1936). This family is of uncertain relationships, but the included genera have a distinctive morphology.

The family Diplagnostidae is essentially reserved for agnostoids that are commonly modified axiolobate (in the sense of Öpik, 1967) and frequently zonate. Thus the family includes the subfamilies Diplagnostinae, Oidalagnostinae, and Pseudagnostinae. The Diplagnostinae have a characteristically zonate pygidium in combination with an axiolobate or only slightly modified axiolobate condition; the cephalon has an often sulcate and occasionally bilobate anterior glabellar lobe and angulate glabellar culmination. Frequently, a transverse depression is developed behind the pygidial axial node in the anterior half of the posterior lobe. Such characteristics tend to unite the genera *Diplagnostus, Linguagnostus*, *Dolichagnostus,* and *Tasagnostus* into a close morphological group.

Öpik (1967, 1979) also included the genera *Baltagnostus* (Lochman in Lochman & Duncan, 1944) and *Oedorhachis* (Resser, 1938) in the subfamily Diplagnostinae. In the former, it is only the type species, *B. centerensis,* that is convincingly zonate. Other species assigned to this genus by subsequent workers are simplimarginate or have thickened posterior pygidial borders that are not really zonate in the sense of *Diplagnostus* or *Linguagnostus:* they are quasizonate, having a gentle doubling of the border. Similar are the species attributed by Öpik (1979) to *Pseudoperonopsis* (Harrington, 1938), which form a well-defined group stratigraphically but will require generic reassessment when the type species, *Agnostus sallesi* (Munier-Chalmas & Bergeron in Bergeron, 1899), is revised. As noted by Öpik (1967, p. 69), specimens illustrated as *Peronopsis fallax* by Westergård (1946, pl. 2, fig. 18–24) also have an incipient zonation. All the above may, therefore, form a second group of taxa that lies intermediate between the basically nonzonate Peronopsidae and

the typically zonate Diplagnostinae. Species assigned to *Oedorhachis* are generally acceptably zonate but are also trispinose and have a variably laterally expanded posterior pygidial axial lobe, a combination of characteristics that sets them slightly apart from other Diplagnostinae.

The subfamily Oidalagnostinae also has a zonate pygidium, but there is a gap in the pygidial collar. The pygidia have a modified axiolobate condition, the posterior lobe is subquadrate and extends to the pygidial collar, and a third marginal spine is situated sagittally. The morphologies of the constituent genera, *Oidalagnostus* and *Cristagnostus* are readily related to and probably derived from Diplagnostinae. A major feature in their phylogeny is the separation of the anterior portion of the posterior axial lobe as seen in *Diplagnostus,* apparently as a third axial ring, and the manifestation of lateral bosses as appendages to this third segment (see WESTERGÅRD, 1946, pl. 9, fig. 6 for extreme condition). These features seem to foreshadow the development of the accessory furrows and deuterolobe that characterize Pseudagnostinae.

The Pseudagnostinae are usually simplimarginate diplagnostids, which develop a deuterolobe proper and accessory furrows. They are linked to other groups of Diplagnostidae by the occasional presence of a third pygidial spine, as in *Pseudagnostus (Sulcatagnostus),* and triannulate anterior part of axis, as in *Xestagnostus.* The Pseudagnostinae are a large group of genera that exhibit a wide range of deuterolobe morphology and degrees of effacement. Relationships of genera and subgenera are determined by the situation of the axial glabellar node relative to the F2 and F3 furrows (SHERGOLD, 1975, 1977, 1980), falling into groups related to *Pseudagnostus, Neoagnostus,* and *Rhaptagnostus,* respectively. Degree of effacement varies from nearly total in *Litagnostus* to extreme scrobiculation in *Neoagnostus (Machairagnostus). Agnostotes (Agnostotes)* (ÖPIK, 1963) and *A. (Pseudoglyptagnostus),* with its synonym *Glyptagnostotes* (LAZARENKO, 1966), has been classified by authors in Glyptagnostinae (for example, XIANG & ZHANG, 1985), but they are here classified among the Pseudagnostinae because their pygidia seem to be typically deuterolobate (see particularly LAZARENKO, 1966, pl. 2, fig. 1–2, 5–6, 8, 10–12). Characters of the cephalon of Glyptagnostinae, like the elaborate development of the lateral glabellar lobes and division of the anterior lobe by a median sulcus, are apparent in the scrobiculate subgenus *Pseudoglyptagnostus* but much less marked in the more effaced *Agnostotes.* Neither subgenus possesses the typical posterior axial lobe with its secondary axial node and associated transverse depression. ÖPIK (1963, 1967) has explored alternative possibilities for the classification of *Agnostotes* within the Diplagnostidae.

The definition of the deuterolobe has been debated (see PRATT, 1992, for discussion and opinion different from that below). It is a composite posterior pygidial lobe that comprises both axial and pleural elements and that extends therefore to the posterior border furrow and is anterolaterally at least circumscribed by accessory furrows. Possibly, then, such genera as *Oxyagnostus* should be excluded from Pseudagnostinae and such forms as *Idolagnostus* included. Some others, for example *Formosagnostus,* judging from its relationship with *Nahannagnostus* (i.e., the *bulgosus* species group of *Pseudagnostus;* see SHERGOLD, 1977), seem to indicate derivation from Agnostidae and suggest that the subfamily Pseudagnostinae could be polyphyletic. Further revision is required to solve such issues. FORTEY (1980b, p. 28) has regarded the Pseudagnostinae as somehow related to the Metagnostidae because some of them possess what might be taken to be an intranotular axis behind the defined extent of the pygidial axis. He also noted the glabellar furrow patterns, the deliquiation of the border furrows, common pygidial articulating device, and the occurrence of a common prosopon. However, many morphological trends found among agnostoids are subsequently reiterated in apparently unrelated groups. Features of Pseudagnostinae are found in Middle Cambrian Oidalagnostinae

(Diplagnostidae) and in Glyptagnostinae (Agnostidae). The transverse division of the cephalic acrolobe of the latest Cambrian genus *Trisulcagnostus* may be observed also in Condylopygidae.

Clavagnostidae has been long recognized as an independent family, like Condylopygidae, of unknown origin and with unknown descendants. It has been discussed at length by Öpik (1967), whose subfamilial division into Clavagnostinae and Aspidagnostinae is followed here. Clavagnostidae are distinguished by the fused anterior and posterior glabellar lobes and generally shortened glabella. Clavagnostinae have a relatively simple pygidium, characterized by an acuminate axis posteriorly bisected by a transverse furrow somewhat similar to that of Glyptagnostinae. In Aspidagnostinae the pygidial axis has both F1 and F2 furrows, the posterior transverse one, and a secondary axial node, also rather reminiscent of Glyptagnostinae. The posterior border of taxa in Clavagnostinae is, however, zonate, and there is a gap in the collar as in *Oidalagnostus.* A hint of a third marginal pygidial spine in Aspidagnostinae also recalls *Oidalagnostus. Utagnostus* is temporarily placed with the Clavagnostidae by virtue of its trispinose pygidium and nature of its cephalic spines.

The family name Metagnostidae was revived by Fortey (1980b, p. 24) to embrace some of the genera previously most commonly referred to Geragnostidae (Howell, 1935b; see also Howell in Moore, 1959, p. 176). Fortey (1980b, p. 27) also included the genera *Segmentagnostus* and *Corrugatagnostus,* those genera with a chevronate furrow separating the two main glabellar lobes. This taxonomic scheme is followed herein with modifications, notably some of those introduced by Zhiyi Zhou (1987).

Two, long-accepted families, Phalacromidae and Sphaeragnostidae are unclassified at superfamilial rank. The former is based on the genera, *Phalacroma, Lisogoragnostus,* and *Dignagnostus* and the latter on *Sphaeragnostus* alone.

Phalacromidae, concept and composition, has been discussed at some length by Öpik

(1961b) and Jago (1976). It has been regarded as polyphyletic (Öpik, 1967, p. 82). We follow Öpik (1961b, p. 54) in recognizing the validity of the family, but restrict it to the genera noted above. All other genera previously associated with Phalacromidae (*Phalagnostus, Grandagnostus, Valenagnostus, Phoidagnostus*) are classified elsewhere. The inclusion here of *Dignagnostus* (Hajrullina in Repina, Petrunina, & Hajrullina, 1975) is based on pygidial characteristics, and there is no certainty that associated cephala illustrated by this author are correctly assigned. If the association of cephala and pygidia illustrated by Hajrullina is correct, then *Dignagnostus* must be rejected from Phalacromidae, which would then be restricted to *Phalacroma* as indicated by Öpik (1967). Pygidia of *Dignagnostus grandis* and *Phalacroma bibullatum* are unified by the long (sag.), wide (tr.), and laterally expanded axis; effacement of transverse furrows; shape and position of the axial node; and retention of a transverse depression behind the axial node, a characteristic feature of *Peronopsis* and *Diplagnostus,* which may indicate the derivation of Phalacromidae. If cephala assigned to *Dignagnostus* are ignored, species of Phalacromidae are relatively large and mostly effaced.

Effacement also is responsible for the isolation of Sphaeragnostidae. The genus *Sphaeragnostus* is widely distributed during the Ordovician and quite characteristic. The cephalon is completely effaced, and the pygidial axis an unfurrowed, spheroidal structure of substantial width (tr.). Thoracic axial structures are also very wide (tr.), limiting the extent of the pleurae. There is no guarantee that Sphaeragnostidae or Phalacromidae are true Agnostina, as the presence of a cephalothoracic aperture is not confirmed in either group.

Twenty-one genera are left unclassified at familial level. Mostly this is because their type specimens are not readily interpreted due to effacement of diagnostic morphology (*Agnostogonus, Delagnostus, Leiagnostus, Monaxagnostus, Phoidagnostus, Glaberagnostus, Grandagnostus, Skryjagnostus,* and

Valenagnostus) or adverse preservation (*Archaeagnostus, Armagnostus, Blystagnostus, Hastagnostus,* and *Quadragnostus*), or both (*Ciceragnostus* and *Gallagnostus*). *Plurinodus* is a diminutive genus that may prove supra-generically classifiable when more material becomes available. *Phaldagnostus* may be classifiable when it is properly illustrated. Pratt (1992) has recently erected the family Phalagnostidae for the effaced genus *Phalagnostus,* whose relationships with other agnostoids, particularly *Grandagnostus* and *Valenagnostus,* have not been thoroughly explored.

Four genera are rejected from Agnostida. Two of them, *Discagnostus* (Öpik, 1963), the sole representative of the family Discagnostidae, and *Mallagnostus* (Howell, 1935b), on which Mallagnostidae (Howell, 1935b) is based, are considered better classified among Eodiscina. *Gallagnostoides,* founded by Kobayashi (1939b, p. 580) with *Aeglina boia* (Hicks, 1875, p. 185, pl. 10, fig. 9, 9a) as type species, is a mid-Arenig species of the cyclopygid subgenus *Microparia (Microparia)* Hawle & Corda, according to Fortey and Owens (1987, p. 172). *Pseudotrinodus* (Kobayashi & Hamada, 1971), from the Devonian of western Malaysia, is referred to Aulacopleurinae by Thomas and Owens (1978, p. 74).

Acknowledgments

Superfamily AGNOSTOIDEA M'Coy, 1849

[*nom. transl.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, *ex* Agnostinae M'COY, 1849, p. 402]

Agnostina with basal glabellar lobes anteriorly expanded, anterior glabellar lobe not laterally expanded. *Lower Cambrian–Upper Ordovician.*

Family AGNOSTIDAE M'Coy, 1849

[Agnostidae M'COY, 1849, p. 402] [=Micragnostidae HOWELL, 1935b, p. 233; Glyptagnostidae WHITEHOUSE, 1936, p. 101; Rudagnostidae LERMONTOVA, 1951b, p. 7]

En grande tenue to effaced; border furrows nondeliquiate to deliquiate; cephalic border narrow and pygidial border of variable width; acrolobes usually unconstricted; median preglabellar furrow absent to well developed. Glabella with variably shaped anterior lobe; F3 straight or curved; F2 absent to well developed; glabellar culmination rounded, subquadrate, or obtusely angular; glabellar node from midway between F1 and F2 to in front of F2; basal lobes variable in size, usually simple, occasionally incorporating lateral portions of M2 lobe. Pygidium with usually long axis, commonly reaching border furrow, commonly constricted across M2; F1 variably impressed or effaced; M1 usually trilobate; F2 variably impressed or effaced; posterior lobe usually long and semiovate, ogival, semicircular, or bulbous, commonly with either a secondary axial node in posterior half or with a terminal node. *Middle Cambrian–Lower Ordovician.*

Subfamily AGNOSTINAE M'Coy, 1849

[Agnostinae M'COY, 1849, p. 402]

Pygidium bispinose or nonspinose, with agnostoid or basic articulating device; pygidial axis simple, axiolobate, usually long but not reaching border furrow; F1 and F2 variably impressed; posterior lobe with or without terminal node. *Middle Cambrian–Lower Ordovician.*

Agnostus BRONGNIART, 1822, p. 38 [**Entomostracites pisiformis* WAHLENBERG, 1818, p. 42; SD JAEKEL, 1909, p. 399; lectotype cephalon (WAHLENBERG, 1818, pl. 1, fig. 5; SD SHERGOLD, LAURIE, & SUN, 1990, p. 32), Vg819a, PM, Uppsala]. Generally with relatively narrow borders. Cephalon with median preglabellar furrow; anterior glabellar lobe ogival or rounded; posterior lobe tapering forward; axial node level with or slightly behind variably developed F2; basal lobes variable in size. Pygidium with long (sag.), variably wide (tr.), and tumid axis, usually not reaching border furrow, lacking median postaxial furrow; marginal spines present. *upper Middle Cambrian–lower Upper Cambrian:* Cosmopolitan.

A. (Agnostus) [=*Battus* DALMAN, 1827, p. 151 (type, *Entomostracites pisiformis* WAHLENBERG, 1818, p. 42, pl. 1, fig. 5; SD JAEKEL, 1909, p. 399)]. Cephalon with ogival anterior glabellar lobe, basal lobes of moderate to large size. Pygidium with long (sag.), relatively narrow (tr.), posteriorly pointed, or narrowly rounded axis; F1 and F2 very weak or effaced. *upper Middle Cambrian–lower Upper Cambrian:* northern Greenland; Sweden, Norway, Denmark, England, Wales, Canada (New Brunswick, Newfoundland), *L. laevigata–A. pisiformis* Zones; Australia (Queensland), *E. eretes* Zone. *upper Middle Cambrian:* Argentina.——FIG. 217,*1a,b.* **A. (A.) pisiformis* (WAHLENBERG), Upper Cambrian (*A. pisiformis* Zone), Sweden (Hönsäter, Hallevad-Billingen, Västergötland); *a,* lectotype, cephalon, PM Vg819a, ×7.55 (new); *b,* paralectotype, pygidium, PM Vg819b, ×6.95 (new).

A. (Homagnostus) HOWELL, 1935c, p. 15 [**Agnostus pisiformis* LINNAEUS var. *obesus* BELT, 1867, p. 294; OD; lectotype (BELT, 1867, pl. 12, fig. 4a; SD RUSHTON in ALLEN, JACKSON, & RUSHTON, 1981, pl. 16, fig. 2), I.7646, BMNH, London]. Pygidium with posteriorly broadly rounded axis extending nearly to posterior border furrow. Axis constricted across M2 with posterior lobe variably but always laterally expanded; F2 well developed; F1 always impressed laterally and only occasionally impressed medially; M1 variably tripartite. *Upper Cambrian:* northern Greenland; England, Wales, *O. gibbosus–O. cataractes* Subzones; Sweden, Norway, Denmark, *Olenus* Zone; Russia (Novaya Zemlya, Yakutia, Altay Mountains), Kazakhstan, *Pedinocephalina/Toxotis–Irvingella* Zones; China (Zhejiang, Shandong, Liaoning), *G. stolidotus* Zone; South Korea, *Chuangia* Zone; Australia (Queensland), *G. reticulatus* Zone; USA (Alabama, Alaska, Oklahoma, Texas, Nevada, Wyoming), *Aphelaspis–Elvinia* Zones; Canada (Newfoundland, Northwest Territories), *?Cedaria minor* and *Irvingella major* Zones.——FIG. 217,*2a,b.* **A. (H.) obesus* (BELT), Upper Cambrian (*Olenus* Zone); *a,* lectotype, northern Wales (Afon Mawddach, Dolmelynllyn), ×8 (Allen, Jackson, & Rushton, 1981, pl. 16, fig. 2); *b,* exoskeleton, BMNH TE6, England (Nuneaton district), ×6.67 (Rushton, 1978, pl. 25, fig. 4).
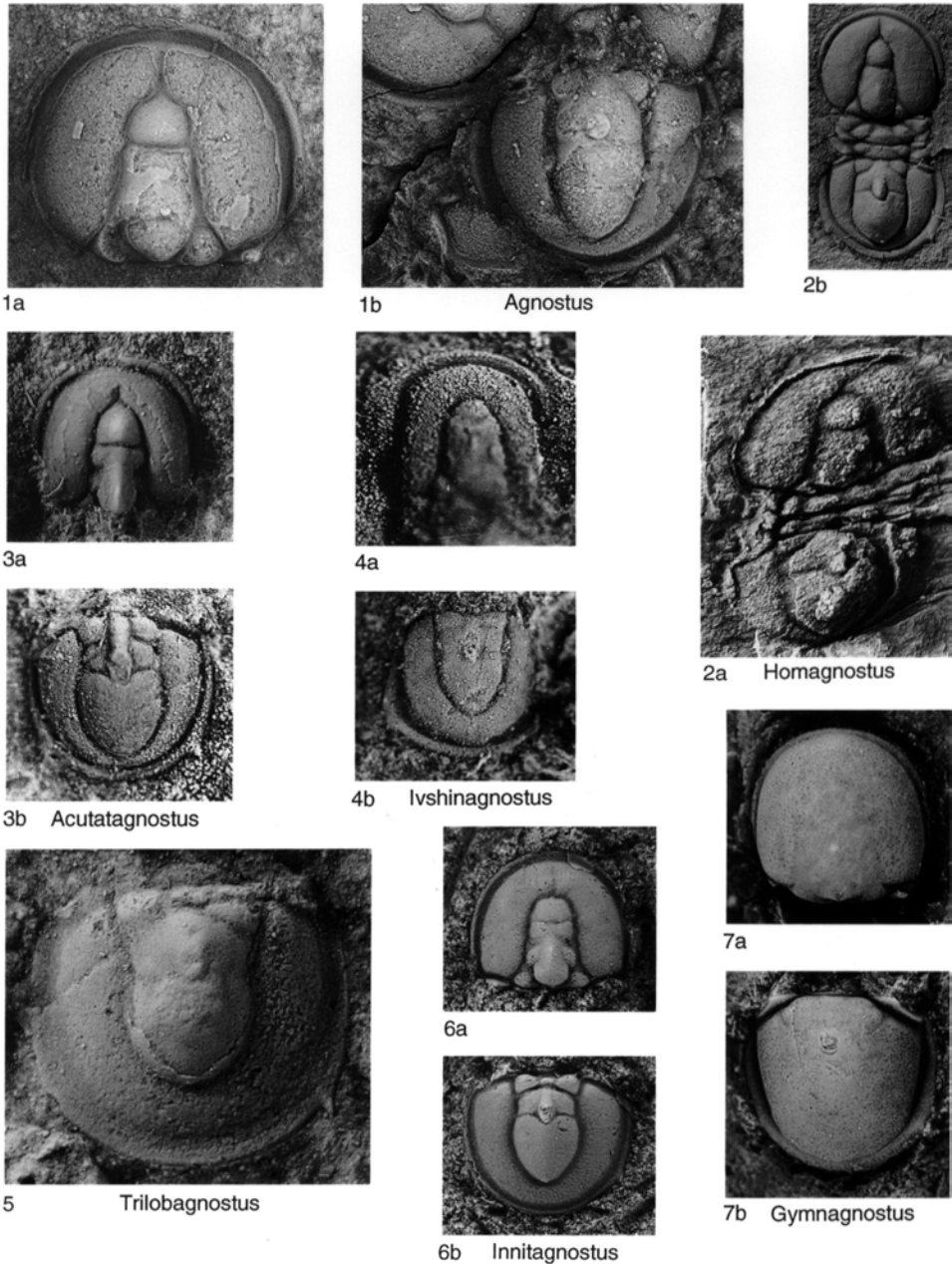
FIG. 217. Agnostidae (p. 339–344)

Acutatagnostus ERGALIEV, 1980, p. 91 [**A. acutatus;* OD; holotype (ERGALIEV, 1980, pl. 11, fig. 16), 1950/184, GMAN, Alma-Ata]. Like *Innitagnostus* but with median preglabellar furrow only evident proximally; anterior glabellar lobe long and ogival; F2 well developed but F1 weak. Pygidium with retrally located spines; long axis extending almost to posterior border furrow; M1 and M2 clearly trilobate; F1 only laterally impressed. *Upper Cambrian (Sakian):* Kazakhstan, *H. longiformis–P. curtare* Zones.——FIG. 217,3a,b. **A. acutatus* ERGALIEV, Upper Cambrian (*Oncagnostus longifrons* Zone),

Kazakhstan (Kirshabakty River, Lesser Karatau mountains); *a,* holotype, cephalon, GMAN 1950/184, ×11; *b,* pygidium, GMAN 1950/185, ×12 (Ergaliev, 1980, pl. 11, fig. 16–17).

?Gymnagnostus Robison & Pantoja-Alor, 1968, p. 776 [*G. gongros;* OD; holotype (Robison & Pantoja-Alor, 1968, pl. 97, fig. 29), 158892, USNM, Washington, D.C.]. Almost effaced, but cephalon retaining very narrow borders, faint axial glabellar node, and partly outlined basal lobes. Pygidium with broader border, faintly constricted acrolobe, and weakly defined axial furrows and terminal node, which indicate the short axis; axial node prominent; posterolateral spines advanced. *Upper Cambrian:* Mexico, *Cordylodus proavus* Zone; Bolivia, *Neoparabolina argentina* Zone.——Fig. 217,7a,b. *G. gongros,* Mexico (Santiago Ixtaltepec, Nochixtlán region, Oaxaca), *Cordylodus proavus* Zone; *a,* cephalon, USNM 158887, ×10; *b,* holotype, pygidium, USNM 158892, ×10 (new).

Innitagnostus Öpik, 1967a, p. 98 [*I. innitens;* OD; holotype (Öpik, 1967, pl. 58, fig. 2), CPC 5853, AGSO, Canberra]. Median preglabellar furrow variably developed. Glabella with broad, trapeziform anterior lobe; F3 well impressed, nearly straight; posterior lobe with well-developed F1 and F2; lateral portions of M2 commonly separated from midmost glabella by weak longitudinal (exsag.) furrows; glabellar node located from midway between F1 and F2 to level with F2; basal lobes of moderate size, trapezoidal. Pygidial axis of moderate length, constricted across M2; M1 trilobate; F1 well impressed, bent forward; F2 straight laterally, bent rearward by strong axial node. Posterior lobe ogival to semiovate, usually narrowly rounded posteriorly, not reaching border furrow. Median postaxial furrow absent. *Upper Cambrian:* China (Guizhou, Hunan); Australia (Queensland), Mindyallan–Idamean (*E. eretes* to *S. diloma* Zones); Russia (Siberia), Kazakhstan, *G. stolidotus* to *P. curtare* Zones; Canada (Northwest Territories, British Columbia, Newfoundland), *Glyptagnostus reticulatus* to *Olenaspella regularis* Zones; USA (Alabama, Nevada, Texas), *Aphelaspis* Zone.——Fig. 217,6a,b. *I. innitens,* Upper Cambrian (Mindyallan, *G. stolidotus* Zone), western Queensland (Boulia district); *a,* holotype, cephalon, CPC 5853, ×8; *b,* topotype, pygidium, CPC 5854, ×8 (new).

?Ivshinagnostus Ergaliev, 1980, p. 65 [*I. ivshini;* OD; holotype (Ergaliev, 1980, pl. 13, fig. 2), 1950/204, GMAN, Alma-Ata]. Anteriorly expanding cephalon and posteriorly expanding pygidium; median preglabellar furrow absent. Glabella strongly tapered, with small, rounded anterior lobe; posterior lobe with F2 furrows very weak, F1 furrows weak, basal furrows weak; glabellar node a short distance behind F2 furrows; basal lobes indistinct. Pygidium bispinose; axis tapered, unconstricted, short; F1 weak; M1 weakly trilobate; F2 very weak. *Upper Cambrian (Sakian):* Kazakhstan, *I. ivshini* Zone.——Fig. 217,4a,b. *I. ivshini,* Kazakhstan (Kirshabakty River, Lesser Karatau mountains); *a,* cephalon, GMAN 1950/203, ×5.5; *b,*

holotype, pygidium, GMAN 1950/204, ×6.8 (Ergaliev, 1980, pl. 13, fig. 2–3).

Lotagnostus Whitehouse, 1936, p. 101 [*Agnostus trisectus* Salter, 1864b, p. 10; holotype by monotypy (Salter, 1864b, pl. 1, fig. 11), BGS 8768, London]. Variably effaced, with usually nondeliquiate border furrows and unconstricted acrolobes, with or without a median preglabellar furrow. F3 furrow straight or bent backward; posterior lobe with well-developed F2 furrows; glabellar node located from midway between F1 and F2 furrows to level with F2 furrow. Basal lobes large, triangular, in some species incorporating the narrow (tr.) portions of the M2 lobe. Pygidium bispinose; axis long (sag.); M1 trilobate; F1 impressed at least laterally; M2 trilobate; F2 always impressed. Posterior lobe elongate, semiovate to ogival, with well-developed terminal node. *Upper Cambrian.*

L. (Lotagnostus). Commonly scrobiculate, variably deliquiate. Median preglabellar furrow present. Glabella with long (sag.), subpentagonal anterior lobe; posterior lobe with F2 furrow well developed, in some species curving forward to intersect F3 furrow, isolating anterolateral lobes. Pygidial axis weakly constricted across M2; F1 clearly impressed. *uppermost Cambrian:* Argentina; England, Wales, *P. minor* Zone; Sweden, *P. minor–P. scarabaeoides* Zones; Canada (Nova Scotia, Quebec), *Peltura* Zone, (Newfoundland), Sunwaptan; China (Xinjiang, Zhejiang, Hunan, Anhui, Guizhou), *L. (L.) punctatus, L. (L.) hedini, H. regalis* Zones & zones correlated with them; Kazakhstan, *E. scrobicularis* Zone; USA (Vermont, Maryland), *upper Trempealeauan.* ——Fig. 218,1a,b. *L. (L.) trisectus* (Salter) *sensu* Westergård, 1922, Upper Cambrian (*Peltura minor* Zone), Sweden (Andrarum, Skåne); *a,* cephalon, SGU 127, ×7.2; *b,* pygidium, SGU 128, ×7.2 (new).——Fig. 218,1c. *L. (L.) trisectus* (Salter), Upper Cambrian (Merioneth Series, *Peltura scarabaeoides* Zone), northern Wales (Dolgellau); plastoholotype, pygidium, wax impression, BGS 8768, ×8 (new).

L. (Eolotagnostus) Zhou in Zhiqiang Zhou, Li, & Qu, 1982, p. 217 [*E. gansuensis;* OD; holotype (Zhiqiang Zhou, Li, & Qu, 1982, pl. 57, fig. 10), Tr 008, XIGMR, Beijing]. Cephalon weakly scrobiculate and pygidium nonscrobiculate; median preglabellar furrow absent or weakly developed. Glabella with long (sag.), semiovate to ogival anterior lobe; posterior lobe with F2 furrows angled slightly forward. Pygidial axis variably constricted across M2, with F1 impressed laterally and medially effaced. *uppermost Cambrian:* China (Gansu, Xinjiang, Zhejiang), *L. punctatus–Hedinaspis* Zone; Kazakhstan, *E. scrobicularis* Zone; Australia (Tasmania), Iverian.——Fig. 218,2a,b. *L. (E.) gansuensis* (Zhou), Upper Cambrian (Fengshanian), China (Gansu); *a,* paratype, cephalon, XIGMR Tr 007, ×5; *b,* holotype, pygidium, XIGMR Tr 008, ×5 (Zhiqiang Zhou, Li, & Qu, 1982, pl. 57, fig. 9–10).
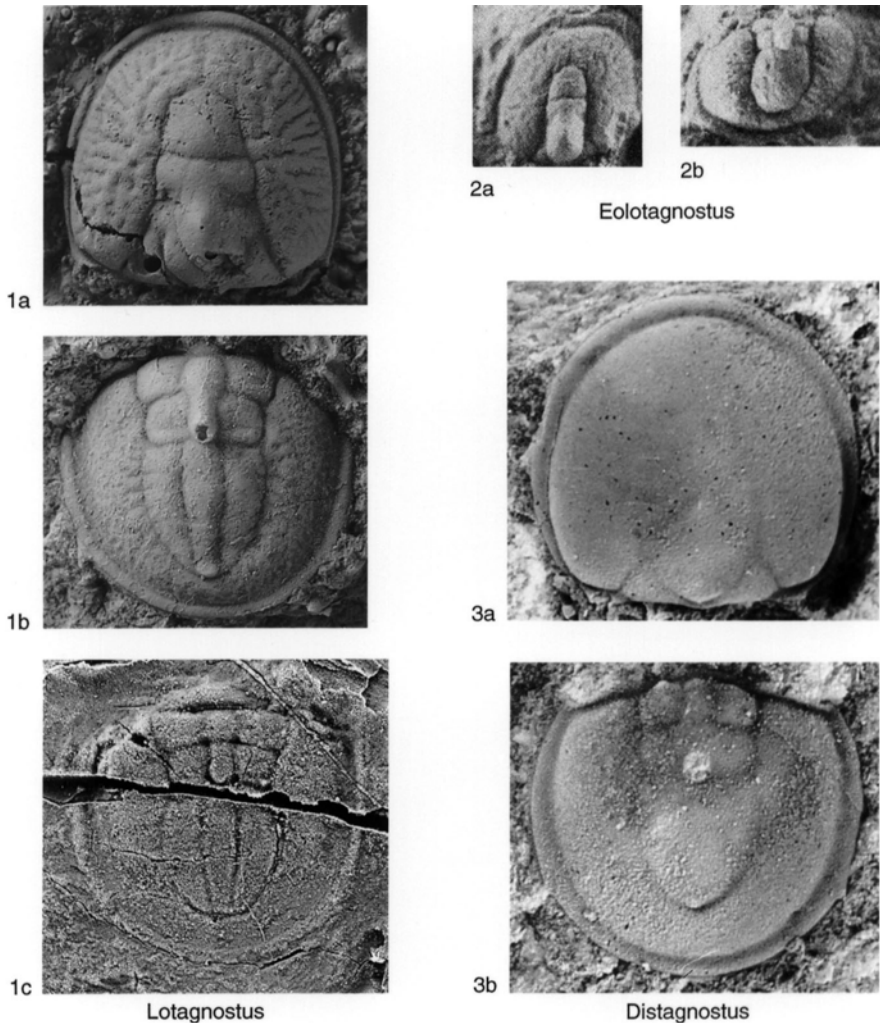
Fig. 218. Agnostidae (p. 341–342)

L. (**Distagnostus**) SHERGOLD, 1972, p. 17 [*D. ergodes;* OD; holotype (SHERGOLD, 1972, pl. 4, fig. 3), CPC 9667, AGSO, Canberra]. Exoskeleton largely effaced with only traces of axial furrows on both cephalon and pygidium. Pygidial axis weakly constricted across M2; F1 and F2 weakly impressed. *uppermost Cambrian:* Canada (Quebec); Argentina; Australia (Queensland), *R. bifax* or *N. denticulatus* to *R. clarki maximus* or *R. papilio* Zones; USA (Nevada), *S. pyrene* Zone.——FIG. 218,*3a,b.* **L. (D.) ergodes** (SHERGOLD), Upper Cambrian (Iverian, *Rhaptagnostus clarki maximus* or *R. papilio* Assemblage-Zone), western Queensland (Momedah anticline); *a,*

paratype, cephalon, CPC 9671, ×10; *b,* holotype, pygidium, CPC 9667, ×12 (Shergold, 1972, pl. 4, fig. 1–3).

Micragnostus HOWELL, 1935b, p. 233 [*Agnostus calvus* LAKE, 1906, p. 23; OD; lectotype (LAKE, 1906, pl. 2, fig. 18; SD FORTEY, 1980b, p. 23), A548, SM, Cambridge]. En grande tenue; nonscrobiculate; border furrows nondeliquiate; acrolobes unconstricted; median preglabellar furrow absent. Glabella with semiovate anterior lobe; F3 straight; posterior lobe parallel-sided with F2 weakly developed or absent; glabellar culmination broadly rounded; glabellar node level with or slightly behind F2. Basal lobes small. Pygidium

minutely bispinose; axis relatively short, unconstricted or weakly constricted over M2; M1 trilobate; F1 traversing axis; F2 well impressed, slightly deflected by axial node. Posterior lobe semiovate. Median postaxial furrow absent. *Upper Cambrian–Lower Ordovician (Arenig):* Wales, Spitsbergen, *Asaphellus–D. bifidus* Zones; Argentina, *N. argentina–K. meridionalis* Zones; Sweden, *M. dalecarlicus* Zone.——Fig. 219,*4.* *M. calvus* (Lake), Lower Ordovician (Tremadoc), northern Wales (Nant Rhos Ddu); lectotype, SM A548, ×10 (new).

Oncagnostus Whitehouse, 1936, p. 84 [*Agnostus hoi* Y. Sun, 1924, p. 28; OD; lectotype (Y. Sun, 1924, pl. 2, fig. 2c; SD X. Sun, 1989, p. 70), 515, NIGP, Nanjing]. En grande tenue; nonscrobiculate; usually with deliquiate border furrows in both shields. Median preglabellar furrow absent. Glabella with semiovate, subpentagonal, or subquadrate anterior lobe; F3 straight; posterior lobe usually short with F2 variably developed; axial node level with or slightly behind F2. Pygidium bispinose; F1 impressed only laterally, curving forward to articulating furrow to isolate subtriangular to ovate anterolateral lobes; F2 well developed. *Upper Cambrian (G. reticulatus Zone)–Lower Ordovician (K. meridionalis Zone).*

O. (Oncagnostus) [=*Eurudagnostus* Lermontova, 1951b, p. 7 (type, *E. grandis* Lermontova, 1951a, p. 8, pl. 2, fig. 1–4)]. Pygidial axis long (sag.), broad (tr.), and nearly parallel sided, with posterior lobe relatively broad. *Upper Cambrian (Glyptagnostus reticulatus to Peltura scarabaeoides Zones):* Sweden, *P. aciculata* Zone; Russia (Siberia), Kazakhstan, *P. pseudangustilobus* to *T. trisulcus* Zones; China (Hebei, Hunan, Liaoning), *Chuangia* to *L. bella* or *A. sinensis* Zones; South Korea, *Chuangia* to *Eochuangia* Zones; Australia (Queensland), *S. diloma* to *R. maximus* or *R. papilio* Zones; Antarctica (northern Victoria Land), *Dunderbergia* Zone; USA (Alaska, Montana, Wyoming, Nevada, Texas), *Aphelaspis* to *Elvinia* Zones; Canada (Newfoundland), Sunwaptan.——Fig. 219,*2a–c.* *O. (O.) hoi* (Sun), Upper Cambrian (Changshanian, *Changshania* Zone); *a,b,* China (Kushan, Changqingxian, Shandong); *a,* cephalon, NIGP 89034, *b,* pygidium, NIGP 89031, both ×10 (X. Sun, 1989, pl. 1, fig. 1–7); *c,* lectotype, pygidium, NIGP 515, China (Renzhuang, near Tangshan, Hebei), ×10 (Y. Sun, 1924, pl. 2, fig. 2c).——Fig. 219,*2d,e. O. (O.) tumidosus* (Hall & Whitafield), Upper Cambrian (Dresbachian, *Dunderbergia* Zone), USA (Eureka district, Nevada); *d,* plesiotype, cephalon, USNM 136831a, ×13; *e,* plesiotype, pygidium, USNM 136831b, ×13 (Palmer, 1960, pl. 4, fig. 1–2).

O. (Kymagnostus) Hohensee in Hohensee & Stitt, 1989, p. 861 [*K. harti;* OD; holotype (Hohensee & Stitt, 1989, fig. 3.1), 16666a, UMC, Columbia]. Cephalic border narrow; pygidial border wide, flattened. Pygidial axis long (sag.), broad (tr.), nearly parallel sided or expanding posteriorly, axial furrows commonly effaced around posterior lobe. *Upper Cambrian:* USA (Arkansas, Texas), *Elvinia* Zone.——Fig. 219,*1a,b.* *O. (K.) harti* (Hohensee), USA (Ouachita Mountains, Arkansas); *a,* holotype, cephalon, UMC 16666a, ×16, *b,* paratype, thoracopygon, UMC 16667, ×16 (Hohensee & Stitt, 1989, fig. 2–3.1).

O. (Strictagnostus) Shergold, 1975, p. 54 [*Geragnostus (Strictagnostus) chronius;* OD; holotype (Shergold, 1975, pl. 13, fig. 5), CPC 11732, AGSO, Canberra]. Cephalon anteriorly expanding with anteriorly tapering acrolobe. Pygidium posteriorly flared with posteriorly tapering, gently constricted acrolobe; short (sag.), posteriorly tapering pygidial axis, commonly slightly constricted at M2; posterior lobe short, semiovate, terminating well in advance of posterolateral spine bases. *Upper Cambrian–Lower Ordovician:* Australia (Queensland), *R. bifax* or *N. denticulatus* to *R. maximus* or *R. papilio* Zones; Argentina, Bolivia, *K. meridionalis* Zone; USA (Texas), *M. typicalis* Zone; South Korea, *Asaphellus* Zone; China (Anhui), Upper Cambrian; Afghanistan, Tremadoc; Kazakhstan, *T. trisulcus* Zone.——Fig. 219,*3a,b.* *O. (S.) chronius* (Shergold), Australia (Black Mountain, western Queensland); *a,* topotype, cephalon, CPC 11730, Upper Cambrian (Iverian, *Rhaptagnostus clarki maximus* or *R. papilio* Assemblage-Zone), ×15; *b,* holotype, pygidium, CPC 11732, Upper Cambrian (Iverian, *Rhaptagnostus bifax* or *Neoagnostus denticulatus* Assemblage-Zone), ×15 (Shergold, 1975, pl. 13, fig. 3, 5).

Trilobagnostus Harrington, 1938, p. 148 [*Agnostus innocens* Clark, 1923b, p. 122; OD; holotype (Ludvigsen, Westrop, & Kindle, 1989, pl. 1, fig. 25), 1697, MCZ, Cambridge] [=*Rudagnostus* Lermontova, 1951a, p. 7 (type, *A. princeps* var. *rudis* Salter, 1864b, p. 4, pl. 1, fig. 3)]. Nonscrobiculate; unconstricted acrolobes; median preglabellar furrow generally absent. Glabella with straight or gently posteriorly curved F3; short posterior lobe with F2 usually absent; glabellar node level with F2 furrows. Pygidium widest at M1; F1 generally only impressed laterally, curving forward to isolate lateral lobes; posterior lobe relatively long (sag.); posterolateral spines retral. *Upper Cambrian–Lower Ordovician (Tremadoc):* Wales, Sweden, Germany, Czech Republic, Poland, *P. acutidens* Zone–lower Tremadoc; Turkey, lower Tremadoc; China (Anhui, Guizhou, Hebei, Shanxi, Liaoning, Jilin, Zhejiang, Hunan), *L. punctatus* to *Yosimuraspis* Zones; South Korea, *"Dictyites"* Zone; Australia (Queensland), *R. maximus* or *R. papilio* Zone; Argentina, Bolivia, Colombia, *N. argentina* Zone; Mexico, *C. proavus* Zone; USA (Alaska, Montana, Nevada, Texas, Oklahoma, Vermont), *Saratogia* or *Drumaspis* to *C. proavus* Zones; Canada (Quebec, Newfoundland, British Columbia), Sunwaptan.——Fig. 217,*5.* *T. innocens* (Clark), uppermost Cambrian (Sunwap-

tan), Canada (Lévis, Quebec); holotype, pygidium, MCZ 1697, ×14 (Ludvigsen, Westrop, & Kindle, 1989).

Subfamily AMMAGNOSTINAE Öpik, 1967

[Ammagnostinae Öpik, 1967, p. 137]

Pygidium generally bispinose with broad, flattened border; pygidial axis long, broad, reaching border furrow, with long, expanded posterior lobe having well-developed secondary axial node in posterior half; F1 effaced or weakly impressed laterally, curving forward to intersect articulating furrow, isolating anterolateral lobes; F2 variably impressed and deflected by well-developed axial node. *upper Middle Cambrian–lower Upper Cambrian.*

Ammagnostus Öpik, 1967, p. 137 [**A. psammius;* OD; holotype (Öpik, 1967, pl. 66, fig. 3), CPC 5937, AGSO, Canberra]. En grande tenue or with pygidial axial furrows effaced posteriorly. Median preglabellar furrow absent. Glabella with ogival to subpentagonal anterior lobe; F3 straight or concave forward; a broad, anteriorly tapering posterior lobe with variably developed F2 furrow and broadly rounded glabellar culmination; glabellar node immediately behind F2 furrows. *Upper Cambrian.*

A. **(Ammagnostus)** [=*Glyptagnostus (Lispagnostus)* Öpik, 1967, p. 169 (type, *G. (L.) lenis;* OD); *Agnostoglossa* Öpik, 1967, p. 145 (type, *A. bassa;* OD)]. Pygidial axis usually weakly constricted across M2 and with F2 effaced or weakly impressed. *lower Upper Cambrian:* northern Greenland; Australia (Queensland), *E. eretes* to *G. stolidotus* Zones; Kazakhstan, *K. simplex* to *G. stolidotus* Zones; China (Zhejiang), *L. sinensis* Zone, (Hunan), *A. integriceps* or *Chatiania* Zone; ?USA (Montana), *Cedaria* Zone; ?Antarctica, *Aphelaspis* Zone.——Fig. 220,*2a,b. *A. (A.) psammius,* Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone); *a,* paratype, cephalon, CPC 5936, Australia (Boulia area, western Queensland), ×8; *b,* holotype, pygidium, CPC 5937, Australia (Duchess area, western Queensland), ×8 (new).

A. **(Tentagnostus)** X. Sun, 1989, p. 75 [**Pseudagnostus adchinensis* Schrank, 1975, p. 595; OD; holotype (Schrank, 1975, pl. 2, fig. 1), T934.1, HMB, Berlin]. Pygidial axis strongly constricted across M2 and with F2 strongly impressed. *lower Upper Cambrian (Changshanian):* China (Liaoning), *K. quadriceps* fauna.——Fig. 220,*1a,b. *A. (T.) adchinensis* (Schrank), Upper Cambrian (Changshanian), China (Saima, Fengchenxian, Liaoning); *a,* holotype, cephalon, HMB T934.1, ×13.5; *b,* paratype, pygidium, HMB T904.1, ×10.2 (Schrank, 1975, pl. 2, fig. 1, 4).

Formosagnostus Ergaliev, 1980, p. 92 [**F. formosus;* OD; holotype (Ergaliev, 1980, pl. 5, fig. 11), 1950/92, GMAN, Alma-Ata] [=*Kunshanagnostus* Qian & Zhou, 1984, p. 173 (type, *K. kunshanensis;* OD)]. En grande tenue, with deliquiate or subdeliquiate border furrow and narrow border in cephalon and poorly defined, deliquiate border furrow and broad, flattened border in pygidium. Median preglabellar furrow clearly developed. Glabella with ogival to subpentagonal anterior lobe; F3 bent backward; posterior lobe with well-developed F2 furrows, F1 furrows absent or weakly developed, broadly rounded glabellar culmination; glabellar node immediately behind F2 furrows. Pygidial axis with F1 only impressed laterally, curving forward to intersect articulating furrow and isolating small, subtriangular anterolateral lobes; F2 clearly impressed, deflected strongly backward by long, low axial node. *lower Upper Cambrian:* Antarctica; Kazakhstan, *K. simplex–G. reticulatus* Zones; Australia (Queensland), *E. eretes* Zone; China (Jiangsu, Liaoning).——Fig. 221*a,b. *F. formosus,* Upper Cambrian (Ajusokkanian), Kazakhstan (Lesser Karatau mountains); *a,* holotype, cephalon, GMAN 1950/92, *Kormagnostus simplex* Zone, ×8; *b,* paratype, pygidium, GMAN 1950/133, *Glyptagnostus stolidotus* Zone, ×7.5 (Ergaliev, 1980, pl. 5, fig. 11; pl. 8, fig. 12).

Hadragnostus Öpik, 1967, p. 102 [**H. las;* OD; holotype (Öpik, 1967, pl. 58, fig. 8), CPC 5861, AGSO, Canberra]. Cephalon and pygidium transverse; en grande tenue, with subdeliquiate border furrows and narrow border on cephalon and moderately wide border on pygidium. Median preglabellar furrow broad, short. Glabella relatively long with short (sag.), subtriangular to ogival anterior lobe; F3 straight; posterior lobe with weakly developed F2 and broadly rounded glabellar culmination; glabellar node absent. Pygidial axis tapering forward from middle of posterior lobe with constriction across M2 weak or absent; F1 and F2 furrows effaced. *lower Upper Cambrian:* Australia (Queensland), *E. eretes* to *A. quasivespa* Zones; Iran, *Drepanura* Zone; Canada (Northwest Territories), *Cedaria selwyni* to *C. brevifrons* Zones; USA (Montana), *Crepicephalus* Zone.——Fig. 220,*5. *H. las,* Upper Cambrian (Mindyallan, *Erediaspis eretes* Zone), Australia (Glenormiston district, western Queensland); holotype, pygidium, CPC 5861, ×16 (new).

?Kormagnostella E. Romanenko in Romanenko & Romanenko, 1967, p. 75 [**K. glabrata;* OD; holotype (Romanenko & Romanenko, 1967, pl. 1, fig. 22), 152/166, ZSGU, Novokuznetsk] [=*Litagnostoides* Schrank, 1975, p. 593 (type, *L. minutus;* OD)]. Diminutive, partly effaced, with deliquiate border furrow and narrow border in cephalon and subdeliquiate border furrow and wide, flat border in pygidium. Median preglabellar furrow absent. Glabella with anterior lobe effaced; F3 curved forward; posterior lobe with F1 and F2 furrows absent; glabellar culmination broadly rounded to obtusely angular; glabellar node posteriorly located. Py-
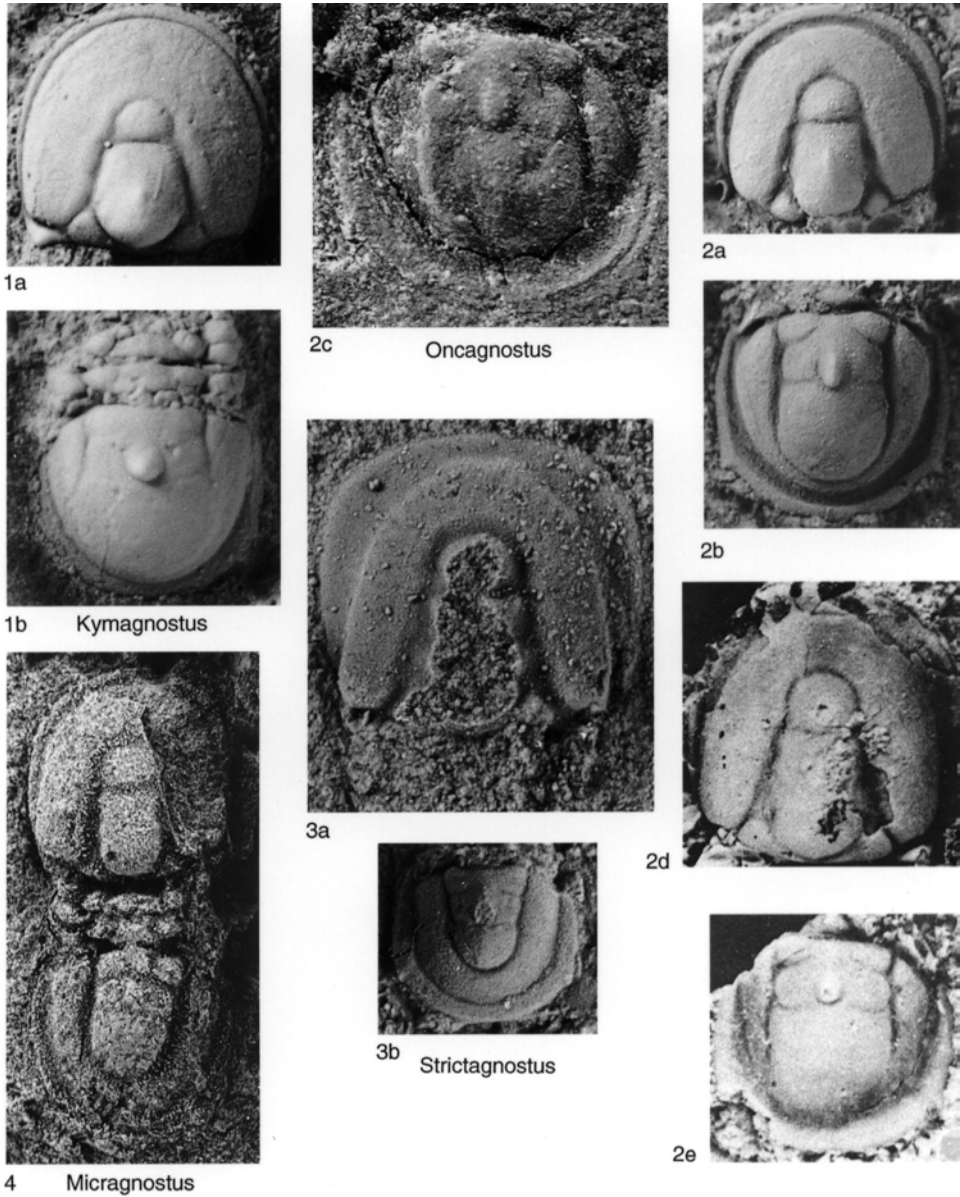
FIG. 219. Agnostidae (p. 343)

gidium nonspinose, axial furrows only impressed anteriorly, adjacent to M1 and anterior portion of M2. Axial node of moderate size. Weakly developed terminal node located adjacent to border furrow. *Upper Cambrian:* Russia (southern Siberia), Ayusokkanian–Sakian; China (Liaoning), *Kaolishania quadriceps* fauna; Australia (Queensland), *S. diloma* Zone.——FIG. 220,*6*. **K. glabrata,* Upper Cambrian (Ayusokkanian, *Glyptagnostus stolidotus*

Zone), southern Siberia (Altay Mountains); holotype, cephalothorax, ZSGU 152/153, and associated pygidium, ZSGU 152/166, ×9 (Romanenko & Romanenko, 1967, pl. 1, fig. 22–23).

Kormagnostus RESSER, 1938, p. 49 [**K. simplex;* OD; syntypes (RESSER, 1938, pl. 9, fig. 11–13), 94842, USNM, Washington, D.C.]. Anterior glabellar lobe effaced, with deliquiate border furrow in cephalon and poorly defined, deliquiate border furrow and
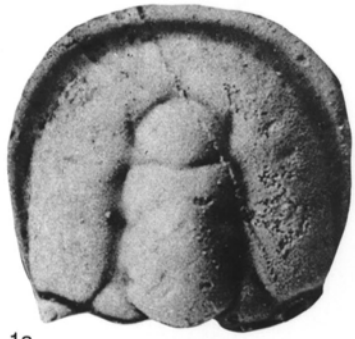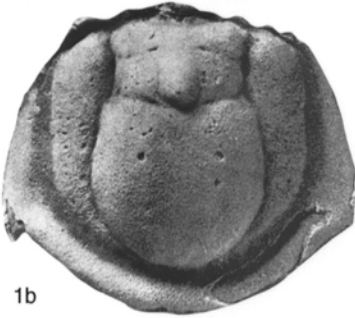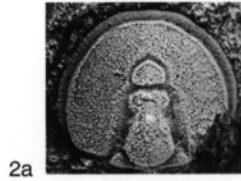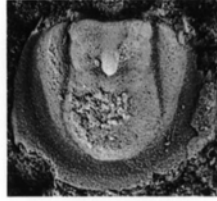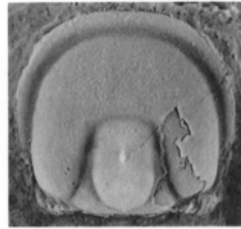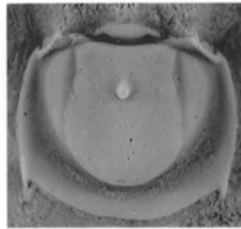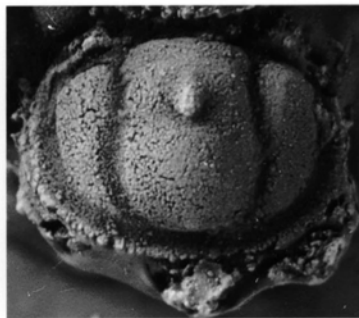
FIG. 220. Agnostidae (p. 344–347)

broad, flattened border in pygidium. Median preglabellar furrow absent. Glabella with straight F3; a broad, anteriorly tapering posterior lobe with weakly developed F2 furrows; a broadly rounded glabellar culmination; and with glabellar node immediately behind F2 furrows. Pygidial axis usually widest across posterior lobe with very slight constriction over M2; F1 and F2 effaced. *uppermost Middle Cambrian–lower Upper Cambrian:* northern Greenland; USA (Alabama, Georgia, Missouri, Montana, Nevada, Tennessee, Texas, Utah, Wyoming), *Bolaspidella* to *Crepicephalus* Zones; Canada (Quebec, Northwest Territories), *Cedaria minor-C. brevifrons* Zones; Argentina, *Bolaspidella* Zone; Australia (Queensland), *E. eretes* Zone, (Tasmania), *P. punctuosus* to *G. nathorsti* Zones; China (Hunan, Guizhou), *Paradamesops jimaensis* or *Cyclolorenzella* Zone; Kazakhstan, *K. simplex* Zone.——Fig. 220,*4a,b.* **K. simplex,* Upper Cambrian (Dresbachian), USA (Rogersville district, Tennessee); *a,* syntype, cephalon, USNM 94842a, ×10; *b,* syntype, pygidium, USNM 94842b, ×10 (new).——Fig. 220,*4c,d. K. seclusus* (Walcott, 1884b), uppermost Middle Cambrian (*Lejopyge laevigata* Zone), northern Greenland (Gustav Holm Dal, Peary Land); *c,* cephalon, MGUH 17.158, ×12; *d,* pygidium, MGUH 17.165, ×8 (Robison, 1988, fig. 11.7,13).

Proagnostus Butts, 1926, p. 76 [**P. bulbus;* OD; lectotype (Butts, 1926, pl. 9, fig. 12; SD Robison, 1988, p. 41, fig. 8.12), 94867, USNM, Washington, D.C.] [=*Agnostascus* Öpik, 1967, p. 147 (type, *A. gravis;* OD); *Agnostascus (Paragnostascus)* Peng, 1992, p. 85 (type, *A. (P.) sinensis;* OD)]. Cephalon narrow, trapeziform or semiovate; with nondeliquiate border furrows and with a narrow border in the cephalon and a wider, flattened border in the pygidium. Median preglabellar furrow well developed. Glabella with subquadrate to semiovate anterior lobe; F3 straight or bent strongly forward; posterior lobe with well-developed F2 furrows; glabellar culmination broadly rounded to obtusely angular; glabellar node in front of F2 furrows. Pygidial spines retral or advanced; axis with well-developed constriction across M2; F1 weakly impressed or effaced; F2 weakly impressed or absent, deflected posteriorly by strong axial node. *upper Middle Cambrian–lower Upper Cambrian:* northern Greenland; USA (Alabama), *Cedaria* Zone; Canada (Northwest Territories), *Cedaria minor* Zone; Australia (Queensland), *E. eretes* Zone, (Tasmania), *L. laevigata* Zone; China (Hunan, Guizhou), *Paradamesops jimaensis-Cyclolorenzella tuma* Zones, (Xinjiang), *Agnostascus orientalis (=Proagnostus orientalis)* Zone; Kazakhstan, *Kormagnostus simplex* Zone; Russia (Siberia), *L. laevigata* to *G. stolidotus* Zones.——Fig. 220,*3a–c.* **P. bulbus; a,* Upper Cambrian (Dresbachian), USA (Cedar Bluff, Alabama), lectotype, exoskeleton, USNM 94867, ×10 (Resser, 1938, pl. 10, fig. 17); *b,c,* latest Middle Cambrian (*Lejopye laevigata* Zone), northern Greenland (Gustav Holm Dal, Peary Land), *b,* pygidium, MGUH 17.128 and *c,* cephalon, MGUH 17.126, ×8 (Robison, 1988, fig. 8.14–15).

Formosagnostus
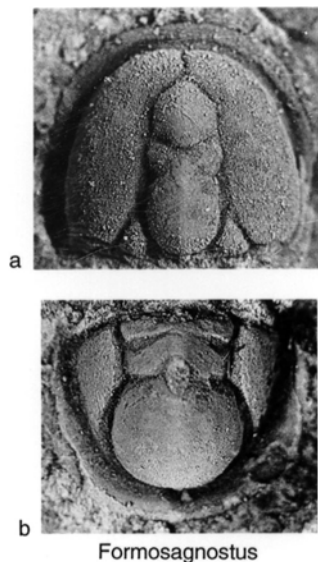
Fig. 221. Agnostidae (p. 344)

Subfamily GLYPTAGNOSTINAE Whitehouse, 1936

[Glyptagnostinae Whitehouse, 1936, p. 101]

Median preglabellar furrow well developed. Glabella with strong F2 furrow and broadly rounded culmination. Axiolobate pygidium with glyptagnostoid articulating device; secondary axial node developed in association with well-defined transverse depression occurring in rear of posterior lobe; median postaxial furrow well developed. *upper Middle Cambrian–lower Upper Cambrian.*

Glyptagnostus Whitehouse, 1936, p. 101 [**G. toreuma;* OD; =*Agnostus reticulatus* Angelin, 1851, p. 8; lectotype (SD Westergård, 1947, pl. 1, fig. 2), Ar 9794, RM, Stockholm] [=*Barrandagnostus* Ivshin in Khalfin, 1960, p. 166 (type, *B. barrandei;* OD)]. Of low convexity; both cephalon and pygidium strongly scrobiculate. Glabella with anterior lobe subpentagonal to subquadrate; commonly with median sulcus; F3 straight or bent forwards. Posterior lobe with very well-developed F1 furrow and with lateral portions of M2 separated from the midmost glabella by longitudinal (exsag.) furrows. Glabellar node located from midway between F1 and F2 to level of F2. Basal lobes large, triangular. Pygidial axis constricted across M2; M1 trilobate; F1 bent forward; M2 trilobate; axial node extending well on to posterior lobe. *lower Upper Cambrian (upper Mindyallan–lower Idamean):*
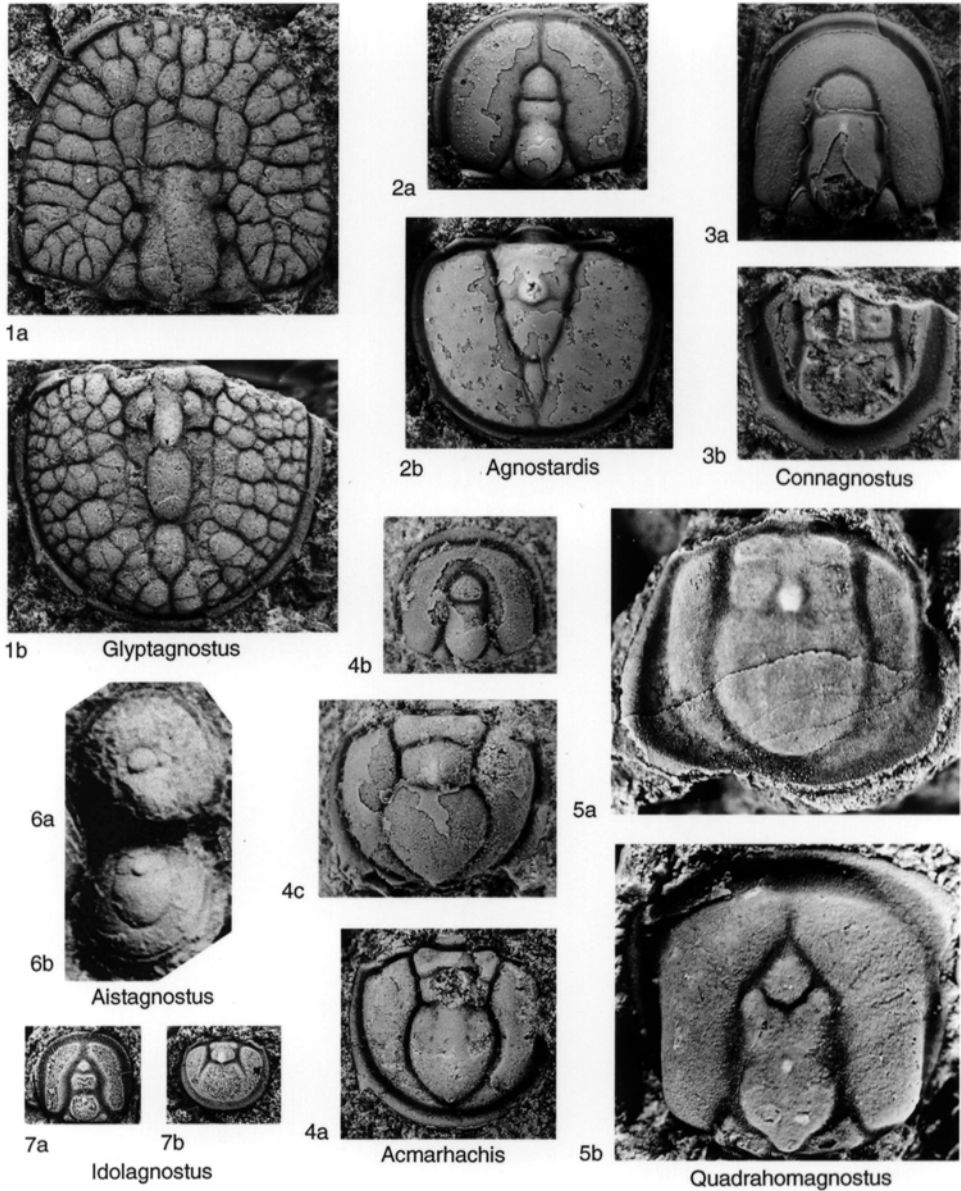
FIG. 222. Agnostidae (p. 348–350)

Cosmopolitan.——FIG. 222,*1a,b.* **G. reticulatus* (ANGELIN), Upper Cambrian (*Olenus* Zone), Sweden (Andrarum, Skåne); *a,* lectotype, cephalon, RM Ar 9794, ×8; *b,* paralectotype, pygidium of ANGELIN (1851), RM Ar 9796, ×8 (new).

Agnostardis ÖPIK, 1963, p. 39 [**A. amplinatis;* OD; holotype (ÖPIK, 1963, pl. 3, fig. 8), CPC 4270, AGSO, Canberra]. Nonscrobiculate or faintly scrobiculate. Glabella with anterior lobe ogival to

subpentagonal; F3 straight or bent backward; posterior lobe lacking F1; with glabellar node located midway between F1 and F2. Basal lobes of moderate size. Pygidial axis tapering posteriorly; F1 and F2 effaced; axial node moderately large. Posterior lobe subtriangular. *upper Middle Cambrian–lower Upper Cambrian:* Australia (Queensland), *G. stolidotus* Zone; China (Gansu, Guizhou), *L. laevigata* Zone.——FIG. 222,*2a,b.* **A. amplinatis,*

Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Wells Creek, Boulia area, western Queensland); *a,* paratype, cephalon, CPC 4265, ×8; *b,* holotype, pygidium, CPC 4270, ×8 (new).

Subfamily UNCERTAIN

Acmarhachis RESSER, 1938, p. 47 [**A. typicalis;* OD; holotype (RESSER, 1938, pl. 10, fig. 5), 94858, USNM, Washington, D.C.] [=*Cyclagnostus* LERMONTOVA, 1940, p. 126 (syntypes, *Cyclagnostus elegans* LERMONTOVA, 1940, p. 127, pl. 49, fig. 10, 10a); *Wanagnostus* QIU in QIU & others, 1983, p. 30 (type, *W. anhuiensis;* OD)]. Median preglabellar furrow weak or absent. Glabella with long ogival to subquadrate anterior lobe; F3 straight; posterior lobe with forwardly directed F2 furrows, occasionally joining to form chevronate furrow; glabellar node located from well behind F2 furrows to near apex of chevronate furrow; basal lobes of moderate to large size, triangular. Pygidium with agnostoid articulating device, axiolobate, strongly constricted across M2; broad, tumid posterior lobe bearing terminal node and sometimes intranotular axis. *Upper Cambrian:* USA (Alaska, Alabama, Nevada, Maryland, Vermont), *Crepicephalus* to *Dunderbergia* Zones; Canada (British Columbia, Northwest Territories), *Cedaria minor-C. brevifrons* Zones; Australia (Queensland), *D. torosa* or *A. janitrix* to *W. iota* or *R. apsis* Zones, (Tasmania), post-Idamean; Kazakhstan, *Kormagnostus simplex* Zone; Russia (Kharaulakh), *L. laevigata* to *P. pseudangustilobus* Zones; China (Zhejiang), *L. sinensis* Zone, (Anhui), zone uncertain.——FIG. 222,*4a–c. *A. typicalis; a,* Upper Cambrian (Dresbachian), USA (McCalla, Alabama), holotype, pygidium, USNM 94858, ×10 (new); *b,c,* Upper Cambrian (Dresbachian, *Crepicephalus* Zone), USA (McGill, Nevada), *b,* cephalon, USNM 143145a and *c,* pygidium, USNM 143145b, ×10 (Palmer, 1962a, pl. 2, fig. 12–13).

Aistagnostus XIANG & ZHANG, 1985, p. 68 [**A. laevigatus;* OD; holotype (XIANG & ZHANG, 1985, pl. 6, fig. 1a,b), T1415a, CAGC, Beijing]. Small, en grande tenue, with axial furrows weakly impressed and nondeliquiate border furrows. Anterior glabellar lobe short, broad, subpentagonal; posterior glabellar lobe short, broad, with median node at midlength; basal lobes simple. Median preglabellar furrow absent. Pygidial axis short, broad, posteriorly rounded, tripartite, with transverse furrows weakly impressed. Median postaxial furrow absent. Pygidial marginal spines small. Possibly belongs to Agnostinae. *Upper Cambrian (Changshanian):* China (Xinjiang), *Agnostotes tianshanicus* Zone.——FIG. 222,*6a,b. *A. laevigatus; a,* paratype, cephalon, CAGC T1415a, ×12; *b,* holotype, pygidium, CAGC T1415b, ×12 (Xiang & Zhang, 1985, pl. 6, fig. 1a,b).

Connagnostus ÖPIK, 1967, p. 128 [**C. venerabilis;* OD; holotype (ÖPIK, 1967, pl. 54, fig. 11a,b), CPC 5809, AGSO, Canberra]. Nonscrobiculate, with nondeliquiate to deliquiate border furrow and narrow border in cephalon; deliquiate border furrow and broad, flattened border in pygidium; cephalic acrolobe unconstricted and pygidial acrolobe unconstricted to weakly constricted; median preglabellar furrow absent. Glabella with semicircular to semiovate anterior lobe; F3 bent slightly forward; F2 weakly developed; glabellar culmination rounded; glabellar node elongate, keel-like, extending from level with F2 nearly to F3; basal lobes of moderate size. Pygidial axis long, broad, extending to or nearly to border furrow, with very weak constriction over M2; F1 clearly impressed, deflected forward by anterior end of axial node; F2 nearly straight, deflected by axial node. Axial node well defined, elongate, ovate. [Possibly an Ammagnostinae or a diplagnostid.] *lower Upper Cambrian:* Australia (Queensland), *A. quasivespa* to *G. stolidotus* Zones; Canada (Northwest Territories), *Cedaria brevifrons* Zone; USA (Alabama), *Glyptagnostus stolidotus* Zone; Russia (Siberia), Nganasan Gorizont.——FIG. 222,*3a,b. *C. venerabilis,* Upper Cambrian (Mindyallan, *G. stolidotus* Zone), Australia (Glenormiston district, western Queensland); *a,* paratype, cephalon, CPC 5812, ×8; *b,* holotype, pygidium, CPC 5809, ×8 (new).

?Idolagnostus ÖPIK, 1967, p. 104 [**I. agrestis;* OD; holotype (ÖPIK, 1967, pl. 60, fig. 8), CPC 5766, AGSO, Canberra]. Small; nonscrobiculate; median preglabellar furrow well developed to absent. Glabella with small, triangular to ogival anterior lobe; F3 well developed and nearly straight; F2 usually well developed as transglabellar furrow, straight or curved forward; glabellar node a short distance behind F2 furrow; glabellar culmination elevated, broadly rounded to obtusely angular; basal lobes of moderate size. Pygidium nonspinose; axis long, strongly constricted across M2; F1 clearly impressed, curved forward; F2 clearly impressed, deflected rearward by axial node; posterior lobe expanded, subcircular, extending to or nearly to border furrow; with or without small terminal node. [Possibly belongs within Diplagnostidae, Pseudagnostinae; unassigned because of configuration of glabellar furrows and greatly expanded posterior lobe of pygidial axis.] *Upper Cambrian:* Australia (Queensland), Mindyallan–Idamean (*E. eretes* to *S. diloma* Zones); China (Qinghai), lower Upper Cambrian.——FIG. 222,*7a,b. *I. agrestis,* Upper Cambrian (Mindyallan, *G. stolidotus* Zone), Australia (Selwyn Range district, western Queensland); *a,* holotype, cephalon, CPC 5766, ×8; *b,* paratype, pygidium, CPC 5872, ×8 (new).

Quadrahomagnostus CHU, 1959, p. 91 [**Homagnostus (Quadrahomagnostus) subquadratus;* OD; holotype (CHU, 1959, pl. 1, fig. 21), 9429, NIGP, Nanjing]. Nonscrobiculate; median preglabellar furrow very weak to absent. Glabella with small to moderate-sized, subrhombic to subcircular anterior lobe; F3 curved strongly rearward; F2 effaced or weakly impressed, crossing glabella, and curved forward; glabellar node immediately behind F2 furrow; glabellar culmination narrowly rounded to angular; basal

lobes of moderate to large size. Pygidial axis long, parallel-sided or expanding slightly rearwards, nearly reaching border furrow. [Unassigned because of glabellar characteristics.] *lower Upper Cambrian:* China (Henan, Liaoning), *B. paronai* to *D. premesnili* Zones.——Fig. 222,*5a,b. Q. subquadratus* (Zhu), Upper Cambrian (Gushanian); *a,* paratype, pygidium, NIGP 9431, China (Wutingshan, Yentai, Liaoning), *Drepanura premesnili* Zone, ×10; *b,* holotype, cephalon, NIGP 9429, China (Yaobao, Tienshihfu, Liaoning), *Blackweldleria paronai* Zone, ×10 (Chu, 1959, pl. 1, fig. 21, 23).

Family PTYCHAGNOSTIDAE Kobayashi, 1939

[Ptychagnostinae Kobayashi, 1939a, p. 151] [=Triplagnostinae Kobayashi, 1939a, p. 145; Lejopyginae Harrington in Kobayashi, 1939a, p. 128; Tomagnostinae Kobayashi, 1939a, p. 148; Canotagnostidae Rusconi, 1951, p. 13]

Usually en grande tenue, with nondeliquiate border furrows and unconstricted acrolobes; usually with median preglabellar furrow and elongate basal lobes; axial glabellar node variable in position. Pygidium usually simplimarginate, rarely weakly zonate, nonspinose or bispinose; with basic articulating device; axiolobate with F1 furrow well developed, F2 furrow rarely absent; posterior axial lobe usually long, acuminate or rounded posteriorly, occasionally with a transverse depression in anterior half; median postaxial furrow usually present. *Middle Cambrian–lower Upper Cambrian.*

Ptychagnostus Jaekel, 1909, p. 401 [*Agnostus punctuosus* Angelin, 1851, p. 8; OD (publication date discussed by Shergold & Laurie, 1991); lectotype (SD Westergård, 1946, p. 78, pl. 12, fig. 3a,b), Ar 9539, RM, Stockholm]. Scrobiculate; prosopon finely granulose or pustulose. Anterior glabellar lobe semiovate; posterior glabellar lobe evenly convex, with F2 furrows well developed, glabellar node slightly behind to slightly in front of F2 furrow; basal lobes divided or entire. Pygidium nonspinose; axis with small node on M2; median postaxial furrow present. *Middle Cambrian:* Argentina; China (Liaoning); Sweden, Denmark, Norway, uppermost *H. parvifrons* to *P. punctuosus* Zones; Australia (Queensland), *P. punctuosus* to *D. notalibrae* Zones; Kazakhstan, *P. punctuosus* Zone; Russia (Siberian Platform), *A. henrici* Zone; England, Canada (Newfoundland), *P. davidis* Zone; USA (Utah, Nevada), *A. atavus* to *P. punctuosus* Zones, (New York), *Bolaspidella* Zone.——Fig. 223,*1a,b. *P. punctuosus* (Angelin), Middle Cambrian (*Ptychagnostus punctuosus* Zone), Sweden (Andrarum, Skåne); *a,* lectotype, cephalon, RM Ar 9539, ×8; *b,* paralectotype, pygidium, RM Ar 9540, ×8 (new).

Acidusus Öpik, 1979, p. 100 [*Ptychagnostus (Acidusus) acidusus;* OD; holotype (Öpik, 1979, pl. 46, fig. 2–3), CPC 14248, AGSO, Canberra] [=?*Canotagnostus* Rusconi, 1951, p. 13 (type, *C. huarpeanus;* OD)]. Commonly scrobiculate; prosopon smooth or pustulose; nonspinose or with cephalic spines, axial spine on posterior thoracic segment, and pygidial marginal spines. Anterior glabellar lobe ogival, semiovate or trapeziform; posterior glabellar lobe tapering strongly anteriorly, evenly convex to slightly posteriorly inflated, with F2 furrows well developed; glabellar node located slightly in front of F1 furrows; basal lobes divided or entire. Pygidial axis with moderate to large, elongate node on M2 strongly deflecting F2 furrow; posterior lobe long, with or without small terminal tubercle; median postaxial furrow occasionally absent. *Middle Cambrian:* Sweden, *T. fissus* or *A. atavus* Zone; Sweden, Norway, Denmark, *S. brachymetopa* Zone; Australia (Queensland), *A. atavus* to *A. cassis* Zones, (Tasmania), *A. cassis* or *P. agra* Zone; Kazakhstan, *A. atavus* Zone, beds with *Pianaspis recta;* Russia (Siberian Platform), *T. fissus, A. henrici, L. allachjunensis* Zones, (Altay-Sayan), *A. limbataeformis* Zone; USA (Alaska), *Bolaspidella* Zone, (Utah), *B. fimbriatus* to *B. contracta* Subzones; China (Zhejiang, Hunan), *P. atavus* to *L. armata* Zones, (Guizhou), zone uncertain.——Fig. 223,*2. *A. acidusus* (Öpik), Middle Cambrian (Undillan, *Doryagnostus notalibrae* Zone), Australia (northwestern Mt. Isa district, western Queensland); holotype, exoskeleton, CPC 14248, ×9 (new).

Goniagnostus Howell, 1935c, p. 13 [*Agnostus nathorsti* Brögger, 1878, p. 68; OD; holotype (Brögger, 1878, pl. 5, fig. 1), not traced, PMO, Oslo] [=?*Huarpagnostus* Rusconi, 1950b, p. 92 (type, *H. costatus;* OD)]. Usually scrobiculate; spinose, with or without cephalic spines and occipital spine, with axial spine and fulcral spines on the posterior thoracic segment and pygidial marginal spines. Anterior glabellar lobe depressed, subtriangular; posterior glabellar lobe broad, very strongly convex in posterior half, with F2 furrows very well developed; axial glabellar node located behind F1 furrows; basal lobes divided or entire, anterior extremities indistinct, associated with a well-developed apodemal pit. Pygidial axis with spine on M2 strongly deflecting F2 furrow rearward; posterior lobe with strong tubercle near midlength, centered on a variably developed rosette; median postaxial furrow well developed. *Middle Cambrian–lower Upper Cambrian.*

G. (Goniagnostus). Cephalon without arcuate scrobicules. Posterior lobe of pygidial axis with rosette weakly developed or absent. *upper Middle Cambrian:* Sweden, Norway, Denmark, *L. lundgreni* or *G. nathorsti* to *S. brachymetopa* Zones; Australia (Northern Territory, Queensland), *P. punctuosus* to *G. nathorsti* Zones; England, ?late *P. davidis* Zone; Canada (New Brunswick, Newfoundland), *P. hicksi* Zone; Turkestan Mountain Range, *H. brevifrons* beds; Russia (Siberian Platform), *A. henrici* to *L. laevigata* or *A. truncata* Zones. *Middle*
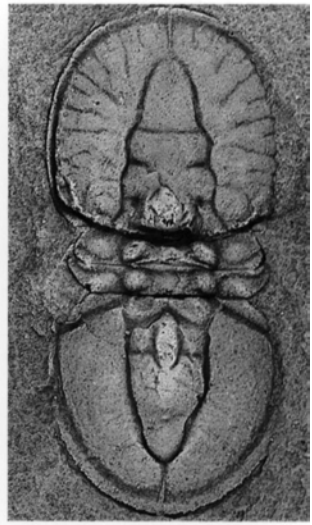
FIG. 223. Ptychagnostidae (p. 350–352)

Cambrian: China (Qinghai); Argentina.——Fig. 223,*3a–c* . *G. (G.) nathorsti* (Brögger), Middle Cambrian (*Goniagnostus nathorsti* Zone); *a*, exoskeleton, PMO 19887, Norway (Krekling, Oslo district), ×8 (new); *b,c,* Sweden (Baskemölla, Skåne), *b*, cephalon, SGU 4957, ×8, *c*, pygidium, SGU 4958, ×8 (new).

G. (**Allobodochus**) Öpik, 1979, p. 144 [*Ptychagnostus (G.) fumicola* Öpik, 1961b, p. 81; OD; holotype (Öpik, 1961b, pl. 20, fig. 14a,b), CPC 3598, AGSO, Canberra]. Cephalon lacking arcuate scrobicules; glabella with very strongly developed F1 and F2 furrows, commonly with the midmost glabella separated from the outer glabella by weak longitudinal (exsag.) furrows. Posterior pygidial axial lobe with very well developed rosette. *upper Middle Cambrian–lower Upper Cambrian:* Sweden, England, *L. laevigata* Zone; Australia (Queensland, Tasmania), *A. cassis* to *E. eretes* Zones; Kazakhstan, *?G. nathorsti* to *L. armata* Zones, *L. laevigata* Zone, early *K. simplex* Zone; China (Hunan, Guizhou), *P. jimaensis* or *C. tuma* Zone, (Zhejiang), *P. triangularis* to *L. sinensis* Zones.——Fig. 223,*4a.* *G. (A.) fumicola* (Öpik), Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Tobermory area, Northern Territory); holotype, pygidium, CPC 3598, ×8 (new).——Fig. 223,*4b.* *G. (A.) spiniger* (Westergård), Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Tobermory area, Northern Territory); paratype, cephalon, CPC 14342, ×8 (new).

G. (**Criotypus**) Öpik, 1979, p. 144 [*G. (C.) oxytorus;* OD; holotype (Öpik, 1979, pl. 57, fig. 1–2), CPC 14309, AGSO, Canberra]. Cephalon with well-developed, arcuate scrobicules. Posterior lobe of pygidial axis with rosette usually absent, rarely weakly developed. *Middle Cambrian:* Australia (Queensland), *A. atavus* to *E. opimus* Zones.——Fig. 223,*5a.* *G. (C.) lemniscatus,* Middle Cambrian (Floran, *Euagnostus opimus* Zone), western Queensland (Camooweal area), holotype, cephalon, CPC 14311, ×8 (new).——Fig. 223,*5b.* *G. (C.) oxytorus,* Middle Cambrian (Floran, *Acidusus atavus* Zone), western Queensland (Camooweal area), holotype, exoskeleton, CPC 14309, ×8 (new).

Lejopyge Hawle & Corda, 1847, p. 51 [*Battus laevigatus* Dalman, 1828, p. 136; OD; lectotype (SD Westergård, 1946, p. 134, pl. 13, fig. 21a,b), Ar 287b, RM, Stockholm] [=*Miagnostus* Jaekel, 1909, p. 401 (type, *Battus laevigatus* Dalman, 1828, *sensu* Jaekel, 1909, p. 401, fig. 21); *Pseudophalacroma* Pokrovskaya, 1958, p. 79 (type, *P. creba* Pokrovskaya, 1958, p. 79, pl. 3, fig. 4–6)]. Strongly convex, with very narrow cephalic border; en grande tenue to largely effaced; uncommonly scrobiculate; prosopon smooth; variably spinose. Anterior glabellar lobe narrow, subtriangular; posterior glabellar lobe with F2 furrows usually absent; glabellar node midway between F1 and F2; basal lobes small, simple. Pygidial axis with small node

on M2 slightly deflecting F2 furrow rearward. *upper Middle Cambrian:* Sweden, Norway, Denmark, *P. punctuosus* to *L. laevigata* Zones; Australia (Queensland, Tasmania), *P. punctuosus* to *C. quasivespa* Zones; England, *P. forchhammeri* Zone; Kazakhstan, Uzbekistan, *L. armata* to *L. laevigata* Zones, *H. brevifrons* beds; Russia (Siberian Platform), *L. lundgreni* Subzone to *L. laevigata* or *A. truncata* Zone; China (Zhejiang), *P. triangularis* to *L. sinensis* Zones, (Guizhou), *L. laevigata,* Zone, (Hunan), *L. laevigata, Paramphoton* Zone; USA (New York), *Bolaspidella* Zone, (Utah, Nevada), *P. punctuosus* to *L. laevigata* Zones; Greenland, *L. laevigata* Zone; Canada (Newfoundland, Northwest Territories), *Cedaria minor* Zone. *Middle Cambrian:* Alaska; China (Qinghai); ?Argentina.——Fig. 224,*5a,b.* *L. laevigata* (Dalman), Middle Cambrian (*Lejopyge laevigata* Zone), Sweden (Kinnekulle, Västergötland); *a*, paralectotype, pygidium, RM Ar 287a, ×12; *b*, lectotype, cephalon, RM Ar 287b, ×12 (new).

Myrmecomimus Öpik, 1979, p. 136 [*M. tribulis;* OD; holotype (Öpik, 1979, pl. 36, fig. 1, 1a, 2), CPC 14179, AGSO, Canberra]. Small; strongly convex; en grande tenue or with anterior glabellar lobe, median preglabellar furrow, and median postaxial furrow effaced; nonscrobiculate; nonspinose or with short cephalic spines. Posterior glabellar lobe very strongly convex, subhexagonal or subcircular, lateral glabellar furrows absent; basal lobes elongate, entire. Thorax nonspinose. Pygidial axis usually short, with very strongly inflated M2 and posterior lobe. *Middle Cambrian:* Australia (Queensland), *P. punctuosus* to *D. notalibrae* Zones; Russia (Siberian Platform), *Pseudanomocarina* Zone.——Fig. 223,*6.* *M. tribulis,* Middle Cambrian (Undillan, *Doryagnostus notalibrae* Zone), Australia (northwestern Mt. Isa, western Queensland); holotype, exoskeleton, CPC 14179, ×9 (new).

Onymagnostus Öpik, 1979, p. 107 [*O. angulatus;* OD; =*Agnostus gibbus* var. *hybridus* Brögger, 1878, p. 62; lectotype herein designated (Brögger, 1878, p. 62), 28906, PMO, Oslo] [=*Onymagnostus (Agnostonymus)* Öpik, 1979, p. 114 (type, *O. (A.) semiermis;* OD)]. Usually en grande tenue; very strongly convex, particularly in the pygidium; borders in both shields moderately wide; axial furrows variably impressed; median postaxial furrow absent; uncommonly scrobiculate; nonspinose or with very small pygidial marginal spines. Anterior glabellar lobe low, semiovate; posterior glabellar lobe evenly convex, with F2 furrows weak to well developed; glabellar node a short distance behind F2 furrows; basal lobes short to slightly elongate, entire, commonly indistinct anteriorly. Pygidial axis very long, with large node on M2 strongly deflecting F2 furrow; posterior lobe very long, semiovate to subtriangular, narrowly rounded posteriorly. *Middle Cambrian:* Sweden, Norway, Denmark, *T. fissus* or *A. atavus* to *L. lundgreni* or *G. nathorsti* Zones; Australia (Queensland, Northern Territory), late *T. gibbus* to *G. nathorsti* Zones, (Tasmania), *P. punctuosus* or *G. nathorsti* Zone; England, Wales, *P.*

1a Pentagnostus

1b

2a

2b Onymagnostus

3a

3b

Tomagnostus

4b

4a Zeteagnostus

5a Lejopyge

5b
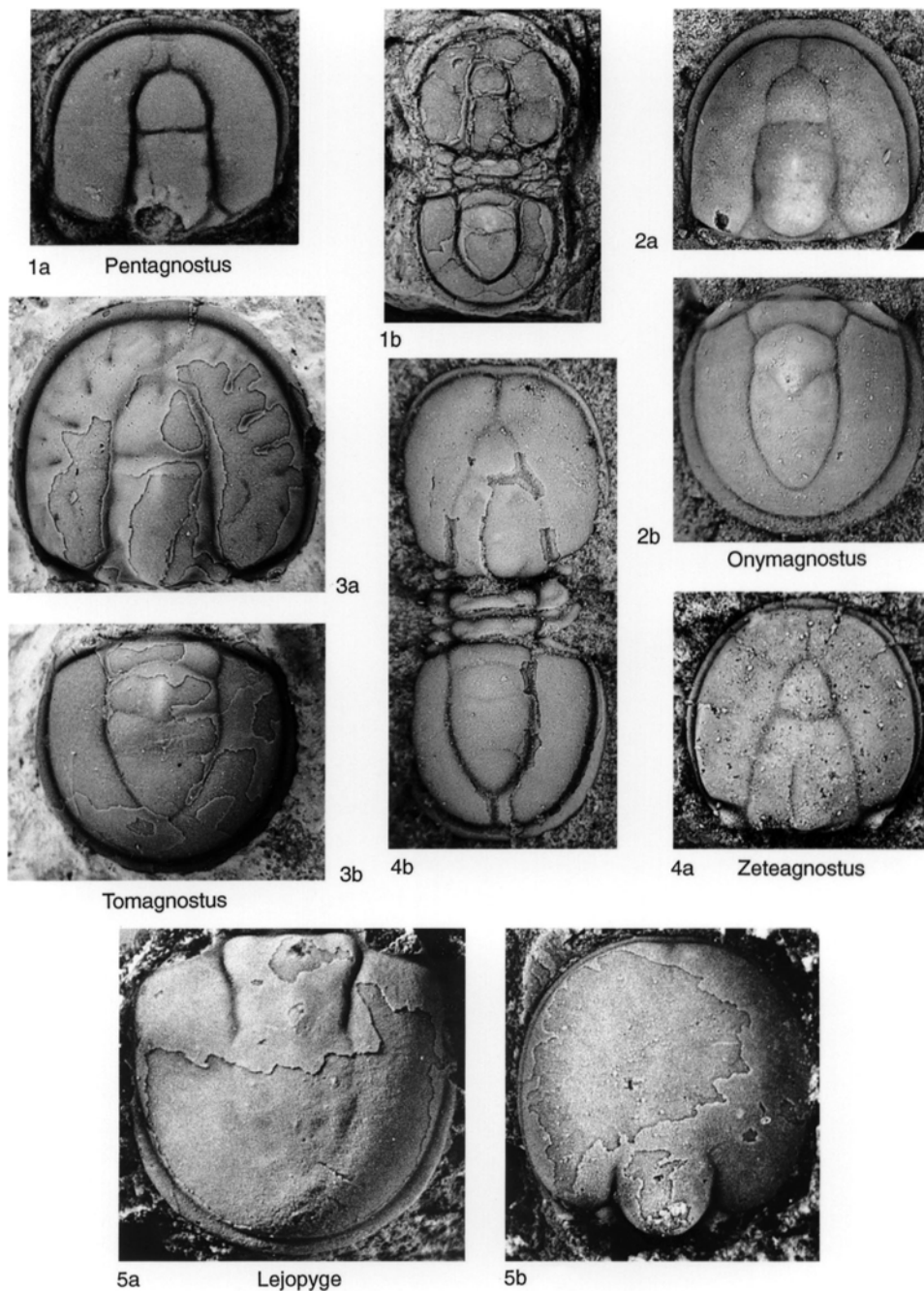
FIG. 224. Ptychagnostidae (p. 332-355).

aurora to early *P. davidis* Zone; Canada (Newfoundland, New Brunswick), *P. hicksi* to *P. forchhammeri* Zones; Russia (Siberian Platform), ?*Kounamkites*

Zone, *T. fissus* or *P. hicksi* to *A. limbataeformis* Zones; Kazakhstan, Uzbekistan, *Pseudanomocarina* Zone; Czechoslovakia, *E. pusillus* Zone; USA

(Utah), *T. gibbus* Zone, *B. contracta* Subzone.——Fig. 224,*2a,b*. **O. hybridus* (Brögger), Middle Cambrian (*Ptychagnostus punctuosus* Zone), Norway (Krekling, Oslo district); *a,* cephalon, PMO 28088, ×7.5 (new); *b,* lectotype (here chosen), pygidium, PMO 28096, original syntype of Brögger (1878, pl. 5, fig. 4b), ×7.5 (new).

Pentagnostus Lermontova, 1940, p. 127 [**P. anabarensis;* OD; lectotype (Lermontova, 1940, pl. 35, fig. 10c; SD Shergold, Laurie, & Sun, 1990, p. 41), 56/9182, CNIGR, St. Petersburg]. Median preglabellar furrow variably developed; median postaxial furrow weak or absent; rarely scrobiculate; nonspinose or with small pygidial marginal spines. Anterior glabellar lobe long, semiovate; posterior glabellar lobe with subparallel sides, evenly convex or slightly inflated posteriorly with F2 furrows weakly to moderately well developed; axial glabellar node located midway between F1 and F2 furrows; basal lobes short or slightly elongate, entire. Pygidial axis with small node on M2 slightly deflecting F2 furrow. *lower Middle Cambrian:* Antarctica (Shackleton Range); Sweden, Norway, *P. insularis* to *T. gibbus* Zones; England, *P. pinus* Zone; Australia (Northern Territory, New South Wales), *T. gibbus* Zone; Russia (Siberian Platform), *Kounamkites* to *T. fissus* Zones, (Altay-Sayan), zone uncertain; Canada (British Columbia), *Bathyuriscus-Elrathina* Zone.——Fig. 224,*1a,b*. **P. anabarensis,* Middle Cambrian (Amgaian, *Triplagnostus gibbus* Zone), Russia (Anabar River, Yakutia); *a,* paralectotype, exoskeleton, CNIGR 53/9182, ×10; *b,* lectotype, cephalon, CNIGR 56/9182, ×10 (Lermontova, 1940, pl. 35, fig. 10, 10c).

Tomagnostus Howell, 1935c, p. 15 [**Agnostus fissus* Lundgren in Linnarsson, 1879, p. 23; OD; neotype (SD Westergård, 1946, pl. 7, fig. 22), 4840, SGU, Uppsala]. Usually scrobiculate; borders of moderate width; nonspinose or with small pygidial marginal spines. Median preglabellar furrow commonly weakly developed. Anterior glabellar lobe subquadrate to semiovate, usually sulcate; posterior glabellar lobe usually with well-developed F2 furrows. Axial glabellar node elongate, from a short distance behind to in front of F2 furrows; basal lobes slightly elongate, commonly indistinct anteriorly. Pygidial axis with well-developed F2 furrows; moderate to small node on M2; posterior lobe with well-developed transverse depression near midlength; median postaxial furrow rarely present. Weak, narrow (sag.) pygidial collar present in some specimens. *Middle Cambrian:* USA (South Carolina); Sweden, Denmark, England, *T. gibbus* to *H. parvifrons* Zones; Russia (Siberia), *Kounamkites, Pseudanomocarina, T. fissus-P. hicksi* to *A. henrici* Zones; Canada (Newfoundland), *P. hicksi* to *P. davidis* Zones; Czechoslovakia, *E. pusillus* Zone; Australia (Northern Territory), *?A. atavus* Zone.——Fig. 224,*3a,b*. **T. fissus* (Lundgren), Middle Cambrian (*Triplagnostus gibbus* Zone), Sweden (south of Brantevik, Skåne); *a,* neotype, cephalon, SGU 4840, ×9; *b,* topotype, pygidium, SGU 4839, ×9 (new).

Triplagnostus Howell, 1935c, p. 14 [**Agnostus gibbus* Linnarsson, 1869, p. 81; OD; types not identified]. Rarely scrobiculate; spinose. Median preglabellar furrow well developed. Anterior glabellar lobe subtriangular, semiovate or subpentagonal. Posterior glabellar lobe strongly convex in entirety or only in posterior half, with axial glabellar node located level with F1 furrows; basal lobes divided or entire. Pygidial axis with spine or large node on M2 deflecting F2 furrow rearward. Median postaxial furrow well developed or absent. *Middle Cambrian.*

T. (Triplagnostus) [=*Solenagnostus* Whitehouse, 1936, p. 86 (type *Agnostus longifrons* Nicholas, 1916, p. 453, pl. 39, fig. 1); *T. (Aristarius)* Öpik, 1979, p. 125 (type, *T. (A.) aristarius;* OD)]. Anterior glabellar lobe low, subtriangular to semiovate; posterior glabellar lobe very strongly convex in posterior half; F2 furrows variably developed. Pygidial axis with spine or large node on M2 strongly deflecting F2 furrow rearward; posterior axial lobe long, semiovate to subtriangular, usually with small median tubercle near midlength. *Middle Cambrian:* England; Poland; Antarctica; Canada (Newfoundland); Sweden, Norway, Denmark, *T. gibbus* to *T. fissus* or *A. atavus* Zones; Australia (Queensland), *T. gibbus* to *G. nathorsti* Zones; Russia (Siberian Platform), upper *Kounamkites, T. gibbus, T. fissus, Pseudanomocarina* Zones; Kazakhstan, lower *A. atavus* Zone; USA (New York), *Bathyuriscus-Elrathina* Zone, (Utah, Nevada), *T. gibbus* Zone.——Fig. 225,*1a,b*. **T. (T.) gibbus* (Linnarsson), Middle Cambrian (*Triplagnostus gibbus* Zone), Exsulans Limestone; *a,* cephalon, SGU 4891, Sweden (Brantevik, Skåne), ×8; *b,* pygidium, SGU 4890, Sweden (Andrarum, Skåne), ×8 (new).

T. (Aotagnostus) Öpik, 1979, p. 133 [**A. culminosus;* OD; holotype (Öpik, 1979, pl. 34, fig. 1), CPC 14166, AGSO, Canberra]. Anterior glabellar lobe slightly to strongly inflated, subtriangular to subpyriform; posterior glabellar lobe short, tapering forward, very strongly convex with F2 furrows very weak to absent. Pygidial axis with large spine or node on gibbous M2 strongly deflecting F2 furrow; posterior lobe of short or moderate length, semiovate; median postaxial furrow well developed. *upper Middle Cambrian:* Australia (Queensland), *E. opimus* to *G. nathorsti* Zones.——Fig. 225,*2*. **T. (A.) culminosus* (Öpik), upper Middle Cambrian (Undillan, *Doryagnostus notalibrae* Zone), Australia (northwest of Mt. Isa, western Queensland); holotype, exoskeleton, CPC 14166, ×9 (new).

Zeteagnostus Öpik, 1979, p. 105 [**Z. incautus*; OD; holotype (Öpik, 1979, pl. 45, fig. 1), CPC 14242, AGSO, Canberra]. Commonly scrobiculate. Anterior glabellar lobe subtriangular; posterior glabellar lobe evenly convex with F2 furrows weakly developed or absent and with axial glabellar node from a short distance in front of F1 furrow to a short distance behind F2 furrow; basal lobes divided or en-

tire, variably distinct. Pygidial axis with F2 furrow straight or slightly deflected rearward; median postaxial furrow present. *Middle Cambrian:* Australia (Queensland), *A. atavus* to *E. opimus* Zones; ?Sweden, *T. fissus* or *A. atavus* Zone; Russia (Siberia), *T. gibbus* or *T. fissus* Zone; Kazakhstan, *Z. intermedius* Zone (*sensu* ROBISON, 1984, p. 20); USA (Utah), *T. gibbus* Zone; China (Liaoning, Shandong), Canada (Newfoundland), lower Middle Cambrian.——FIG. 224,4a,b. *Z. incautus,* Middle Cambrian (Floran, *Acidusus atavus* Zone), Australia (northwest of Mt. Isa, western Queensland); *a,* holotype, cephalon, CPC 14242, ×14 (new); *b,* exoskeleton, CPC 14239, ×14 (new).

Family SPINAGNOSTIDAE Howell, 1935

[Spinagnostidae HOWELL, 1935a, p. 218] [=Quadragnostidae HOWELL, 1935a, p. 219, *sensu* ÖPIK, 1961b, p. 55; Cyclopagnostidae HOWELL, 1937, p. 1165]

En grande tenue or with anterior glabellar lobe variably effaced; usually nonscrobiculate; with nondeliquiate border furrows and narrow to moderately wide borders; unconstricted acrolobes; cephalon nonspinose; median preglabellar furrow well developed to absent. Glabella with ogival, semiovate, subpentagonal, or effaced anterior lobe; F3 straight, variably bent forward or effaced; posterior lobe with F2 usually developed; glabellar culmination usually broadly rounded; glabellar node from level with F1 to slightly in front of F2; basal lobes small, simple. Pygidium nonspinose or bispinose, with axis usually long, not reaching border furrow, ogival, and constricted across M2; F1 and F2 usually effaced; axial node of moderate size; median postaxial furrow usually present. *upper Lower Cambrian–middle Upper Cambrian.*

Subfamily SPINAGNOSTINAE Howell, 1935

[Spinagnostidae HOWELL, 1937, p. 1161] [=Cyclopagnostinae HOWELL, 1937, p. 1161; Hypagnostinae IVSHIN, 1953, p. 15; Euagnostinae ÖPIK, 1979, p. 73]

Commonly nonscrobiculate, with most species variably effacing the anterior glabellar lobe and some also effacing F3; cephalic border usually narrow; pygidial border wider; median preglabellar furrow usually absent, rarely weakly developed. Anterior glabellar lobe semiovate, subpentagonal, or

1a
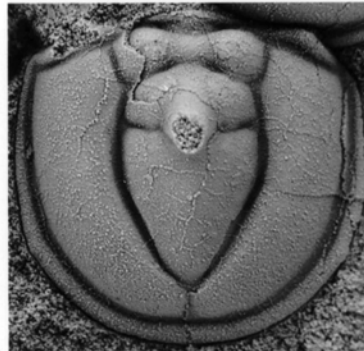
1b

Triplagnostus

2

Aotagnostus

FIG. 225. Ptychagnostidae (p. 354).

more commonly effaced; posterior lobe with F2 weak or absent; glabellar node located from short distance behind F2 to short distance in front of F2. *upper Lower Cambrian–Upper Cambrian.*

Hypagnostus JAEKEL, 1909, p. 399 [*Agnostus parvifrons* LINNARSSON, 1869, p. 82; OD; lectotype (LINNARSSON, 1869, pl. 2, fig. 56; SD WESTERGÅRD, 1946, p. 116), 4769, SGU, Uppsala] [=*Spinagnostus* HOWELL, 1935a, p. 219 (type, *S. franklinensis;* OD); *Cyclopagnostus* HOWELL, 1937, p. 1166 (type, *C. hesperius;* OD); *H. (Breviagnostus)* LIU, 1982, p. 296 (type, *H. (B.) brachyaxonus;* OD); *H. (Metahypagnostus)* QIU in QIU & others, 1983, p. 41 (type, *H. (M.) brachydolonus* ZHOU & YANG in QIU & others, 1983, p. 42, pl. 13, fig. 16–17, pl. 14, fig. 1)]. Commonly weakly scrobiculate. Glabella with effaced anterior lobe; F3 bent forward, rounded or chevronate; posterior lobe short, variably ovate, with F2 weak or absent; glabellar node level with or slightly in front of F2 furrows. Pygidium usually nonspinose; axis usually long, broadly ogival or less commonly short and posteriorly rounded. Median postaxial furrow usually developed. *Middle Cambrian–lower Upper Cambrian:* Argentina; Sweden, Wales, *H. parvifrons* to *L. laevigata* Zones; England, *H. parvifrons* to *A. pisiformis* Zones; Norway, *P. tessini* to *P. forchhammeri* Zones; Denmark, *P. tessini* Zone; Czechoslovakia, *P. (P.) gracilis* Zone; USA (Vermont, New York), *Bolaspidella* Zone, (Alaska), late Dresbachian, (South Carolina), zone uncertain; Canada (Newfoundland, New Brunswick, Quebec), *H. parvifrons* Zone; Australia (Queensland, Tasmania), *P. atavus* to *E. eretes* Zones; China, *H. parvifrons* to *G. stolidotus* Zones; Russia (Salair, Altay, southeastern Siberia), Turkestan Mountain Range, Kazakhstan, *P. atavus* Zone, *T. fissus* or *P. hicksi* to *L. laevigata* or *A. truncata* Zones; Kazakhstan, *K. simplex* to *G. reticulatus* Zones.——FIG. 226,5a,b. *H. parvifrons* (LINNARSSON), Middle Cambrian (*Hypagnostus parvifrons* Zone), Sweden (Hällekis, Kinnekulle, Västergötland); *a,* lectotype, cephalon, SGU 4769, ×9; *b,* paralectotype, pygidium, SGU 4768, ×9 (new).

Cotalagnostus WHITEHOUSE, 1936, p. 92 [*Agnostus lens* GRÖNWALL, 1902, p. 65; OD; syntypes (GRÖNWALL, 1902, pl. 1, fig. 8–9), 149, 150, MGUH, Copenhagen]. Like *Hypagnostus* but with glabellar F3 effaced and commonly with axial furrows surrounding posterior lobe of pygidial axis effaced. *Middle Cambrian:* Argentina; China (Hunan, Guizhou); Sweden, *P. atavus* to *P. forchhammeri* Zones; Denmark, *P. davidis* Zone; Norway, *P. paradoxissimus* to *P. forchhammeri* Zones; England, Wales, *H. parvifrons* to *P. punctuosus* Zones; Canada (Newfoundland, Nova Scotia), late *P. hicksi* to early *P. davidis* Zones; USA (Utah, Alaska), *B. contracta* Subzone; Australia (Queensland), *D. notalibrae* Zone; Russia (southeastern Siberia), *T. fissus* or *P. hicksi* to late *P. davidis* Zones, (Kemerov), *P.*

forchhammeri Zone.——FIG. 226,1a,b. *C. lens* (GRÖNWALL), Middle Cambrian (*Hypagnostus parvifrons* Zone), Denmark (Borregaard, Øle Aa, Bornholm); *a,* syntype, cephalon, MGUH 149, ×10; *b,* syntype, pygidium, MGUH 150, ×12 (new).

Eoagnostus RESSER & HOWELL, 1938, p. 216 [*E. roddyi;* OD; holotype (RESSER & HOWELL, 1938, pl. 3, fig. 4), 90796, USNM, Washington, D.C.]. Small; nonscrobiculate; with moderately wide borders; median preglabellar furrow absent. Glabella with anterior lobe very faintly outlined or effaced, semiovate; F3 straight; posterior lobe strongly inflated posteriorly, overhanging occipital band; glabellar node absent; glabellar culmination rounded or obtusely angular. Pygidium nonspinose; axis of moderate length, strongly convex, semiovate, narrowly rounded posteriorly; axial node indistinct; median postaxial furrow weakly developed. *upper Lower Cambrian:* USA (Pennsylvania, Vermont, New York), *Olenellus* to *Paedumias* to *Bonnia* faunas.——FIG. 227,1a. *E. roddyi,* Lower Cambrian (*Bonnia* to *Olenellus* Zones), USA (Lancaster, Pennsylvania); holotype, exoskeleton, USNM 90796, ×10 (new).——FIG. 227,1b,c. *E. acrorhachis,* Lower Cambrian (*Bonnia* to *Olenellus* Zones), USA (Hatch Hill, New York); *b,* paratype, cephalon, MCZ 8548/3, ×10; *c,* paratype, pygidium, MCZ 8545/4, ×10 (new).

Euagnostus WHITEHOUSE, 1936, p. 87 [*E. opimus;* OD; holotype (WHITEHOUSE, 1936, pl. 8, fig. 11), 3195, UQF, Brisbane]. Glabella with anterior lobe broadly semiovate or variably effaced; F3 straight; posterior lobe broad with F2 weak to absent; glabellar node a short distance behind F2. Pygidial axis long, ogival, almost reaching border furrow, slightly constricted across M2; F1 and F2 effaced; median postaxial furrow well developed. *Middle Cambrian:* Canada (Newfoundland); Australia (Queensland), *E. opimus* to *D. notalibrae* Zones; USA (Utah, Nevada), *T. gibbus* to *P. punctuosus* Zones.——FIG. 226,7a. *E. opimus,* Middle Cambrian (Floran, *Euagnostus opimus* Zone), Australia (northwest of Mt. Isa, western Queensland); holotype, pygidium, UQF 3193, ×8.8 (new).——FIG. 226,7b. *E. neptis* (=*E. opimus* WHITEHOUSE), Middle Cambrian (Undillan, *Ptychagnostus punctuosus* Zone), Australia (northwest of Mt. Isa, western Queensland); holotype, exoskeleton, CPC 14068, ×8 (new).

Micagnostus HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 115 [*M. rectus;* OD; holotype (HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 11, fig. 13–14), 483/179, MMG, Tashkent]. Known only from cephalon. Small, nonscrobiculate, with moderately wide border. Glabella short, broad, with anterior lobe weakly outlined, semicircular to semiovate; F3 straight; posterior lobe short, broad; F2 absent; glabellar node indistinct. *Middle Cambrian:* Uzbekistan, *Pseudanomocarina* Zone.——FIG. 226,4. *M. rectus,* Middle Cambrian (Amgaian, *Pseudanomocarina* beds), Uzbekistan (northern Turkestan Mountain
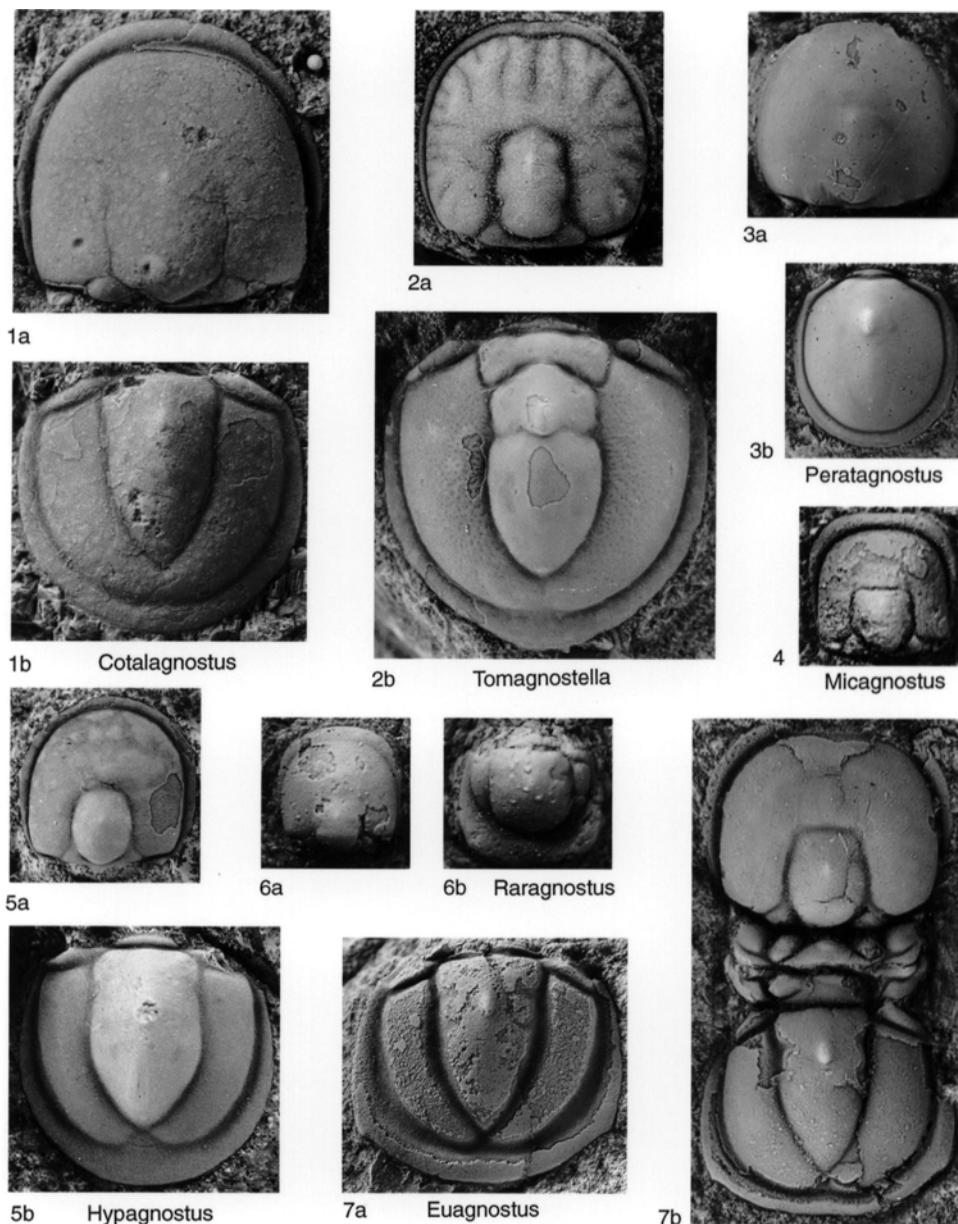
FIG. 226. Spinagnostidae (p. 356–358)

Range); holotype, cephalon, MMG 483/179, ×10 (Repina, Petrunina, & Hajrullina, 1975, pl. 11, fig. 13–14).

Peratagnostus ÖPIK, 1967, p. 86 [**P. nobilis;* OD; holotype (ÖPIK, 1967, pl. 52, fig. 11a–c), CPC 5787, AGSO, Canberra]. Almost completely effaced; nonscrobiculate or weakly scrobiculate; cephalic border absent or very narrow; pygidial border wider, always present. Glabella with vestigial axial furrows defining rear; glabellar node advanced. Pygidium nonspinose, retaining traces of axial furrows defining a narrowly tapering axis that does not reach posterior border furrow; median postaxial furrow effaced. *Upper Cambrian:* Australia
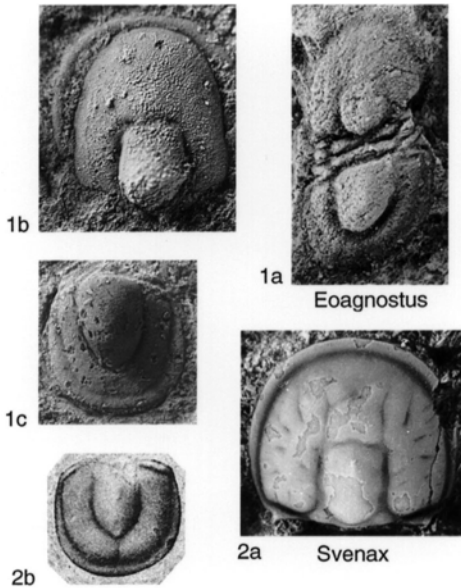
FIG. 227. Spinagnostidae (p. 356–358)

(Queensland), *E. sentum* to *R. apsis* or *W. iota* Zones; South Korea, *Eochuangia* Zone; Kazakhstan, *G. stolidotus* to *H. longiformis* Zones, (Lesser Karatau Mountains), *G. reticulatus* Zone; Russia (Yakutia), *Irvingella* or *C. felix* Zone; Canada (Northwest Territories, Newfoundland), *Olenaspella evansi* to *Irvingella major* Zones; USA (Nevada), *Dunderbergia* Zone, (Alaska), Franconian; China (Zhejiang), *P. fenghwangensis* to *P. clavatus* or *S. kiangshanensis* Zones, (Hunan, Guizhou), zone uncertain.——FIG. 226,*3a,b.* **P. nobilis,* Upper Cambrian (Idamean, *Erixanium sentum* Zone), Australia (Burke River Structural Belt, western Queensland); *a,* paratype, cephalon, CPC 5792, ×8; *b,* holotype, pygidium, CPC 5787, ×8 (new).

Raragnostus HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 117 [**R. mirus;* OD; holotype (HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 12, fig. 17–18), 483/190b, MMG, Tashkent]. Small, nonscrobiculate, with narrow cephalic border and wide, flat pygidial border. Glabella with effaced anterior lobe and with F3 effaced or weakly impressed, bent forward; posterior lobe short; F2 weak to absent; glabellar node a short distance behind F2 furrow. Pygidial axis very broad, long, posteriorly broadly rounded and in contact with border furrow across entire posterior margin; axial node indistinct. *Middle Cambrian:* Uzbekistan, Amgaian–Mayaian; Australia (Queensland), *G. nathorsti* Zone; Sweden, *P. forchhammeri* Zone.——FIG. 226,*6a,b.* **R. mirus,* Middle Cambrian (Amgaian, *Pseudanomocarina* beds), Uzbekistan (northern Turkestan Mountain Range); *a,* paratype, cephalon, MMG 483/190a, ×10; *b,* holo-

type, pygidium, MMG 483/190b, ×10 (Repina, Petrunina, & Hajrullina, 1975, pl. 12, fig. 15, 17).

Svenax ÖPIK, 1979, p. 64 [**Agnostus pusillus* TULLBERG, 1880, p. 36; OD; holotype (TULLBERG, 1880, pl. 2, fig. 30), 407T, LO, Lund]. Weakly scrobiculate. Glabella with semiovate to subpentagonal anterior lobe with adjacent axial furrows weakly impressed; F3 straight or bent slightly forward; posterior lobe with F2 weak; glabellar node level with or slightly in front of F2. Pygidial axis short, broadly ogival, with well-developed constriction across M2; median postaxial furrow clearly developed. *Middle Cambrian:* Sweden, Denmark, Norway, *P. punctuosus* Zone; Australia (Queensland), *P. punctuosus* to *D. notalibrae* Zones.——FIG. 227,*2a,b.* **S. pusillus* (TULLBERG), Middle Cambrian (*Ptychagnostus punctuosus* Zone), Sweden (Andrarum, Skåne); *a,* topotype, cephalon, RM Ar 1988, ×8 (new); *b,* holotype pygidium, LO 407T, ×6 (Westergård, 1946, pl. 4, fig. 12).

Tomagnostella KOBAYASHI, 1939a, p. 150 [**Agnostus exsculptus* ANGELIN, 1851, p. 7; OD; lectotype (TULLBERG, 1880, pl. 1, fig. 10; SD WESTERGÅRD, 1946, p. 118), Ar 2007, RM, Stockholm]. Commonly weakly scrobiculate; median preglabellar furrow occasionally weakly developed, usually absent. Glabella with F3 straight, bent forward, chevronate or rarely effaced; posterior lobe with F2 commonly developed; glabellar node from slightly behind to slightly in front of F2 furrows. Pygidial axis long, commonly reaching border furrow or connected to it by median postaxial furrow; usually strongly constricted across M2; F1 clearly developed, bent forward; F2 variably developed, nearly straight, with a slight median deflection around axial node. *Middle Cambrian–lower Upper Cambrian:* northern Greenland; Sweden, *H. parvifrons* to *L. laevigata* Zones; Norway, England, *L. laevigata* Zone; Russia (Siberia), northern Turkestan Mountain Range, late *P. davidis* to *L. laevigata* Zones; Canada (Northwest Territories), *Cedaria minor* Zone; Australia (Queensland), *G. nathorsti* Zone; China (Zhejiang), *G. stolidotus* Zone, (Hunan, Guizhou), upper Middle Cambrian.——FIG. 226,*2a.* **T. exsculpta* (ANGELIN), upper Middle Cambrian (*S. brachymetopa* Zone), Sweden (Andrarum Limestone, Andrarum, Skåne); lectotype, cephalon, RM Ar 2007, ×10 (new).——FIG. 226,*2b. T. sulcifer* (WALLERIUS), upper Middle Cambrian (*Lejopyge laevigata* Zone), Sweden (Gudhem, Västergötland); topotype, pygidium, SGU 4807, ×9 (new).

Subfamily DORYAGNOSTINAE Shergold, Laurie, & Sun, 1990

[Doryagnostinae SHERGOLD, LAURIE, & SUN, 1990, p. 28]

En grande tenue; nonscrobiculate; with borders of moderate width. Glabella with ogival to semiovate anterior lobe; F3 clear, straight or with slight median forward deflection; posterior lobe with F2 furrows
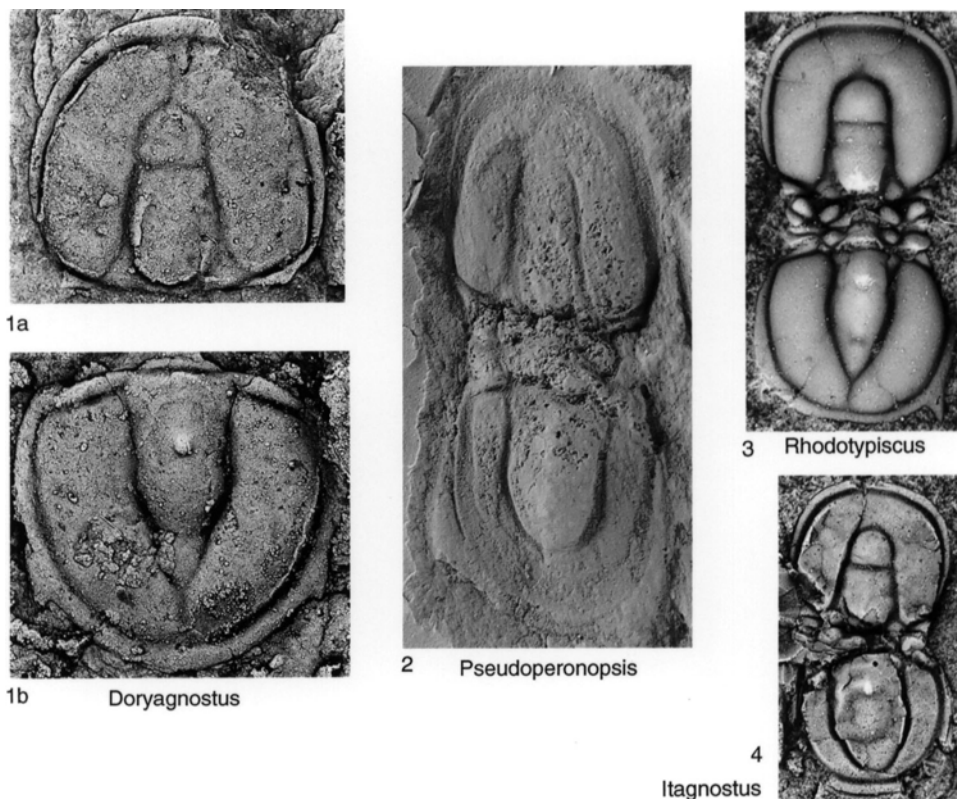
FIG. 228. Spinagnostidae (p. 359–360)

present; glabellar node located from level with F1 to midway between F1 and F2. Pygidium with long, ogival to semiovate posterior lobe; small secondary axial node, commonly associated with a transverse depression in posterior half. *Middle Cambrian.*

Doryagnostus KOBAYASHI, 1939a, p. 148 [**Agnostus incertus* BRÖGGER, 1878, p. 70; OD; lectotype (NIKOLAISEN & HENNINGSMOEN, 1990, fig. 2a), 28200, PMO, Oslo] [=*Ceratagnostus* WHITEHOUSE, 1939, p. 255 (type, *C. magister;* OD]. Median preglabellar furrow well developed, usually expanding into deltoid area anteriorly. Glabella with ogival anterior lobe; posterior lobe with weak F2 furrows; glabellar node midway between F1 and F2 furrows. Pygidium bispinose; axis ogival, acuminate posteriorly; posterior lobe ogival, commonly with transverse depression. *upper Middle Cambrian:* ?northern Greenland; England; Norway, Denmark, *P. tessini* Zone; Sweden, *P. punctuosus* Zone; Canada (Newfoundland), *P. davidis* Zone; Australia (Queens-

land), *E. opimus* to *G. nathorsti* Zones; Russia (southeastern Siberia), late *P. davidis* to *P. forchhammeri* Zones; China (Xinjiang), *G. nathorsti* or *P. punctuosus* Zone, (Hunan, Guizhou), zone uncertain.——FIG. 228,*1a,b.* **D. incertus* (BRÖGGER), Middle Cambrian (*Ptychagnostus punctuosus* Zone), southern Norway (Krekling Station, Oslo district); *a,* paralectotype, cephalon, PMO H2646, ×8; *b,* lectotype, pygidium, PMO 28200, ×8 (Nikolaisen & Henningsmoen, 1990, fig. 2a, 26).

Itagnostus ÖPIK, 1979, p. 60 [**Agnostus elkedraensis* ETHERIDGE, 1902, p. 3; OD; lectotype (SD WHITEHOUSE, 1936, p. 89, pl. 9, fig. 3), 54188, AMF, Sydney]. Median preglabellar furrow absent. Glabella with semiovate anterior lobe; F3 straight; posterior lobe with F2 furrows weak or absent; glabellar node level with or a short distance in front of F1 furrows. Pygidium nonspinose or bispinose; axis broad, long, narrowly rounded posteriorly; posterior lobe semiovate, lacking transverse depression; median postaxial furrow absent. *lower Middle Cambrian:* Australia (Northern Territory), *T. gibbus* Zone; Russia (Siberian Platform), *Oryctocara* to *Kounamkites* Zones; Canada (British Columbia), *Bathyuriscus-Elrathina* Zone; ?Germany, *P. insularis*

Zone; China (Guizhou), Middle Cambrian.——FIG. 228,*4. *I. elkedraensis* (ETHERIDGE), Middle Cambrian (Templetonian, *Triplagnostus gibbus* Zone), Australia (Elkedra area, Northern Territory); lectotype, exoskeleton, AMF 54188, ×8 (new).

Rhodotypiscus ÖPIK, 1979, p. 79 [**R. nasonis;* OD; holotype (ÖPIK, 1979, pl. 16, fig. 1), CPC 14072, AGSO, Canberra]. Median preglabellar furrow usually weakly developed or absent. Glabella with semiovate anterior lobe; F3 straight; posterior lobe with well-developed F2 furrows; glabellar culmination strongly inflated; glabellar node level with or a short distance in front of F1 furrow. Pygidium bispinose; axis elongate ogival, acuminate posteriorly; posterior lobe ogival, commonly with well-developed transverse depression; median postaxial furrow present. *Middle Cambrian:* Canada (Quebec); Australia (Queensland), *E. opimus* Zone; USA (Utah), *T. gibbus* to lower *P. punctuosus* Zones, (Alaska), Middle Cambrian; ?Russia (Siberia), *T. fissus* Zone; China (Xinjiang), *G. nathorsti* or *P. punctuosus* Zone.——FIG. 228,*3. *R. nasonis,* Middle Cambrian (Floran, *Euagnostus opimus* Zone), Australia (Camooweal area, western Queensland); holotype, exoskeleton, CPC 14072, ×8 (new).

Subfamily UNCERTAIN

Pseudoperonopsis HARRINGTON, 1938, p. 149 [**Agnostus sallesi* MUNIER-CHALMAS & BERGERON in BERGERON, 1889, p. 337; OD; holotype (MUNIER-CHALMAS & BERGERON, 1889, pl. 3, fig. 5), not identified]. With tendency to efface F1 and F2 furrows of pygidial axis; deliquiate border furrows; unconstricted acrolobes. Cephalon with vestigial median preglabellar furrow; axial glabellar node at midlength of posterior lobe. Pygidium simplimarginate or narrowly (sag.) zonate; generally with short (sag.), pointed axis; with or without median postaxial furrow; with posterolateral spines. *Middle Cambrian:* France, *Paradoxides* beds; Spain, *Badulesia* to *Solenopleuropsis* Zones; USA (Utah), *B. contracta* Subzone; Australia (Queensland), *A. atavus* to *D. notalibrae* Zones; China (Liaoning, Shandong), *Crepicephalina* Zone.——FIG. 228,*2. *P. sallesi* (MUNIER-CHALMAS & BERGERON), Middle Cambrian (horizon with *Conocoryphe levyi*), France (Coulouma, Champs du Travers, Montagne Noire); plesiotype, UM Thoral H24, ×5 (new).

Family PERONOPSIDAE
Westergård, 1936

[Peronopsidae WESTERGÅRD, 1936, p. 28]

Usually en grande tenue; commonly scrobiculate; with nondeliquiate border furrows and unconstricted acrolobes; cephalon nonspinose; median preglabellar furrow occasionally weakly developed. Glabella with subrectangular, trapeziform, semicircular, or semiovate anterior lobe; F3 straight or bent rearward; posterior lobe with F1 and F2 well developed; glabellar culmination narrowly rounded; glabellar node from a short distance behind F2 to a short distance in front of F2; basal lobes simple, inset behind a well-developed F1 furrow. Pygidium simplimarginate, nonspinose or bispinose; axis long, nearly reaching border furrow, ogival to subtriangular, variably constricted across M2; F1 well developed to effaced; F2 well developed to effaced, straight or deflected around axial node; posterior lobe semiovate to ogival with a usually well-developed transverse depression at about midlength or in anterior half. *Middle Cambrian.*

Peronopsis HAWLE & CORDA, 1847, p. 115 [**Battus integer* BEYRICH, 1845, p. 44; OD; lectotype (PEK & VANĚK, 1971, p. 270, pl. 1, fig. 6), Beyrich Collection 86(530), HMB, Berlin] [=*Mesospheniscus* HAWLE & CORDA, 1847, p. 46 (type, *M. cuneifer;* OD); *Mesagnostus* JAEKEL, 1909, p. 397 (type, *Battus interger* BEYRICH, 1845, p. 44, fig. 19)]. Nonscrobiculate; narrow border in cephalon and wide, flat border in pygidium; median preglabellar furrow absent. Glabella with subquadrate to semiovate anterior lobe; posterior lobe with glabellar node a short distance behind F2. Pygidium nonspinose or bispinose; axis strongly convex, broadly ogival; F1 weak; F2 weak or absent, straight; posterior lobe broadly ogival, narrowly rounded to acuminate posteriorly, with a weakly developed transverse depression at about midlength. *Middle Cambrian:* ?Sweden; Czech Republic, *P. (P.) gracilis* Zone.——FIG. 229,*1a,b. *P. integra* (BEYRICH), Middle Cambrian (*Paradoxides gracilis* Zone), Czech Republic (Jince, Bohemia); *a,* topotype, exoskeleton, SBNM Br-190/56, ×10 (Horný & Bastl, 1970); *b,* lectotype, pygidium, HMB Beyrich Collection 86(530), ×10.7 (Pek & Vaněk, 1971, pl. 1, fig. 6–7).

Diplorrhina HAWLE & CORDA, 1847, p. 46 [**D. triplicata*; SD PEK & VANĚK, 1971, p. 271; lectotype (SD ŠNAJDR, 1958, pl. 4, fig. 9), Hawle Collection 745/66, NMP, Prague]. Commonly scrobiculate, with moderately wide border in cephalon and wider border in pygidium; median preglabellar furrow absent or weakly developed. Glabella with subrectangular, trapeziform, or semicircular anterior lobe; F3 bent rearward, rounded or chevron shaped; posterior lobe with glabellar node from a short distance behind to slightly in front of F2 furrows. Pygidium bispinose; axis of low convexity, ogival to subtriangular; F1 well developed to effaced, bent forward; F2 well developed or effaced, straight; posterior lobe acuminate posteriorly. *Middle Cambrian:* Czech Republic, *P. (E.) pusillus* to *P. (P.) gracilis* Zones; Sweden, *H. parvifrons* to *S. brachy-*
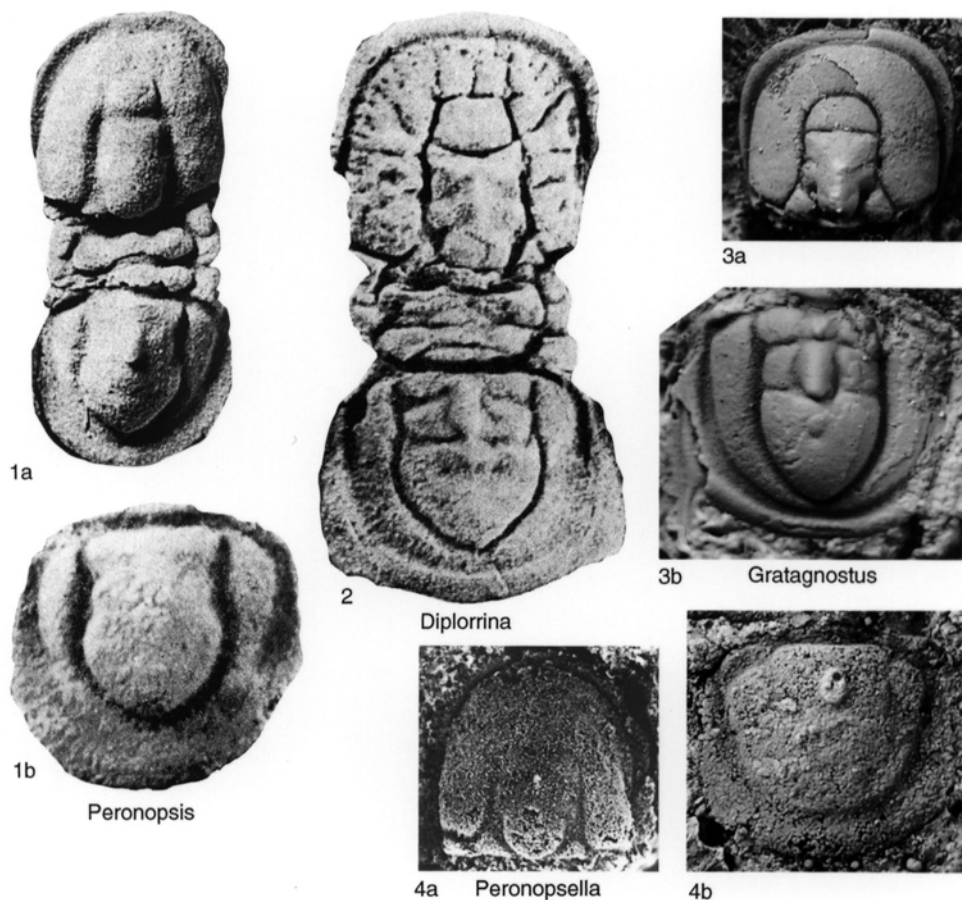
FIG. 229. Peronopsidae (p. 360–362)

metopa Zones; England, Canada (Newfoundland), upper *P. hicksi* to lower *P. davidis* Zone.——FIG. 229,*2*. **D. triplicata,* Middle Cambrian (*Eccaparadoxides pusilla* Zone), Czech Republic (Skryje, Bohemia); lectotype, exoskeleton, NM Hawle Collection 745/66, ×10 (Pek & Vaněk, 1971, pl. 1, fig. 1).

Gratagnostus HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 113 [**G. latus;* OD; holotype (HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 11, fig. 10), 483/189, MMG, Tashkent]. Nonscrobiculate; narrow to moderately wide border in cephalon and wider border in pygidium; median preglabellar furrow absent. Glabella with trapeziform to semicircular anterior lobe; posterior lobe with glabellar node midway between F1 and F2. Pygidium bispinose; axis broad, ogival; F1 well developed; F2 well developed, deflected around axial node; posterior lobe narrowly rounded posteriorly. *Middle Cambrian:* Uzbekistan, *Pseudanomocarina* Beds; England, *P. aurora* to *T. fissus* Zones; Sweden,

T. fissus or *A. atavus* Zone; Canada (Newfoundland), *P. bennetti* Zone.——FIG. 229,*3a,b*. **G. latus,* Middle Cambrian (Amgaian Stage beds with *Pseudanomocarina*), Uzbekistan (Shodymira region, southern Tyan-Shan Range); *a,* paratype, cephalon, MMG 483/176a, ×10; *b,* holotype, pygidium, MMG 483/189, ×10 (Repina, Petrunina, & Hajrullina, 1975, pl. 11, fig. 10, 12).

Peronopsella SDZUY, 1968, p. 88 [**P. pokrovskajae;* OD; holotype (SDZUY, 1968, pl. 1, fig. 1), 24000, SMF, Frankfurt am Main]. Similar to *Peronopsis* but cephalon with F3 and F2 and axial furrows surrounding anterior half of glabella effaced. Pygidium with F1, F2, and usually axial furrows surrounding posterior axial lobe effaced. *Middle Cambrian:* Spain (Asturias), *C. ovata* beds, *Acadolenus* to *Badulesia* Zones, (Zaragoza), *Badulesia* to *Pardailhania* Zones; Germany, *P. paradoxissimus* beds, *T. gibbus* to *A. atavus* Zones; England, lower *T. fissus* Zone; Canada (Newfoundland), *P. bennetti* Zone.—— FIG. 229,*4a,b*. **P. pokrovskajae,* Middle Cambrian

(beds with *Acadoparadoxides*), Spain (Riosol, Asturias); *a,* holotype, cephalon, SMF 24000, ×16; *b,* paratype, pygidium, SMF 24001, ×12 (Sdzuy, 1968, pl. 1, fig. 1, 6).

Family DIPLAGNOSTIDAE
Whitehouse, 1936

[Diplagnostidae WHITEHOUSE, 1936, p. 90]

Variably effaced; commonly scrobiculate; usually with deliquiate border furrows; with pygidial border simplimarginate or variably zonate; cephalon nonspinose; cephalic acrolobe usually unconstricted; pygidial acrolobe commonly constricted; median preglabellar furrow variably developed. Glabella with anterior lobe variable in shape; F3 variably impressed, straight to V-shaped; posterior lobe with glabellar culmination variably rounded to angular; glabellar node from slightly behind F2 to near F3; basal lobes of moderate to large size, simple. Pygidium with basic or glyptagnostoid articulating device; bispinose or occasionally posteriorly angulate or trispinose; axis of variable length, commonly deuterolobate; F1 variably impressed or effaced; M1 commonly trilobate; F2 usually impressed, deflected by axial node; in axiolobate forms, posterior lobe with transverse depression; deuterolobate forms with well-developed terminal node. *Middle Cambrian–Lower Ordovician.*

Subfamily DIPLAGNOSTINAE
Whitehouse, 1936

[Diplagnostinae WHITEHOUSE, 1936, p. 90]

En grande tenue; usually nonscrobiculate; with variably zonate pygidial border. Glabella with subquadrate to semicircular anterior lobe; F3 variably impressed, straight; posterior lobe with variably developed F2 and F1; glabellar node from slightly behind to slightly in front of F2. Pygidium usually bispinose, occasionally posteriorly angulate or trispinose; axis of variable length, usually slightly constricted over M2; F1 and F2 well developed to effaced; posterior lobe variable in shape, usually with transverse depression; pygidial collar usually present, incipient, arcuate or sinuous. *Middle Cambrian–lower Upper Cambrian.*

Diplagnostus JAEKEL, 1909, p. 396 [**Agnostus planicauda* ANGELIN, 1851, p. 7; OD; location of types unknown (topotypes illustrated by WESTERGÅRD, 1946, pl. 8, fig. 22–24)] [=*Enetagnostus* WHITEHOUSE, 1936, p. 91 (type, *E. humilis;* OD)]. Cephalon commonly scrobiculate; deliquiate to subdeliquiate border furrows with narrow border in cephalon and zonate border in pygidium; unconstricted acrolobes; median preglabellar furrow well developed to absent. Glabella with trapeziform to subrectangular anterior lobe, commonly with median sulcus; F3 clearly impressed; F2 well developed or absent; glabellar node level with or slightly in front of F2 furrows. Pygidium bispinose; axis long, broad, ogival, commonly extending to border furrow or connected to it by median postaxial furrow; F1 clearly impressed laterally; F2 clearly impressed; posterior lobe ogival to subtriangular, commonly with poorly defined transverse depression at about midlength; pygidial collar always well defined, extending across entire posterior margin between pygidial marginal spines, but not extending onto acrolobe. *Middle Cambrian:* Argentina; northern Greenland; Sweden, *P. punctuosus* to *L. laevigata* Zones; Denmark, Norway, *L. laevigata* Zone; England, *P. aurora* to *T. fissus* Zones; France, *Paradoxides* beds; Canada (Newfoundland), *P. davidis* Zone; Turkestan Mountain Range, Kazakhstan (Tyan-Shan Range), Amgaian; Russia (southeastern Siberia), *T. fissus* to *L. laevigata* Zones; China (Zhejiang), *P. triangularis* to *L. armata* Zones, (Hunan, Guizhou, Qinghai), upper Middle Cambrian; Australia (Queensland, Tasmania), *P. atavus* to *L. laevigata* Zones.——FIG. 230,*1a,b.* **D. planicauda* (ANGELIN), Middle Cambrian (*Goniagnostus nathorsti* Zone), Sweden (Andrarum, Skåne); *a,* topotype, cephalon, SGU 4870, ×9; *b,* topotype, pygidium, SGU 4871, ×9 (new).

Acadagnostus KOBAYASHI, 1939a, p. 113 [**Agnostus acadicus* HARTT in DAWSON, 1868, p. 655; OD (*fide* ÖPIK, 1979, p. 62)] [=*Axagnostus* LAURIE, 1990, p. 318 (type, *Agnostus fallax* LINNARSSON, 1869, p. 81, pl. 2, fig. 54–55)]. Nonscrobiculate to weakly scrobiculate; surface smooth. Cephalon with deliquiate border furrow; median preglabellar furrow absent; glabella with semicircular to transversely quadrate anterior lobe; posterior glabellar lobe with well-developed F2 furrows and with glabellar node level with or immediately behind F2 furrows. Pygidium subquadrate, bispinose; occasionally with incipient or restricted zonation; border furrow deliquiate; median postaxial furrow commonly present; axis never reaching border furrow, bullet-shaped, commonly unconstricted; F1 and F2 absent to very weakly developed; axial node large; secondary axial node commonly developed on posterior lobe. *Middle Cambrian:* Norway; Turkey; Sweden, *T. (T.) gibbus* to *A. atavus* Zones; Canada (Newfoundland, New Brunswick), *P. davidis* to *P. forchhammeri* Zones; Australia (Queensland), *P. punctuosus* to *G. nathorsti* Zones; USA (Nevada, Utah), *Bolaspidella contracta* Subzone, *P. praecurrens* to early *A. atavus* Zones, (New York), *Bathyuriscus-Elrathina* Zone,
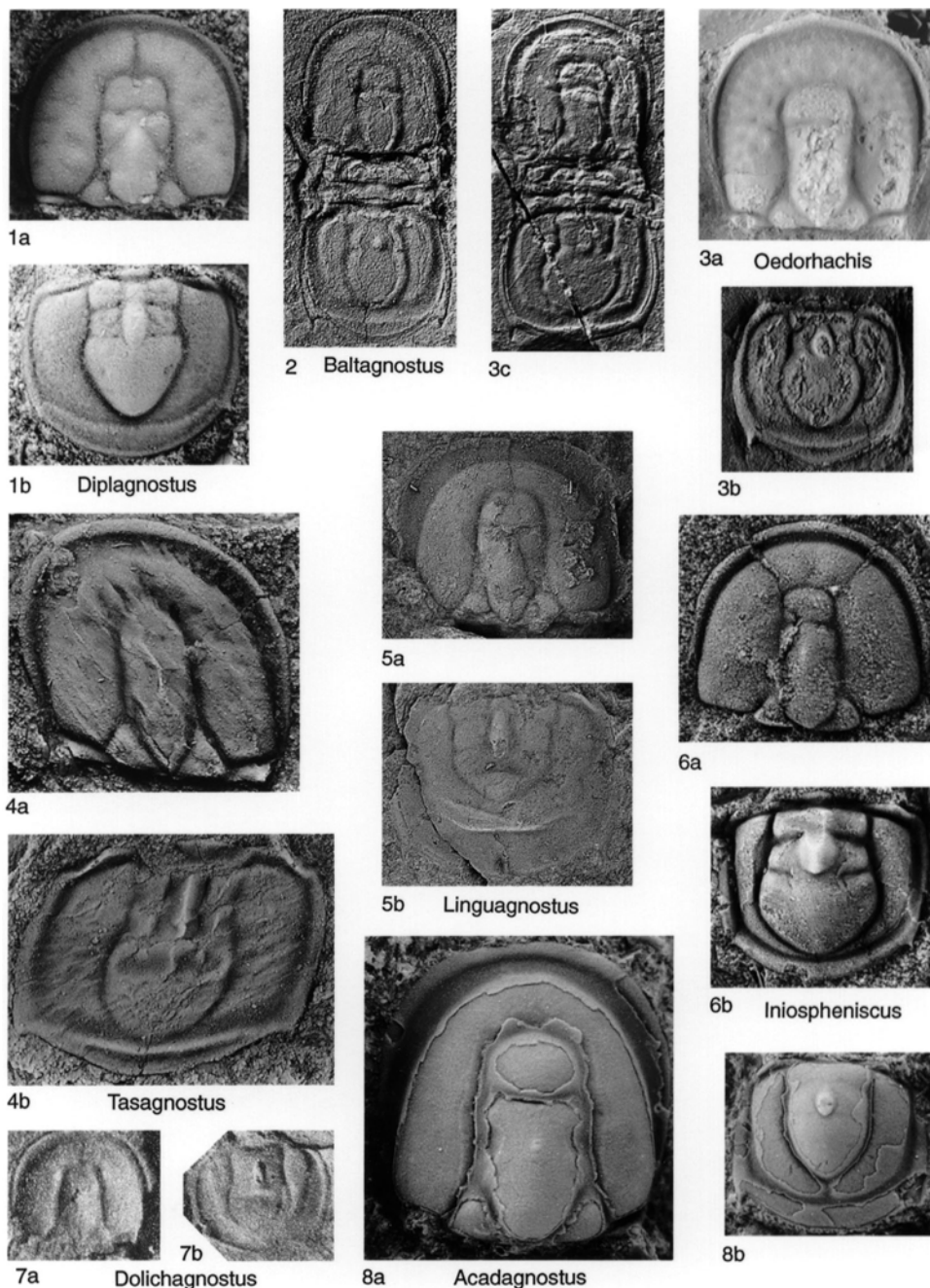
FIG. 230. Diplagnostidae (p. 362–365)

(Texas), *Bolaspidella* Zone, (South Carolina), zone uncertain; Russia (Siberia), *T. fissus, Pseudanomocarina, A. henrici* Zones, (Kirgizia), Amgaian–Mayaian; China (Hunan, Guizhou), *D.* sp. cf. *D. richthofeni* to lower *P. jimaensis-C. tuma* Zones, (Xinjiang), *G. nathorsti* or *P. punctuosus* Zone.——FIG. 230,*8a,b.* *A. fallax* (LINNARSSON), Middle Cambrian (*Triplagnostus gibbus* Zone), Sweden

(Djupadalen, Västergötland); *a,* cephalon, SGU 4717, ×9; *b,* lectotype, pygidium, SGU 4716, ×9 (Laurie, 1990, fig. 1b,d).

Baltagnostus LOCHMAN in LOCHMAN & DUNCAN, 1944, p. 132 [**Proagnostus? centerensis* RESSER, 1938, p. 48; OD; holotype (RESSER, 1938, pl. 10, fig. 18), 94868, USNM, Washington, D.C.]. Nonscrobiculate, with deliquiate border furrows; unconstricted acrolobes; median preglabellar furrow absent. Glabella with subquadrate to subpentagonal anterior lobe; F3 clear; posterior lobe with weak F2 furrows; glabellar culmination narrowly rounded or angular; glabellar node about level with F2 furrows. Pygidium bispinose; axis long, reaching border furrow; F1, F2 effaced; posterior lobe semiovate, broadly rounded posteriorly; pygidial collar arcuate, short (tr.), indistinct. *Middle Cambrian:* USA (Alabama, Montana, Nevada, New York, Tennessee, Texas, Utah), *Bolaspidella* Zone; Canada (Quebec), China (Liaoning), upper Middle Cambrian; southern Korea, *Tonkinella* Zone; Australia (Queensland), *E. opimus* to *D. notalibrae* Zones.——FIG. 230,*2. *B. centerensis* (RESSER), upper Middle Cambrian (Marjuman, zone uncertain), USA (Moshat, Alabama); holotype, exoskeleton, USNM 94868, ×8 (new).

Dolichagnostus POKROVSKAYA, 1958, p. 34 [**D. admirabilis;* OD; holotype (POKROVSKAYA, 1958, pl. 3, fig. 1), 3534/3, GIN, Moscow]. Nonscrobiculate, with broad, deliquiate border furrows; pygidial acrolobe commonly constricted; median preglabellar furrow commonly well developed. Glabella with trapeziform anterior lobe; F3 weak; posterior lobe with F2 weak or absent; glabellar culmination narrowly rounded or angular; glabellar node about level with F2 furrows. Pygidium bispinose and angulate posteriorly; axis long, extending to pygidial collar, broadly rounded posteriorly; F1, F2 effaced; posterior lobe long, with transverse furrow in anterior half; pygidial collar sinuous, extending on to acrolobe. *upper Middle Cambrian:* Russia (Siberia), *L. laevigata* Zone; Australia (Queensland), *L. laevigata* Zone.——FIG. 230,*7a,b. *D. admirabilis,* Middle Cambrian (Mayaian, *Anomocarioides limbataeformis* Zone), Russia (Yakutia); *a,* holotype, cephalon, GIN 3534/3a, ×3; *b,* pygidium, GIN 3534/3b, ×3 (Pokrovskaya, 1958, pl. 3, fig. 1a, 3).

?Iniospheniscus ÖPIK, 1979, p. 50 [**I. talis;* OD; holotype (ÖPIK, 1979, pl. 9, fig. 1), CPC 14021, AGSO, Canberra]. Nonscrobiculate, with subdeliquiate to deliquiate border furrows; pygidial border commonly incipiently zonate; acrolobes unconstricted; median preglabellar furrow absent. Glabella with subrectangular anterior lobe; F3 well developed; posterior lobe with weak F2 furrows; glabellar node about level with F2 furrows. Pygidium bispinose; axis long, reaching border furrow, expanding rearwards; F1, F2 impressed laterally; posterior lobe very broad, semiovate, rounded posteriorly, lacking transverse depression; pygidial collar absent or very short (tr.), indistinct. *Middle Cambrian:* Australia (Queensland), *A. atavus* to *P. punctuosus* Zones; China (Shandong, Liaoning),

Amphoton Zone.——FIG. 230,*6a,b. *I. talis,* Middle Cambrian (Undillan, *Ptychagnostus punctuosus* Zone), Australia (Camooweal district, western Queensland); *a,* cephalon, CPC 14026, ×8; *b,* holotype, pygidium, CPC 14021, ×13 (new).

Linguagnostus KOBAYASHI, 1939a, p. 142 [**Agnostus kjerulfi* BRÖGGER, 1878, p. 65; OD; lectotype (SD WESTERGÅRD, 1946, p. 124, pl. 8, fig. 32), 28684, PMO, Oslo]. Nonscrobiculate; deliquiate border furrows; zonate pygidial border; pygidial acrolobe commonly constricted; median preglabellar furrow absent. Glabella with trapeziform to subrectangular anterior lobe, commonly with median sulcus; F3 clearly impressed; F2 weakly developed or absent; glabellar culmination narrowly rounded or angular; glabellar node about level with F2 furrows. Pygidium bispinose or trispinose, commonly with postaxial notch on margin; axis short, broadly ogival, unconstricted or slightly constricted across M2; F1 effaced to clearly impressed laterally; F2 effaced to clearly impressed; posterior lobe short, broad, subtriangular, with transverse depression at about midlength. Pygidial collar sinuous, extending onto acrolobe. *upper Middle Cambrian:* Sweden, England, *P. punctuosus* Zone; Denmark, *P. davidis* Zone; Norway, *P. forchhammeri* Zone; Wales, *P. paradoxissimus* Zone; Russia (Siberia, Tuva), Turkestan Mountain Range, Tadzhikistan; Kazakhstan, *L. laevigata, Anopolenus, L. allachjunensis* Zones; China (Hunan, Guizhou, Qinghai, Zhejiang), *L. armata* Zone; Australia (Queensland, Northern Territory), *T. gibbus* to *L. laevigata* Zones.——FIG. 230,*5a,b. *L. kjerulfi* (BRÖGGER), Middle Cambrian (*Paradoxides forchhammeri* beds), Norway (Krekling, Oslo district); *a,* paralectotype, cephalon, PMO 28682, ×5.5; *b,* lectotype, pygidium, PMO 28684, ×5.5 (new).

Oedorhachis RESSER, 1938, p. 50 [**O. typicalis;* OD; holotype (RESSER, 1938, pl. 10, fig. 16, 22, 28), 94866, USNM, Washington, D.C.]. Similar to *Tasagnostus* but with incipient zonation only and lacking transverse furrow in posterior pygidial axial lobe. *upper Middle Cambrian–lower Upper Cambrian:* northern Greenland; ?Sweden; Australia (Queensland), *G. nathorsti* to *A. quasivespa* Zones; Argentina, *Bolaspidella* Zone; Canada (Northwest Territories), *Cedaria minor* Zone; USA (Alabama, Tennessee), *G. stolidotus* Zone; China (Liaoning, Qinghai), *Blackweldería* Zone.——FIG. 230,*3a–c. *O. typicalis; a,b,* upper Middle Cambrian (*Lejopyge laevigata* Zone), northern Greenland (Gustav Holm Dal, Peary Land); *a,* cephalon, MGUH 17.115, ×8, *b,* pygidium, MGUH 17.118, ×8 (Robison, 1988, fig. 4, 8.1); *c,* Late Cambrian (Dresbachian, *Crepicephalus* Zone), USA (Cedar Bluff, Alabama), holotype, exoskeleton, USNM 94866, ×6 (new).

Tasagnostus JAGO, 1976, p. 161 [**T. debori;* OD; holotype (JAGO, 1976, pl. 26, fig. 1), 86869e, UTGD, Hobart]. Nonscrobiculate, with broad, deliquiate border furrows; zonate pygidial border; acrolobes unconstricted; median preglabellar furrow weak. Glabella with trapeziform to subpentagonal anterior

lobe; F3 weak; posterior lobe with F2 weak or absent; glabellar culmination acutely angular; glabellar node about level with F2 furrows. Pygidium bispinose; axis long, constricted across M2; F1, F2 effaced; posterior lobe slightly bulbous, broadly rounded posteriorly, extending to pygidial collar, with well-developed transverse furrow in anterior half; pygidial collar extending across entire posterior margin betwen pygidial spines, but not extending onto acrolobe. *upper Middle Cambrian:* Australia (Tasmania), *L. laevigata* to *?D. torosa* or *A. janitrix* Zones.——FIG. 230,*4a,b.* **T. debori,* Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Christmas Hills, northern Tasmania); *a,* paratype, cephalon, UTGD 86877e, ×7.7; *b,* holotype, pygidium, UTGD 86869e, ×7.4 (Jago, 1976, pl. 26, fig. 1, 9).

Subfamily OIDALAGNOSTINAE Öpik, 1967

[Oidalagnostinae ÖPIK, 1967, p. 134]

En grande tenue; scrobiculate; zonate pygidial border; commonly constricted pygidial acrolobe; median preglabellar furrow usually weak. Glabella with trapeziform to subrectangular anterior lobe; F3 well developed, straight; posterior lobe with variably developed F2; glabellar culmination narrowly rounded; glabellar node about level with F2 furrows. Pygidium trispinose; axis long, extending to pygidial collar or posteriorly effaced; F1 and F2 variably impressed; posteroaxis variably quadrate with deep, transverse depression in anterior half defining a third anterior annulation and posterior portion subrectangular, tumid or effaced. *upper Middle Cambrian–lower Upper Cambrian.*

Oidalagnostus WESTERGÅRD, 1946, p. 65 [**O. trispinifer;* OD; holotype (WESTERGÅRD, 1946, pl. 9, fig. 6), 4879, SGU, Uppsala] [=*Ovalagnostus* LU in LU, ZHU, & others, 1974, p. 81 (type, *Oidalagnostus changi* LU in WANG, 1964, p. 30, pl. 3, fig. 11)]. Median preglabellar furrow weakly developed. Pygidial axis long, extending to pygidial collar; posteroaxis with tumid, subrectangular posterior portion; posterior portion commonly separated from pleural field by paired bosses and weak accessory furrows; pygidial collar arcuate, with median depression. *uppermost Middle Cambrian–lower Upper Cambrian:* northern Greenland; Sweden, *L. laevigata* Zone; Australia (Queensland, Tasmania), *L. laevigata, C. quasivespa, G. stolidotus* Zones; Canada (Newfoundland), *A. pisiformis* Zone; Russia (northwestern Siberia), *Pedinocephalus* or *Toxotis* Zone, (southern Siberia), *L. laevigata* Zone; China

1 Cristagnostus

2a Oidalagnostus
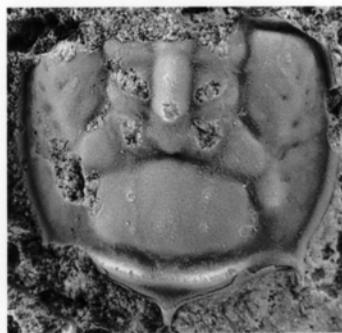
2b

FIG. 231. Diplagnostidae (p. 365–366)

(Zhejiang), *L. armata* to *L. sinensis* Zones, (Hunan), *L. laevigata* Zone.——FIG. 231,*2a,b.* **O. trispinifer,* Middle Cambrian (*Lejopyge laevigata* Zone), Sweden (Gudhem, Västergötland); *a,* cephalon, SGU 4878, ×6; *b,* holotype, pygidium, SGU 4879, ×6 (new).

Cristagnostus RUSHTON, 1978, p. 262 [**C. papilio;* OD; holotype (RUSHTON, 1978, pl. 26, fig. 5), BDA 1320–1321, BGS, London]. Very weakly scrobiculate; median preglabellar furrow variably developed. Pygidial axis with F1 well developed; F2 weak; posteroaxis with only anterior portion

defined by axial furrow and transverse depression; axial furrow effaced behind transverse depression; pygidial collar sinuous, extending on to acrolobe. *uppermost Middle Cambrian–lowest Upper Cambrian:* Russia (southwestern Siberia); England, Canada (Newfoundland), *A. pisiformis* Zone; Russia (northern Siberia), ?uppermost Middle Cambrian.——Fig. 231,*1.* **C. papilio,* Upper Cambrian (*Agnostus pisiformis* Zone), central England (Merevale #3 borehole, Nuneaton); holotype, exoskeleton, BGS BDA 1320, ×9.3 (Rushton, 1978, pl. 25, fig. 5).

Subfamily PSEUDAGNOSTINAE Whitehouse, 1936

[Pseudagnostinae WHITEHOUSE, 1936, p. 97]

En grande tenue to largely effaced; commonly scrobiculate; usually with wide borders; pygidial border usually simplimarginate; pygidial acrolobe commonly constricted; median preglabellar furrow well developed to absent. Glabella with anterior lobe variable in shape; F3 variably impressed, straight to V-shaped, rarely bent forward; posterior lobe with glabellar node from a short distance behind F2 to near F3. Pygidium bispinose, rarely trispinose; axis long, deuterolobate; F1 usually effaced or weak; deuterolobe often effaced, with terminal node. *Upper Cambrian–Lower Ordovician.*

Pseudagnostus JAEKEL, 1909, p. 400 [**Agnostus cyclopyge* TULLBERG, 1880, p. 26; OD; topotypes (WESTERGÅRD, 1922, pl. 1, fig. 7–8), 3066t, 3067t, LO, Lund] [=*Plethagnostus* CLARK, 1923b, p. 124 (type, *P. gyps;* OD)]. Variably convex, spectaculate pseudagnostines; en grande tenue to partly effaced; generally with wide borders; variably deliquiate border furrows; long (sag.), anteriorly rounded or pointed anterior glabellar lobe; simple, terminally angulate posterior lobe; prominent, triangular basal lobes; lateral lobes not well developed; pygidium weakly to strongly deuterolobate, occasionally trispinose. *Upper Cambrian.*
P. (Pseudagnostus). Generally with deliquiate border furrows; median preglabellar furrow usually present; pygidium with single pair of marginal spines in advance of rear of deuterolobe. *Upper Cambrian:* Argentina; Antarctica; Vietnam; Afghanistan; Turkey; Spain; Sweden, England, *O. cataractes* to *L. raphidophorus* Zones; USA (Alaska, Montana, Wyoming, Nevada, Utah, Idaho, Texas, Oklahoma, Tennessee, Virginia, Maryland, Wisconsin), Canada (British Columbia, Alberta, Northwest Territories, Quebec), *Cedaria* to *Ptychaspis* or *Prosaukia* Zones, (Newfoundland), Sunwaptan; Australia (Queensland, Tasmania), *E. eretes* to *P. tertia* or *P. quarta*

Zones; South Korea, *Eochuangia* Zone; Kazakhstan, Russia (northwestern Siberia, Yakutia), *A. pisiformis* to *A. scrobicularis* Zones; China (Zhejiang), *G. stolidotus* to *L. punctatus* Zones.——Fig. 232,*1a,b.* **P. (P.) cyclopyge* (TULLBERG), Upper Cambrian (*Parabolina spinulosa* with *Orusia lenticularis* Zone), Sweden (Andrarum, Skåne); *a,* topotype, cephalon, GMI LO 3066t, ×7; *b,* topotype, pygidium, GMI LO 3067t, ×7 (Shergold, 1977, pl. 15, fig. 1–2).
P. (Pseudagnostina) PALMER, 1962a, p. 21 [**Pseudagnostina contracta;* OD; holotype (PALMER, 1962a, pl. 2, fig. 23), 143151, USNM, Washington, D.C.]. Effaced or partly effaced; strongly spectaculate; with subdeliquiate border furrows; lacking median preglabellar furrow; unconstricted acrolobes; clearly incised, transverse anterior glabellar furrow; pygidium weakly deuterolobate; F1, F2 furrows effaced; posterolateral spines generally close to rear of deuterolobe. *Upper Cambrian:* USA (Alabama, Nevada, Virginia), *Cedaria* to *Crepicephalus* Zones; Canada (Northwest Territories), *Cedaria minor* to *C. brevifrons* Zones; Australia (Queensland), *G. stolidotus* Zone; Kazakhstan, *G. stolidotus* Zone; South Korea, *Drepanura* to *Stephanocare* Zone; China (Hunan, Liaoning, Shandong), Gushanian.——Fig. 232,*4a,b.* **P. (P.) contracta* (PALMER), Upper Cambrian (Dresbachian, *Cedaria* Zone), USA (Woodstock, Alabama); *a,* paratype, cephalon, USNM 143150, ×16; *b,* holotype, pygidium, USNM 143151, ×16 (Shergold, 1977, pl. 15, fig. 11–12).
P. (Sulcatagnostus) KOBAYASHI, 1937b, p. 451 [**Agnostus securiger* LAKE, 1906, p. 20; OD; holotype (LAKE, 1906, pl. 2, fig. 11), 57650, BGS, London]. En grande tenue, with deliquiate border furrows and strongly constricted acrolobes, possessing median preglabellar furrow; pygidium trispinose. *Upper Cambrian:* England, *O. cataractes* Subzone; Canada (Northwest Territories), *Olenaspella regularis* Zone; China (Zhejiang), *L. punctatus* Zone, (?Xinjiang, ?Hunan), zone uncertain; Australia (Tasmania), post-Idamean.——Fig. 232,*5.* **P. (S.) securiger* (LAKE), Upper Cambrian (*Olenus* Zone), England (Nuneaton, Warwickshire); holotype, exoskeleton, BGS 57650, ×6 (Shergold, 1977, pl. 15, fig. 13).
Agnostotes ÖPIK, 1963, p. 43 [**A. inconstans;* OD; holotype (ÖPIK, 1963, pl. 3, fig. 11), CPC 4272, AGSO, Canberra]. Large; variably en grande tenue; variably scrobiculate, with nondeliquiate border furrows, narrow borders, and unconstricted acrolobes; median preglabellar furrow well developed. Glabella with broad anterior lobe; F3 bent forward; posterior lobe with well-developed, forwardly directed F2 furrows and broadly rounded glabellar culmination; glabellar node located level with or slightly in front of F2 furrows. Pygidium bispinose; deuterolobe subcircular to subpyriform, with well-developed terminal node; notular lines usually developed. *Upper Cambrian.*
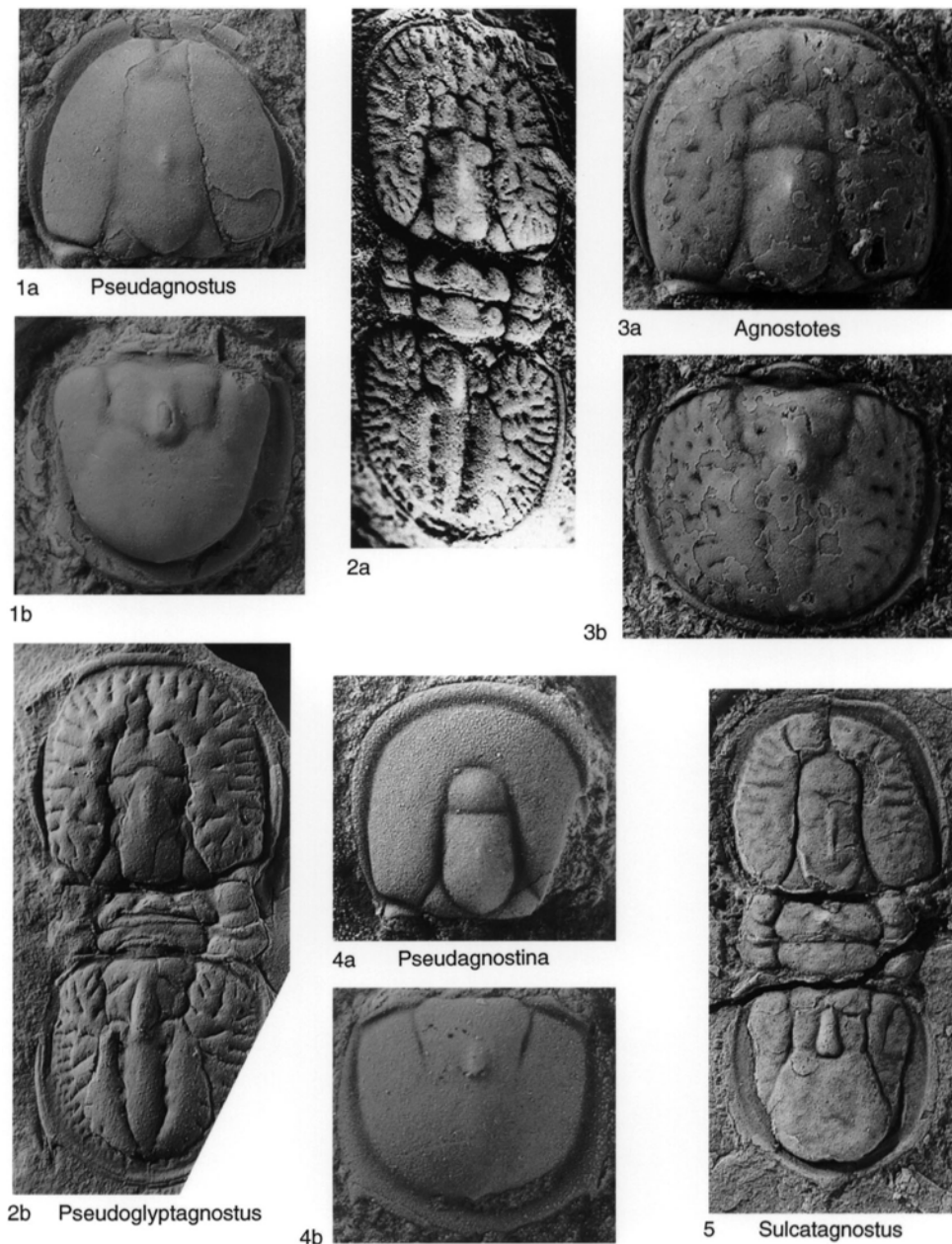
FIG. 232. Diplagnostidae (p. 366–368)

A. (**Agnostotes**). Scrobiculate; axial furrows weakly impressed. Glabella with anterior lobe broad (tr.) and subpentagonal; F3 slightly convex forward; posterior lobe with clearly developed F2; glabellar node level with or slightly in front of F2 furrows. Pygidial axis with weakly impressed accessory furrows; axial node extending slightly onto deuterolobe; deuterolobe subcircular with notular lines erratically developed. *Upper Cambrian:* China (Qinghai); Australia (Queensland), *I. tropica* Zone.——FIG. 232,*3a,b.* *A. (A.) inconstans,* Upper Cambrian (post-Idamean,

Irvingella tropica Zone), Australia (Burke River area, western Queensland); *a,* paratype, cephalon, CPC 4274, ×8.5 (new); *b,* holotype, pygidium, CPC 4272, ×7 (new).

A. (**Pseudoglyptagnostus**) LU in WANG, 1964, p. 32 [**Pseudoglyptagnostus clavatus;* OD; holotype (LU in WANG, 1964, pl. 4, fig. 7), 23719, NIGP, Nanjing] [=*Glyptagnostotes* LAZARENKO, 1966, p. 42 (type, *G. elegans;* OD)]. Both shields strongly scrobiculate. Glabella with anterior lobe broad and trapeziform, with variably developed median sulcus; F3 bent strongly forward; posterior lobe with well-developed F2 and F1; lateral portions of M2 commonly separated from midmost glabella by longitudinal (exsag.) furrows; glabellar node located in front of F2 furrow. Pygidial axis with F1 impressed laterally and F2 clearly impressed; axial node extending well onto deuterolobe; accessory furrows clearly impressed; deuterolobe subpyriform. *Upper Cambrian:* China (Zhejiang), *P. clavatus* to *S. kiangshanensis* Zone, (Hunan), zone uncertain; Kazakhstan, *P. curtare* to *Irvingella* or *C. felix* Zones; Canada (Northwest Territories), *Proceratopyge rectispinata* Zone; USA (Nevada), *Elvinia* Zone.——FIG. 232,*2a.* **A. (P.) clavatus* (LU), Upper Cambrian (Changshanian), China (Hunan); holotype, exoskeleton, NIGP 23719, ×7 (Wang, 1964, pl. 4, fig. 7).——FIG. 232,*2b. A. (P.) elegans* (LAZARENKO), Upper Cambrian (?Sakian, *Irvingella* or *Cedarellus felix* Zone), Russia (Kyutyungda depression, Kharaulakh Mountain Range, Yakutia); holotype, exoskeleton, CNIGR 24/8907, ×5 (Lazarenko, 1966, pl. 2, fig. 1).

Denagnostus JAGO, 1987, p. 213 [**D. corbetti;* OD; holotype (JAGO, 1987, pl. 24, fig. 13), 88463, UTGD, Hobart]. Subovoid or subcircular cephalon and pygidium, almost effaced, with nondeliquiate border furrows; wide anterior cephalic border narrows posteriorly and disappears at about cephalic midlength; glabella faintly outlined, spectaculate; effaced median preglabellar furrow. Pygidium with very weakly outlined axis, acrolobe slightly constricted, marginal spines small, well in advance of rear of deuterolobe; posterior pygidial border faintly zonate. *lower Upper Cambrian:* Australia (Tasmania), Idamean.——FIG. 233,*1a,b.* **D. corbetti,* Upper Cambrian (Idamean), Australia (Denison Range, southwestern Tasmania); *a,* holotype, cephalon, UTGD 88463, *Proceratopyge cryptica* Zone, ×9; *b,* paratype, pygidium, UTGD 88495, *Stigmatoa diloma* Zone, ×9 (Jago, 1987, pl. 24, fig. 13; pl. 25, fig. 2).

Litagnostus RASETTI, 1944, p. 235 [**L. levisensis;* OD; syntypes (RASETTI, 1944, pl. 36, fig. 5–6), 1103a,b, LU, Quebec]. Cephalon and pygidium totally effaced with exception of narrow borders and pygidial axial node; internal molds typically rhaptagnostoid. *Upper Cambrian–Lower Ordovician (Tremadoc):* USA (Minnesota, Wisconsin, Texas); Canada (Alberta), *Taenicephalus* Zone to ?*Ellipsocephaloides silvestris* Subzone, (Newfoundland), Sunwaptan,

(Quebec); England, upper Tremadoc.——FIG. 233,*4a,b.* **L. levisensis,* Upper Cambrian (Sunwaptan, *Keithia subclavata* fauna of LUDVIGSEN & others, 1989), Canada (Boulder 36, Lévis, Quebec); *a,* syntype, cephalon, LU 1103a, ×5; *b,* syntype, pygidium, LU 1103b, ×5 (Rasetti, 1944, pl. 36, fig. 5–6).

Nahannagnostus PRATT, 1992, p. 35 [**Pseudagnostus nganasanicus* ROZOVA, 1964, p. 27; OD; holotype (ROZOVA, 1964, pl. 16, fig. 3), 113/875, CSGM, Novosibirsk]. Cephalon and pygidium strongly convex; median preglabellar furrow well defined; anterior glabellar lobe extremely small; F3 partly effaced; axial glabellar node subcentral or slightly advanced. Pygidium with highly inflated deuterolobe; F1 and F2 mostly effaced; posterolateral spines minute. *Upper Cambrian:* Russia (Siberia), Ayusokkanian; Kazakhstan, *Kormagnostus simplex* Zone; Canada (Northwest Territories, Newfoundland), *Cedaria selwyni* to *Cedaria brevifrons* Zones; USA (Utah, Nevada, Missouri, Texas), *Cedaria* to *Crepicephalus* Zones; Australia (Queensland), *Erediaspis eretes* and *Glyptagnostus stolidotus* Zones; China (Hunan, Zhejiang), *Glyptagnostus stolidotus* Zone.——FIG. 234,*1a,b.* **N. nganasanicus* (ROZOVA), Upper Cambrian (Ayusokkanian, Nganasan Gorizont), Russia (Kulyumbe River, northwestern Siberian Platform); *a,* cephalon, CSGM 113/999, ×10; *b,* holotype, pygidium, CSGM 113/875, ×5 (Rozova, 1964, pl. 16, fig. 3, 11).

Neoagnostus KOBAYASHI, 1955, p. 473 [**N. aspidoides;* OD; holotype (KOBAYASHI, 1955, pl. 7, fig. 5), 12745, GSC, Ottawa]. Spectaculate; partially effaced to en grande tenue, with generally wide borders and subdeliquiate to deliquiate border furrows; acrolobes weakly constricted; cephalon and pygidium frequently subquadrate. Cephalon with variably developed median preglabellar furrow; generally small, rhomboid anterior lobe; variably defined, V-shaped F3; chevronate F2 behind anterolateral lobes of posterior glabellar lobe; anterolateral lobes close together or meeting sagittally. Pygidium with third annulation in anterior part of axis; weakly to strongly deuterolobate, with retral posterolateral spines. *Upper Cambrian–Lower Ordovician.*

N. (**Neoagnostus**) [=*Pseudorhaptagnostus* LERMONTOVA, 1940, p. 126 (type, *P. simplex* LERMONTOVA, 1951a, p. 12, pl. 2, fig. 11–17); *Euplethagnostus* LERMONTOVA, 1940, p. 126 (type, *E. subangulatus;* OD); *Hyperagnostus* KOBAYASHI, 1955, p. 475 (type, *H. binodosus;* OD); *Tarayagnostus* SUAREZ-SORUCO, 1975, p. 133 (type, *T. corrugatus;* OD); *Calagnostus* J. ZHANG & WANG, 1985, p. 332 (type, *C. magezhuangensis;* OD)]. En grande tenue to partly effaced; cephalon nonscrobiculate; glabella proportionately long; median preglabellar furrow variably developed; variably deuterolobate. *Upper Cambrian–Lower Ordovician:* Canada (British Columbia, Newfoundland, Quebec), *Elvinia* to *Missisquoia* Zones; USA (Alaska, Vermont, Arkansas), Franconian–Trempealeauan; Mexico,
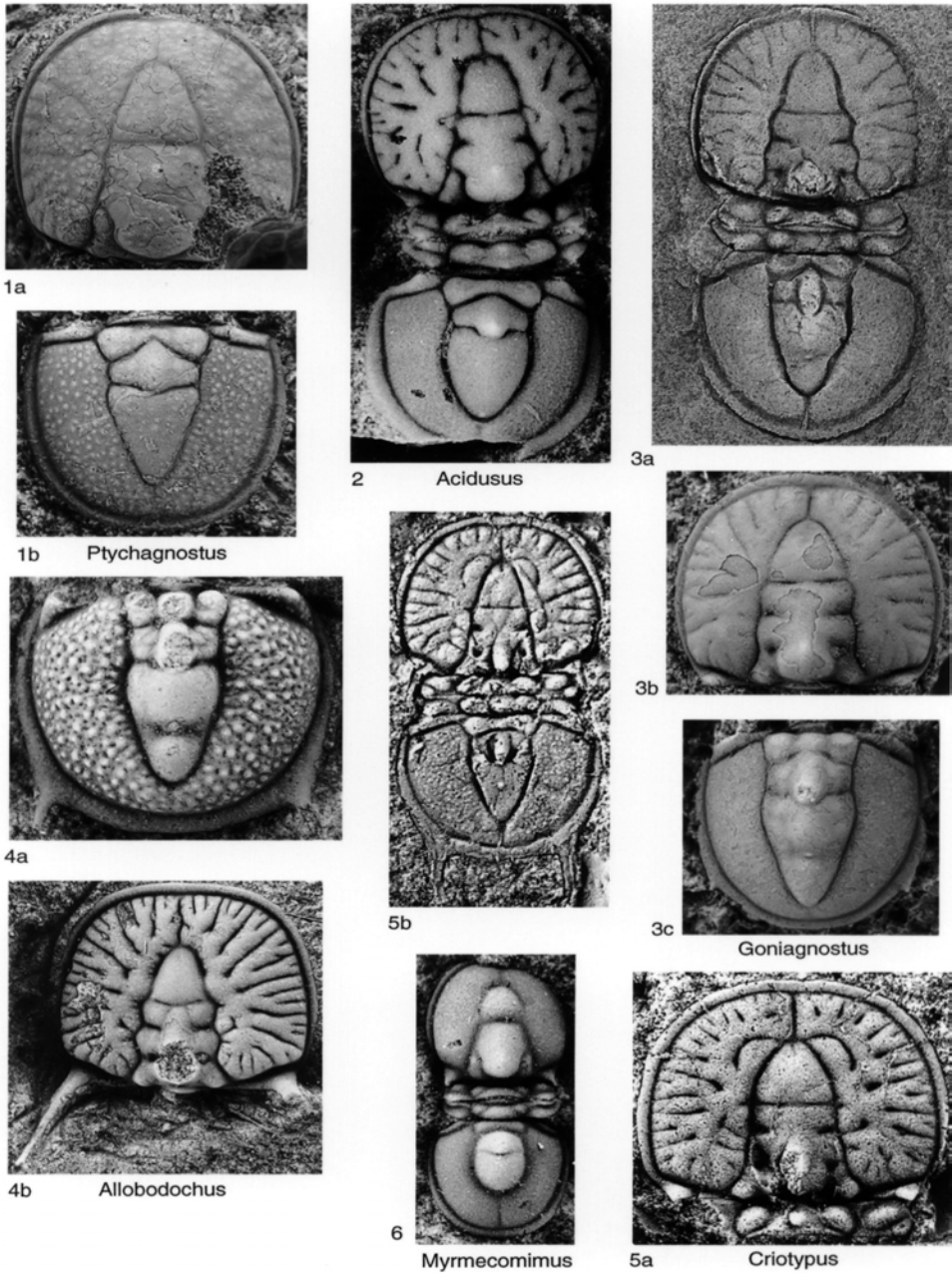
FIG. 233. Diplagnostidae (p. 368–371)

?*Cordylodus proavus* Zone; Australia (Queens-
land, Tasmania), *W. iota* or *R. apsis* to *N.
quasibilobus* or *S. nomas* Zones; China (Anhui,
Guizhou, Shanxi, Zhejiang, Xinjiang, Yunnan),
L. punctatus to *M. perpetis* Zones, (Shandong),

Kaolishania Zone, (Hunan), Tremadoc; South
Korea, *Kaolishania* Zone; Kazakhstan (Altay-
Sayan), Russia (Kuznetsk Alatau, Yakutia),
Irvingella to *M. mutabilis* Zones; Wales,
Tremadoc; ?Argentina, lower Tremadoc; Bolivia,

Neoparabolina argentina Zone.——Fig. 233,*2a.* **N. (N.) aspidoides,* ?Lower Ordovician ("*Symphysurina* fauna"), Canada (Harrogate, British Columbia); holotype, cephalon, GSC 12745, ×7 (Shergold, 1977, pl. 16, fig. 6).——Fig. 233,*2b,c. N. (N.) bilobus* (Shaw), uppermost Cambrian (*Missisquoia* Zone), USA (Highgate Falls, Vermont); *b,* paratype, cephalon, USNM 124467, ×16; *c,* holotype, pygidium, USNM 124468, ×12.5 (Shergold, 1977, pl. 16, fig. 7–8).

N. **(Machairagnostus)** Harrington & Leanza, 1957, p. 64 [**Machairagnostus tmetus;* OD; holotype (Harrington & Leanza, 1957, fig. 7.4), 1297, BAF CB, Buenos Aires]. En grande tenue but with partially effaced glabellar furrows; cephalon scrobiculate, possessing median preglabellar furrow and proportionately short glabella; pygidium nonscrobiculate, weakly deuterolobate, preserving intranotular axis. *uppermost Cambrian:* Argentina, *Neoparabolina argentina* Zone; Kazakhstan, *E. scrobicularis* to *P. asiatica* Zones.——Fig. 233,*5.* **N. (M.) tmetus* (Harrington & Leanza), uppermost Cambrian (*N. argentina* Zone), Argentina (Iruya, Salta); holotype, exoskeleton, BAF CB 1297, ×11.5 (Harrington & Leanza, 1957, fig. 7.4).

Oxyagnostus Öpik, 1967, p. 159 [**O. apicula;* OD; holotype (Öpik, 1967, pl. 63, fig. 6), CPC 5916, AGSO, Canberra]. Both cephalon and pygidium with constricted acrolobes, relatively narrow borders, and deliquiate border furrows. Cephalon lacking median preglabellar furrow; glabellar culmination angular; glabellar node advanced. Pygidium with axis constricted at M2, and long, subpentagonal, laterally expanded posterior lobe; deuterolobe not obvious externally; posterolateral spines slightly in advance of terminal axial node. *Upper Cambrian:* Australia (Queensland), *G. stolidotus* Zone; USA (Alabama), *Crepicephalus* Zone.——Fig. 234,*2a,b.* **O. apicula,* Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Boulia district, western Queensland); *a,* paratype, cephalon, CPC 5917, ×8; *b,* holotype, pygidium, CPC 5916, ×8 (new).

Rhaptagnostus Whitehouse, 1936, p. 97 [**Agnostus cyclopygeformis* Y. Sun, 1924, p. 26; OD; lectotype (Y. Sun, 1924, pl. 2, fig. 1e), 507, NIGP, Nanjing]. Characteristically with subovoid to subcircular cephalon and pygidium; effaced to partly effaced; with nondeliquiate border furrows. Cephalon papilionate, with effaced median preglabellar furrow. Pygidium variably deuterolobate, with weakly constricted acrolobe; marginal spines well in advance of rear of deuterolobe. *Upper Cambrian:* Australia (Queensland), *W. iota* or *R. apsis* to *N. quasibilobus* or *S. nomas* Zones; China (Anhui, Hebei, Liaoning, Shandong, Yunnan, Qinghai, Xinjiang), *Kaolishania* to *Tsinania* Zones, (Zhejiang), *L. punctatus* Zone, (Guizhou), zone uncertain; North and South Korea, Fengshanian, *Tsinania* to *Eoorthis* Zones; Kazakhstan, *E. scrobicularis* to *T. trisulcus* Zones, Russia (Yakutia),
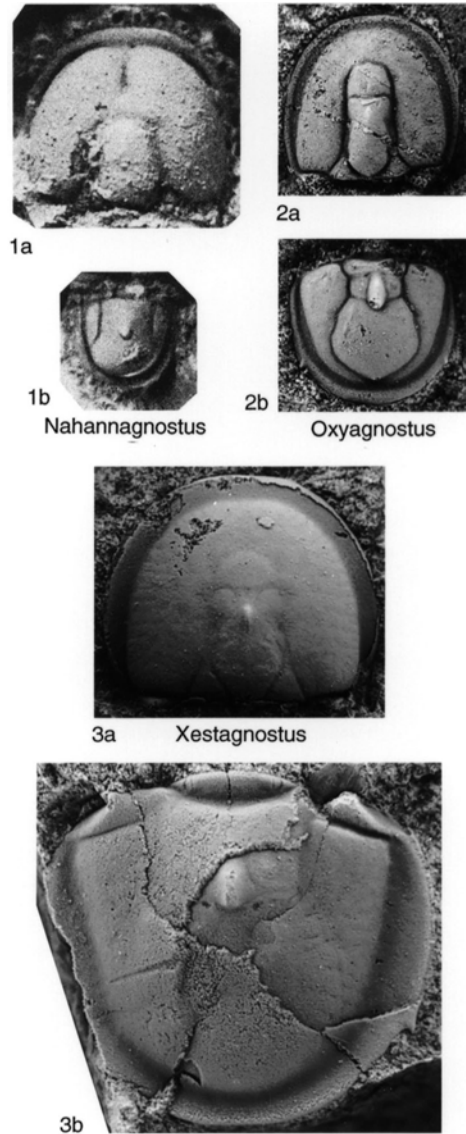
Fig. 234. Diplagnostidae (p. 368–371)

P. perlata Zone; Canada (Northwest Territories, Newfoundland), *Yukonaspis* Zone; USA (Alaska, Montana, Nevada, Vermont), *S. pyrene* to *S. serotina* Subzones; Mexico, pre-*Cordylodus proavus* Zone.——Fig. 233,*3a.* **R. cyclopygeformis* (Sun), Upper Cambrian (Changshanian, *Kaolishania* Zone), China (Kaolishan, Taian, Shandong); lectotype, pygidium, NIGP 507, ×7 (X. Sun, 1989, pl. 5, fig. 10).——Fig. 233,*3b,c. R. convergens* (Palmer), Upper Cambrian (Trempealeauan, *Saukiella pyrene* Subzone), USA (Eureka district, Nevada); *b,*

paratype, cephalon, USNM 123563, ×10; *c,* holotype, pygidium, USNM 123562, ×9.5 (Shergold, 1977).

Trisulcagnostus ERGALIEV, 1980, p. 116 [**T. trisulcus;* OD; holotype (ERGALIEV, 1980, pl. 18, fig. 13), 1950/289, GMAN, Alma-Ata] [=*Pseudagnostus (Tririmagnostus)* QIU, 1983, p. 40 (type, *P. (T.) anhuiensis;* OD)]. Like *Rhaptagnostus,* but with narrow borders and nondeliquiate border furrows, well-defined median preglabellar furrow, and additionally a pair of transverse furrows crossing cephalic acrolobe from axial furrow to border furrow at level of anterolateral lobes of posterior glabellar lobe; pointed anterior lobe, papilionate; pygidium unknown. *Upper Cambrian:* China (Anhui, Hunan); Kazakhstan, *E. scrobicularis* to *T. trisulcus* Zones.——FIG. 233,*6.* **T. trisulcus* ERGALIEV; Upper Cambrian (Batyrbaian, *Trisulcagnostus trisulcus* Zone), Kazakstan (Lesser Karatau Mountains); holotype, cephalon, GMAN 1950/289, ×10.2 (Ergaliev, 1980, pl. 18, fig. 13).

Xestagnostus ÖPIK, 1967, p. 161 [**X. legirupa;* OD; holotype (ÖPIK, 1967, pl. 64, fig. 1), CPC 5922, AGSO, Canberra]. Moderately large; relatively flat; externally effaced. Cephalon lacking median preglabellar furrow; spectaculate; large, triangular basal lobes; glabellar culmination angulate; unconstricted acrolobe; scrobiculate on internal mold. Pygidium with constricted acrolobe; internally scrobiculate pleural lobes; rectangular anteroaxis; effaced accessory furrows; weakly deuterolobate, concave articulating facets; fulcral spines; simple articulating device represented by elliptical, depressed plate; advanced posterolateral spines. *Upper Cambrian:* Australia (Queensland), *A. quasivespa* to *G. stolidotus* Zones.——FIG. 234,*3a,b.* **X. legirupa,* Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Glenormiston area, western Queensland); *a,* paratype, cephalon, CPC 5924, ×8; *b,* holotype, pygidium, CPC 5922, ×8 (new).

Family CLAVAGNOSTIDAE Howell, 1937

[Clavagnostidae HOWELL, 1937, p. 1164] [=Acanthagnostidae QIAN, 1982, p. 640]

En grande tenue; commonly scrobiculate, with nondeliquiate to deliquiate border furrow in cephalon and nondeliquiate border furrow and commonly zonate border in pygidium; unconstricted acrolobes and well-developed cephalic spines. Median preglabellar furrow well developed to absent. Glabella acuminate, rounded, or obtusely angular anteriorly, usually with anterior and posterior lobes fused; F2 absent or weakly developed; glabellar culmination variably rounded, or angular; glabellar node elongate,

located near midlength or in anterior half of glabella; basal lobes of small to moderate size, simple. Pygidium bispinose or trispinose, with long, usually ogival to subtriangular axis; constricted across M2; F1 effaced or clearly impressed, curving forward to articulating furrow to isolate anterolateral lobes; F2 effaced or clearly impressed, strongly deflected by long axial node; posterior axial lobe long, usually ogival, subtriangular or subpyriform, commonly extending to border furrow, with a transverse depression commonly associated with a pair of longitudinal (exsag.) pits at about midlength of lobe. *upper Middle Cambrian–lower Upper Cambrian.*

Subfamily CLAVAGNOSTINAE Howell, 1937

[Clavagnostinae HOWELL, 1937, p. 1164]

Pygidium simplimarginate; axis with F1 and F2 effaced. *upper Middle Cambrian–lower Upper Cambrian.*

Clavagnostus HOWELL, 1937, p. 1164 [**Agnostus repandus* WESTERGÅRD in HOLM & WESTERGÅRD, 1930, p. 13; OD; holotype (HOLM & WESTERGÅRD, 1930, pl. 4, fig. 11), 3131T, LO, Lund] [=*Tomorhachis* RESSER, 1938, p. 51 (type, *T. spinosa;* OD); *Culipagnostus* RUSCONI, 1952, p. 11 (type, *C. chipiquensis;* OD); *Stigmagnostus* C. POULSEN, 1960, p. 15 (type, *?Tomagnostus canotensis* RUSCONI, 1951, p. 14, 26, fig. 29); *Acanthagnostus* QIAN, 1982, p. 640 (type, *A. longispinus;* OD); *Clavagnostus (Leptagnostus)* LU & LIN, 1989, p. 199 (type, *C. (L.) lanceolatus;* OD)]. Nonscrobiculate; median preglabellar furrow variably developed. Glabellar node elongate, located in anterior half of glabella. Pygidium bispinose or trispinose; posterior lobe commonly reaching border furrow or connected to it by median postaxial furrow, with a broad transverse depression and a pair of longitudinal (exsag.) pits at about lobe midlength. *upper Middle Cambrian–lower Upper Cambrian:* USA (Vermont, Alabama); Argentina; Germany; Sweden, *L. laevigata* Zone; Russia (Bennett Island), *P. forchhammeri* Zone, (southwestern Siberia, Altay Mountains, Salair), *L. laevigata* Zone, (northwestern Siberia), *L. armata* to *M. mirabilis* Zones, (southeastern Siberia), *Solenoparia* Zone; Turkestan Mountain Range, *L. laevigata* Zone; Kazakhstan, *L. armata* to *K. simplex* Zone; Canada (Northwest Territories), *Cedaria minor* Zone; Australia (Tasmania), *L. laevigata* Zone, (Queensland), *E. eretes* to *G. stolidotus* Zones; China (Zhejiang), *L. armata* to *G. stolidotus* Zones, (Shandong), *Drepanura* Zone, (Anhui, Hunan, Qinghai), zone uncertain.——FIG. 235,*2a,b.* **C.*
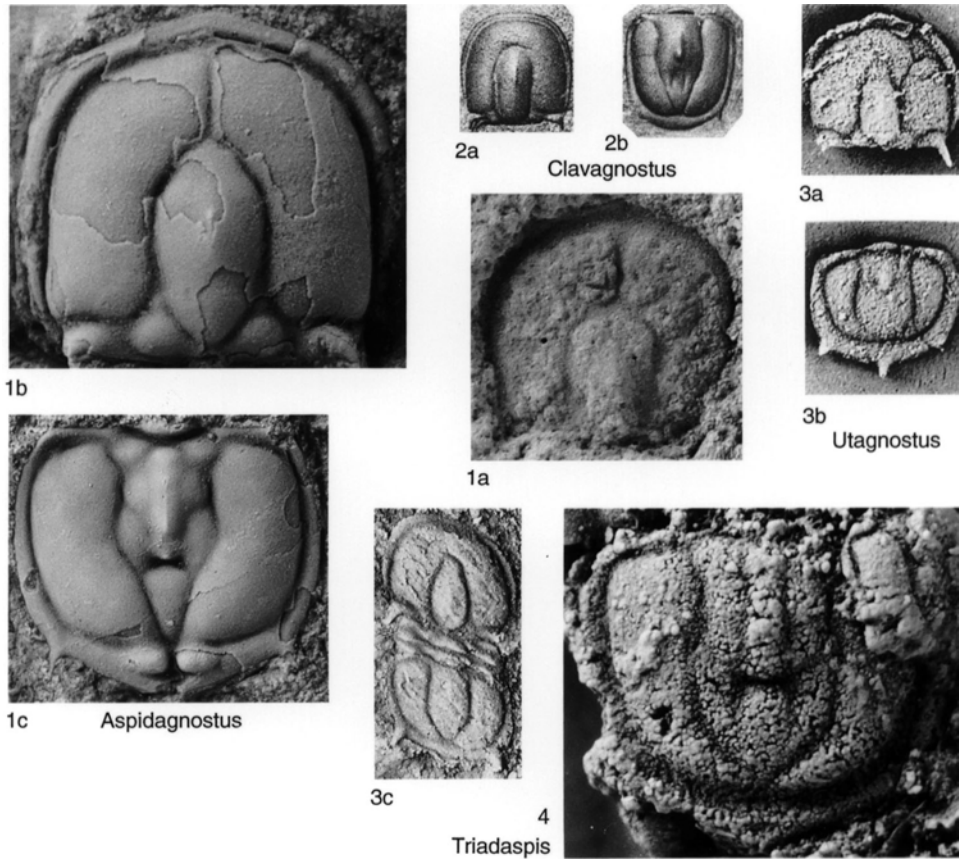
FIG. 235. Clavagnostidae (p. 371–373).

repandus (WESTERGÅRD), Middle Cambrian (*Paradoxides forchhammeri* Stage), Sweden (Andrarum, Skåne); *a,* holotype, cephalon, LO 3131T, ×6; *b,* paratype, pygidium, SGU 5461, ×6; (Westergård, 1946, pl. 4, fig. 19–20).

Subfamily ASPIDAGNOSTINAE Pokrovskaya, 1960

[Aspidagnostinae POKROVSKAYA, 1960, p. 60]

Pygidium trispinose, zonate; F1 impressed laterally, curving forward to articulating furrow to isolate subtriangular anterolateral lobes; F2 strongly deflected by long axial node extending nearly to midlength of posterior axial lobe. *Upper Cambrian.*

Aspidagnostus WHITEHOUSE, 1936, p. 104 [**A. parmatus;* OD; holotype (WHITEHOUSE, 1936, pl. 9, fig. 5), 3213, UQF, Brisbane] [=*Biragnostus* POKROVSKAYA in KHALFIN, 1960, p. 161 (type, *B.*

elenae, nom. nud.; OD)]. Commonly scrobiculate, with nondeliquiate to deliquiate border furrow and anteriorly angulate border in cephalon; median preglabellar furrow well developed. Glabella acuminate or narrowly rounded anteriorly; glabellar culmination narrowly rounded to angular; glabellar node elongate, located at or in front of glabellar midlength; basal lobes small to moderate-sized, commonly divided. Pygidium with weak to well-developed, secondary axial node on posterior lobe; nondeliquiate border furrow and zonate border with collar crossed by deep median gap, commonly flanked by a pair of knobs. *lower Upper Cambrian:* Australia (Queensland, Tasmania), *G. stolidotus* to *G. reticulatus* Zones; Kazakhstan, *G. stolidotus* to *G. reticulatus* Zones; England, *A. pisiformis* Zone; Canada (Northwest Territories), *Cedaria brevifrons* to *G. reticulatus* Zones; USA (Nevada), upper *Crepicephalus* Zone, (Alabama, Nevada), *G. reticulatus* Zone; China (Zhejiang), *G. stolidotus* to *G. reticulatus* Zones. *Upper Cambrian:* Russia (Siberia).——FIG. 235,*1a.* **A. parmatus,* Upper Cambrian (stage and zone uncertain), Australia

(Glenormiston district, western Queensland); holotype, cephalon, UQF 3213, ×12.7 (new).——FIG. 235,*1b,c. A. iniquilinus,* Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Glenormiston district, western Queensland); *b,* holotype, cephalon, CPC 5828, ×16; *c,* paratype, pygidium, CPC 5831, ×12 (new).

Triadaspis ÖPIK, 1967, p. 125 [**T. bigeneris;* OD; holotype (ÖPIK, 1967, pl. 54, fig. 6), CPC 5804, AGSO, Canberra]. Known only from poorly preserved pygidium; with nondeliquiate border furrow; zonate border lacking a gap in the collar. *lower Upper Cambrian:* Australia (Queensland), *E. eretes* Zone.——FIG. 235,*4. *T. bigeneris,* Upper Cambrian (Mindyallan, *Erediaspis eretes* Zone), Australia (Glenormiston district, western Queensland); holotype, pygidium, CPC 5804, ×18 (new).

Subfamily UNCERTAIN

Utagnostus ROBISON, 1964, p. 533 [**U. trispinulus;* OD; holotype (ROBISON, 1964, pl. 82, fig. 25), 141226, USNM, Washington, D.C.]. Small; en grande tenue; nonscrobiculate, with nondeliquiate border furrows; narrow cephalic and broad pygidial border; cephalic spines well developed; median preglabellar furrow absent. Glabella with small, low, semiovate anterior lobe; F3 weakly impressed, nearly straight; glabellar node about level with F2 furrows; basal lobes very small, simple. Pygidium trispinose; F1 effaced; F2 clearly impressed, strongly deflected by elongate axial node; posterior lobe semiovate, broadly rounded posteriorly, of low convexity. *upper Middle Cambrian–lower Upper Cambrian:* USA (Utah), upper *P. punctuosus* to lower *L. laevigata* Zones; Australia (New South Wales), ?*P. punctuosus* Zone.——FIG. 235,*3a,b. *U. trispinulus,* upper Middle Cambrian (*Bolaspidella contracta* Subzone), USA (House Range, western Utah); *a,* paratype, cephalon, USNM 141223, ×9; *b,* holotype, pygidium, USNM 141226, ×10 (Robison, 1964, pl. 82, fig. 21, 25).——FIG. 235,*3c. U. neglectus,* upper Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Christmas Hills, northwestern Tasmania); holotype, exoskeleton, UTGD 86844i, ×11 (Jago, 1976, pl. 23, fig. 13).

Family METAGNOSTIDAE Jaekel, 1909

[Metagnostidae JAEKEL, 1909, p. 398] [=Trinodidae HOWELL, 1935b, p. 233; Geragnostidae HOWELL, 1935b, p. 231; Arthrorhachidae RAYMOND, 1913a, p. 139]

Usually en grande tenue; nonscrobiculate; border furrows nondeliquiate; acrolobes unconstricted; cephalon nonspinose; median preglabellar furrow usually absent. Glabella usually with semiovate, semicircular, or subcircular anterior lobe; F3 effaced, variably chevron shaped or concave forward; posterior lobe with F2 furrows absent or chevron shaped; glabellar culmination broadly rounded or obtusely angular; glabellar node at or near F3 furrow; basal lobes small to moderate-sized, simple. Pygidium with agnostoid articulating device, usually bispinose; axis usually short, not reaching border furrow; F1 impressed laterally, curving forward to articulating furrow, isolating anterolateral lobes; F2 impressed, straight or deflected by axial node; posterior lobe variable in length, trapeziform, subrectangular, semiovate, or subtriangular, commonly with terminal node; median postaxial furrow absent. *?Upper Cambrian–Ordovician.*

Arthrorhachis HAWLE & CORDA, 1847, p. 114 [**Battus tardus* BARRANDE, 1846, p. 35; M; lectotype (BARRANDE, 1852, pl. 49, fig. 1–4) ČD 1812, NMP, Prague] [=*Metagnostus* JAEKEL, 1909, p. 398 (type, *M. erraticus;* OD); *Girvanagnostus* KOBAYASHI, 1939a, p. 174 (type, *Agnostus girvanensis* REED, 1903, p. 4, pl. 1, fig. 2–4)]. Glabellar F3 effaced or with straight medial portion, lateral portions curving forward and outward; posterior lobe with F2 furrows weak; glabellar node immediately behind F3 furrow. Pygidial axis very short, tapering rearward; posterior lobe transverse, subrectangular, trapeziform or subtriangular; commonly with weak terminal node. *Ordovician:* Czechoslovakia, upper Caradoc–Ashgill; Poland, England, Ireland, Uzbekistan, Norway, Denmark, Ashgill; Scotland, Caradoc; Kazakhstan, Tremadoc–Ashgill; Argentina, upper Tremadoc; eastern USA, lower middle Ordovician; Turkey, upper Arenig; France, lower Arenig; Sweden, upper Tremadoc–lower Caradoc; Spitsbergen, upper Canadian; China (Shaanxi), upper middle Ordovician, (Jiangsu), Ashgill; Germany, middle Ordovician.——FIG. 236,*2. *A. tarda* (BARRANDE), Upper Ordovician (Ashgill, *Tretaspis granulata* to *T. seticornis seticornis* horizons), Czechoslovakia (Libomyšl, Bohemia); lectotype, exoskeleton, NM-ČD 1812, ×10 (Pek, 1977, pl. 8, fig. 2).

Anglagnostus HOWELL, 1935b, p. 233 [**Agnostus dux* CALLAWAY, 1877, p. 665; OD; holotype by monotypy (CALLAWAY, 1877, pl. 24, fig. 3), 693, BU, Birmingham]. Type species known from one articulated specimen having short glabella with semiovate anterior lobe; F3 clearly impressed, weakly concave forward; posterior lobe with F2 furrows absent; glabellar culmination broadly rounded; glabellar node not preserved; basal lobes small, transverse. Pygidium minutely bispinose; axis very short, quadrate; posterior lobe transverse, subrectangular with terminal node; F1 and F2 impressed. *Lower Ordovician (Tremadoc):* England; ?France; China (Hunan), *A. latilimbatus* or *T. affinis* Zone.——FIG. 236,*1. *A. dux* (CALLAWAY), England (Shineton, Shropshire); holotype, exoskeleton, BU 693, ×8 (new).
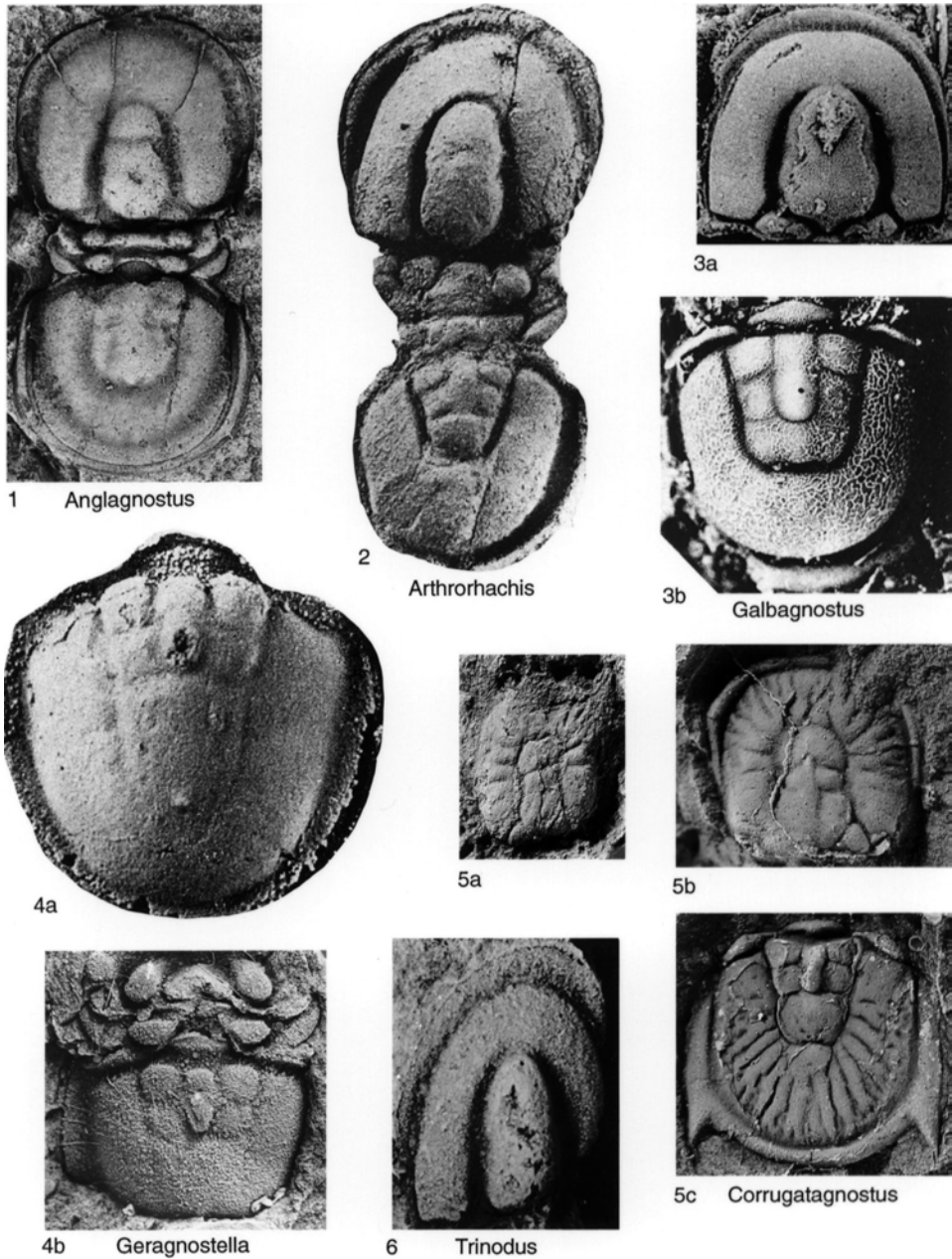
FIG. 236. Metagnostidae (p. 373–377)

Chatkalagnostus Hajrullina & Abdullaev in Abdullaev & Khaletskaya, 1970, p. 20 [*C. mirus;* OD; holotype (Abdullaev & Khaletskaya, 1970, pl. 1, fig. 1), 4/3, IGiG, Tashkent] [=*Oculagnostus* Ahlberg, 1988, p. 116 (type, *Agnostus frici* Holub, 1908, p. 9, pl. 1, fig. 1a,b)]. Large; en grande tenue; usually scrobiculate; border furrows wide, deliquiate; median preglabellar furrow absent. Glabella broad, with large, subquadrate anterior lobe; F3 nearly straight, curving rearward laterally; posterior lobe with F2 furrows well developed, chevronate; glabellar node immediately behind F3 furrow. Py-

gidium bispinose; axis short, slightly constricted across M2; posterior lobe transverse, subrectangular. *Ordovician:* Czech Republic, Llanvirn–lower Llandeilo; Uzbekistan, ?Llandeilo; Sweden, ?Arenig–Llanvirn.——FIG. 237,*5a,b.* **C. mirus,* Lower Ordovician (Llandeilo), Uzbekistan (Pskem Ridge, Karakorum Range); *a,* holotype, cephalon, IGiG 4/3, ×5; *b,* pygidium, IGiG 4/6, ×5 (Abdullaev & Khaletskaya, 1970, pl. 1, fig. 1, 4).

Corrugatagnostus KOBAYASHI, 1939a, p. 173 [**Agnostus perrugatus* BARRANDE, 1872, p. 143; OD; =*A. morea* SALTER, 1864b, p. 7; holotype by monotypy (SALTER, 1864b, pl. 1, fig. 13), 8699, BGS, London] [=*Segmentagnostus* PEK, 1977, p. 17 (type, *Agnostus caducus* BARRANDE, 1872, p. 142, pl. 14, fig. 12–13); *Granulatagnostus* KOLOBOVA, 1981, p. 257 (type, *G. granulatus;* OD)]. En grande tenue; usually scrobiculate; median preglabellar furrow present in more strongly scrobiculate forms. Glabella with semiovate to semicircular anterior lobe; F3 chevron shaped; posterior lobe with F2 variably developed, chevron shaped; glabellar node from immediately behind F3 to well onto anterior glabellar lobe. Pygidial axis very short, tapering rearward or with slight constriction across M2; posterior lobe transverse, subrectangular to trapeziform, usually with weak terminal node. *?Upper Cambrian–Upper Ordovician:* Czechoslovakia, Llandeilo–lower Caradoc; England, Arenig–lower Llanvirn; Scotland, upper Caradoc–Ashgill; Ireland, Ashgill; Belgium, Llandeilo; France, ?lower Arenig; ?Argentina, lower Tremadoc; Russia (Altay Mountains), ?Upper Cambrian; Kazakhstan, middle–upper Caradoc; Uzbekistan, Ashgill; China (Zhejiang, Jiangsu), ?Tremadoc, upper Caradoc–Ashgill; USA (Texas), Lower Ordovician; Poland, Ashgill.——FIG. 236,*5a–c.* **C. morea* (SALTER), Lower Ordovician (Llanvirn); *a,* England (Shelve Inlier, Shropshire), holotype, cephalon, BGS 8699, ×5 (new); *b,c,* England (Old Church Stoke, Shropshire), *b,* cephalon, BGS 92922, ×5; *c,* pygidium, BGS 92923a, ×5 (new).

Dividuagnostus KOROLEVA, 1982, p. 21 [**D. minus;* OD; holotype (KOROLEVA, 1982, pl. 1, fig. 5), 1-358, KazIMS, Alma-Ata] [=*Peziziopsis* JU in QIU & others, 1983, p. 29 (type, *P. typica;* OD)]. Glabella with bulbous, subcircular anterior lobe; F3 strong, chevronate; posterior lobe subcircular, lacking F2; glabellar node from a short distance behind to immediately behind F3 furrow. Pygidial axis short, with well-developed constriction across M2; posterior lobe nearly equidimensional, semiovate to subrectangular, without terminal node. *Lower Ordovician–Upper Ordovician:* Kazakhstan, middle Ordovician; China (Zhejiang), ?Tremadoc, lower Ashgill, (Gansu), Caradoc–Ashgill, (Jiangxi), upper Caradoc; Wales, middle Arenig, Llandeilo–lower Caradoc; England, lower Llandeilo; Australia (New South Wales), upper Gisbornian–lower Eastonian; ?Canada (Newfoundland), Tremadoc.——FIG. 237,*3. D. mccoyi* (SALTER), middle Ordovician (upper Llandeilo), central Wales (Pen-Cerig Lake, Builth-Llandrindod area); exoskeleton, BMNH It 2671, ×5 (C. P. Hughes, 1969, pl. 1, fig. 3).

Galbagnostus WHITTINGTON, 1965, p. 304 [*Agnostus galba BILLINGS, 1865, p. 297; OD; lectotype (WHITTINGTON, 1965, p. 305, pl. 3, fig. 1–2, 4), 689b, GSC, Ottawa]. Glabella short, broad; F3 effaced; F2 weak; glabellar node very advanced, near anterior margin of glabella. Pygidial axis very short, tapering rearwards; posterior lobe transverse, trapeziform, with indistinct median ridge and deepening of axial furrow behind this ridge. *Lower to Middle Ordovician–middle Ordovician:* Canada (Newfoundland), Whiterock; Ireland, ?Sweden, ?Australia, middle Arenig.——FIG. 236,*3a,b.* **G. galba* (BILLINGS), middle Ordovician (Whiterock), Canada (Table Point, western Newfoundland); *a,* lectotype, cephalon, GSC 689b, ×6; *b,* pygidium, GSC 18395, ×15 (Whittington, 1965, pl. 3, fig. 1; pl. 4, fig. 9).

Geragnostella KOBAYASHI, 1939a, p. 171 [**Agnostus tullbergi* NOVÁK, 1883, p. 59; OD; neotype (PEK, 1977, p. 13, pl. 3, fig. 6), 1-356, OMR, Rokycany]. Mostly en grande tenue, with tendency to efface axial furrows surrounding posterior pygidial axial lobe. Glabella with F3 usually effaced or with straight median portion impressed; F2 weak; glabellar node immediately behind F3 furrow. Pygidial axis of moderate length, tapering rearward; posterior lobe semiovate, variably effaced, with strong terminal node. *Ordovician:* Czech Republic, Llanvirn; Spain, lower Llanvirn; Sweden, lower Arenig–Llanvirn; Turkey, lower–upper Arenig.——FIG. 236,*4a,b.* **G. tullbergi* (NOVÁK), Lower Ordovician (Llanvirn); *a,* Czech Republic (Sárka, Bohemia), pygidium, SBNM-ČD 310, ×10 (Pek, 1977, pl. 3, fig. 4); *b,* Czech Republic (Osek, near Rokycany), neotype, pygidium, MR 1-356, ×6.5 (Pek, 1977, pl. 3, fig. 6).

Geragnostus HOWELL, 1935b, p. 231 [**Agnostus sidenbladhi* LINNARSSON, 1869, p. 82; OD; lectotype (LINNARSSON, 1869, pl. 2, fig. 61; SD AHLBERG, 1989, p. 310), 25, SGU, Uppsala] [=*Geratrinodus* KOBAYASHI & HAMADA, 1978, p. 8 (type, *G. perconvexus;* OD); *Neptunagnostella* PEK, 1977, p. 14 (type, *Agnostus consors* HOLUB, 1912, p. 6, pl. 1, fig. 5)]. En grande tenue to nearly entirely effaced. Glabella with semiovate anterior lobe; F3 effaced or with straight median portion, lateral portions curving forward and outward; posterior lobe with weak F2 furrows; glabellar node immediately behind F3 furrow. Pygidial axis of moderate length, commonly constricted across M2; posterior lobe nearly equidimensional, semiovate to subrectangular, commonly with weak terminal node. *Ordovician:* Sweden, upper Tremadoc–Llanvirn; Norway, upper Tremadoc; France, upper Tremadoc–lower Arenig; Czech Republic, Arenig–Llanvirn; Scotland, Llandeilo; England, upper Tremadoc; Canada (Newfoundland), Whiterock; Argentina, Tremadoc; Turkey, Arenig; Tadzhikistan, Arenig; Uzbekistan, Ashgill; China (Hubei, Hunan), Tremadoc–Llanvirn; USA (Nevada), ?Lower Ordovician; Malaysia, ?middle Ordovician.——FIG. 237,*4a,b.* **G. sidenbladhi* (LINNARSSON), Lower Ordovician (upper Tremadoc, *Apatokephalus serratus* Biozone);
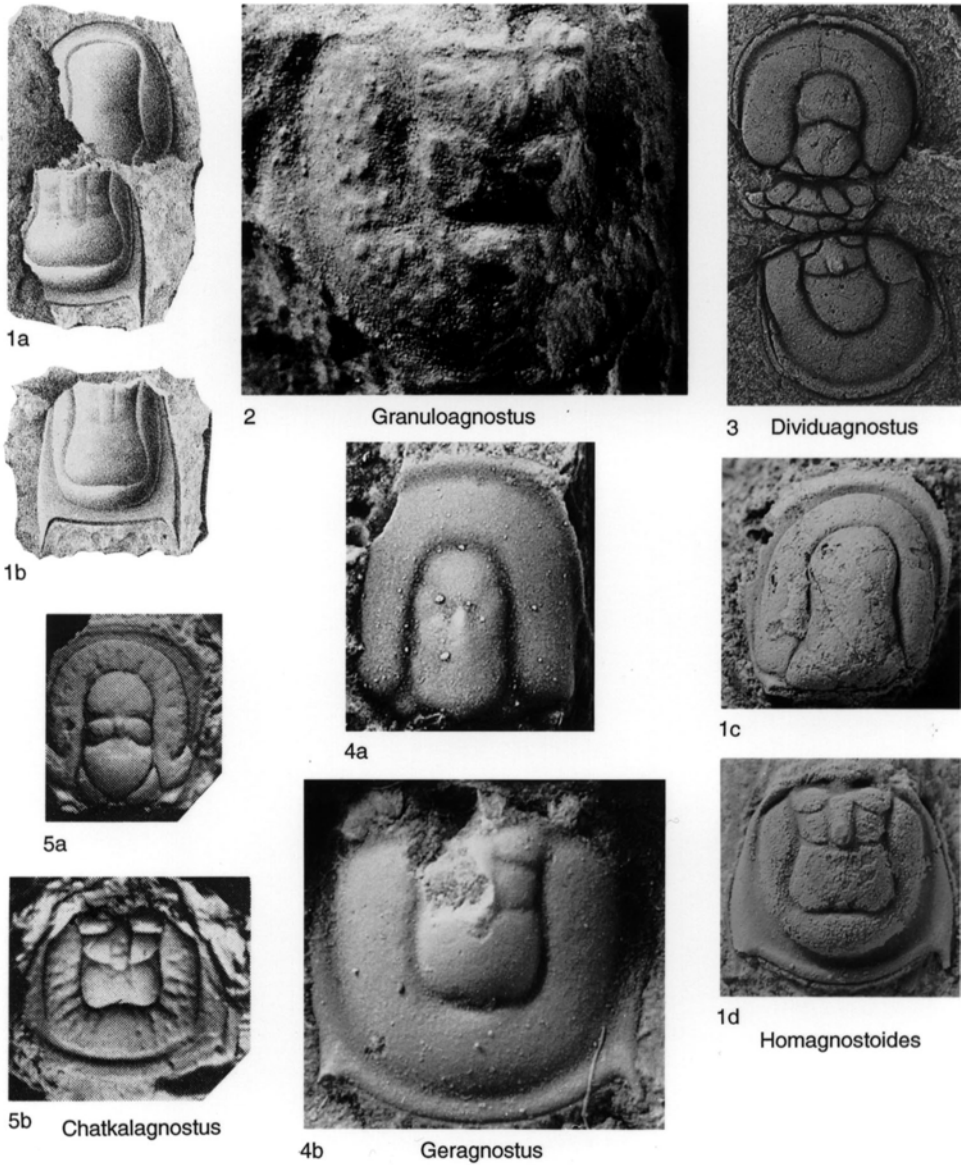
FIG. 237. Metagnostidae (p. 375–377)

a, Sweden (Hunneberg, Västergötland), cephalon, SGU 7886, ×12 (Ahlberg, 1989, fig. 1a,b); *b,* Sweden (Mossebo, Hunneberg, Västergötland), lectotype, pygidium, SGU 25, ×11 (Ahlberg, 1989, fig. 3a).

Granuloagnostus PEK, 1970, p. 129 [**Agnostus dusli* NOVÁK, 1883, p. 58; OD; holotype by monotypy (NOVÁK, 1883, pl. 1, fig. 12a–d), ČD 314, NMP, Prague]. Known only from a pygidium; pygidium similar to that of *Galbagnostus* but with coarsely

pustulose prosopon. *Ordovician (Llanvirn):* Czech Republic.——FIG. 237,*2. *G. dusli* (NOVÁK), Lower Ordovician (Llanvirn), Czech Republic (Osek, Sárka, Bohemia); holotype, pygidium, NM-ČD 314, ×8.5 (Pek, 1970).

Homagnostoides KOBAYASHI, 1939a, p. 178 [**Agnostus ferralsensis* MUNIER-CHALMAS & BERGERON in BERGERON, 1889, p. 342; OD; syntypes (BERGERON, 1889, pl. 4, fig. 8–9), not located]. Pygidium with short (sag.), laterally expanded, flasklike posterior

axial lobe; posteriorly truncate; long axial node extending across entire anteroaxis; acrolobe constricted, lacking median postaxial furrow; borders wide; border furrows nondeliquiate, retral spines. *Ordovician (Tremadoc):* France.——FIG. 237,*1a–d.* **H. ferralsensis* (MUNIER-CHALMAS & BERGERON); *a,b,* Lower Ordovician (Tremadoc, horizon e of COURTESSOLE & PILLET in CAPÈRA, COURTESSOLE, & PILLET, 1978), France (Montagne Noire, Hérault); unlocated syntypes, ×4.7 (Bergeron, 1889, pl. 4, fig. 8–9); *c,d,* Lower Ordovician, southern France (Montagne Noire), *c,* plesiotype, cephalon, IPM B 49009, upper Tremadoc, ×8 (new), *d,* plesiotype, pygidium, IPM B 49010, lower Arenig, ×8 (new).

Trinodus M'COY, 1846, p. 56 [**T. agnostiformi;* M; holotype by monotypy (M'COY, 1846, pl. 4, fig. 3), IV-3, NMING, Dublin]. Name restricted to type specimen, an incomplete and distorted internal mold of a cephalon, by FORTEY (1980, p. 27). *Ordovician (Llandeilo):* Ireland.——FIG. 236,*6.* **T. agnostiformis,* Ireland (Greenville, Wexford County); holotype, cephalon, NMING IV-3, ×8.4 (Whittington, 1950, pl. 68, fig. 1).

Family UNCERTAIN

Agnostogonus ÖPIK, 1967, p. 94 [**A. incognitus;* OD; holotype (ÖPIK, 1967, pl. 57, fig. 8), CPC 5846, AGSO, Canberra]. Cephalon and pygidium effaced but retaining narrow borders, faint indications of basal lobes and furrows, posterior margin of glabella, axial furrows of pygidial anteroaxis, and axial nodes of each shield. [May belong to either Ptychagnostinae or Spinagnostidae.] *lower Upper Cambrian:* Australia (Queensland), *G. stolidotus* Zone.——FIG. 238,*1a,b.* **A. incognitus,* Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Burke River area, western Queensland); *a,* holotype, cephalon, CPC 5846, ×8; *b,* paratype, pygidium, CPC 5847, ×8 (new).

Archaeagnostus KOBAYASHI, 1939a, p. 112 [**A. primigeneus;* OD; lectotype (SD RASETTI & THEOKRITOFF, 1967, p. 195, pl. 20, fig. 20), 18328, USNM, Washington, D.C.]. Small; nonscrobiculate, with nondeliquiate border furrows; cephalon questionably nonspinose; median preglabellar furrow absent. Glabella parallel-sided, with elongate, subquadrate anterior glabellar lobe; F3 deep, straight; posterior lobe strongly inflated posteriorly, lacking F1 and F2; glabellar node posteriorly located; glabellar culmination narrowly rounded or angular; basal lobes small, simple. Pygidium nonspinose; axis of moderate length, broad, rounded posteriorly, not reaching border furrow; F1, F2 effaced; median postaxial furrow absent. *upper Lower Cambrian:* USA (New York).——FIG. 239,*8a,b.* **A. primigeneus,* ?Lower Cambrian (?*Elliptocephala* fauna), USA (Salem, New York); *a,* lectotype, cephalon, USNM 18328, ×17; *b,* paratype, pygidium, USNM 18327, ×14 (new).

Armagnostus HOWELL, 1937, p. 1162 [**A. megalaxis;* OD; holotype (HOWELL, 1937, pl. 2, fig. 15), 9786, YPM(PU), New Haven]. The type species of this genus is based on a poorly preserved, distorted holotype pygidium and eleven paratypes, two of which (one cephalon and one pygidium) were illustrated by HOWELL (1937, pl. 2, fig. 12, 16). These are equally poorly preserved, making this species and hence the genus very difficult to interpret. *upper Middle Cambrian:* USA (Vermont), *Centropleura vermontensis* fauna; Canada (New Brunswick).——FIG. 238,*10.* **A. megalaxis,* upper Middle Cambrian (*Centropleura vermontensis* beds), USA (St. Albans, Vermont); holotype, pygidium, YPM(PU) 9786, ×2 (Howell, 1937, pl. 2, fig. 15).

Blystagnostus ÖPIK, 1961b, p. 95 [**B. laciniatus;* OD; holotype (ÖPIK, 1961b, pl. 23, fig. 5), CPC 3628, AGSO, Canberra]. Agnostoid with short, semiglobose pygidial axis, frill-like border, and granulose prosopon. *Middle Cambrian:* Australia (Queensland), *P. cassis* Zone.——FIG. 238,*9.* **B. laciniatus,* upper Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Burke River area, western Queensland); holotype, pygidium, CPC 3628, ×8 (new).

Ciceragnostus KOBAYASHI, 1937b, p. 442 [**Agnostus barlowi* BELT, 1868, p. 11; OD; lectotype (inferred from LAKE, 1906, p. 17), 58498, BMNH, London]. Largely effaced but preserving faint indication of glabella and pygidial anteroaxis; cephalic border very narrow; pygidial border wider, possibly deuterolobate. [Type species probably referrable to an effaced pseudagnostinid genus. All other species Middle Cambrian and variously assigned.] ?*Lower Ordovician (?Tremadoc):* Wales.——FIG. 239,*2.* **C. barlowi* (BELT), Wales (Dolgellau); lectotype, exoskeleton, BMNH 58498, ×9.3 (Morris & Fortey, 1985, pl. 1, fig. 1).

Delagnostus ÖPIK, 1961b, p. 88 [**D. dilemma;* OD; holotype (ÖPIK, 1961b, pl. 23, fig. 9), CPC 3633, AGSO, Canberra]. Pygidium largely effaced, without border or border furrows except anterolaterally; axial furrows only preserved anteriorly; vestigial axial node and faintly acuminate axis not reaching margin may be apparent; nonspinose; smooth. *upper Middle Cambrian:* Australia (Queensland, Northern Territory), upper *L. laevigata* Zone.——FIG. 239,*9.* **D. dilemma,* upper Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Burke River area, western Queensland); holotype, pygidium, CPC 3633, ×9 (new).

Gallagnostus HOWELL, 1935b, p. 227 [**G. geminus;* OD; holotype (HOWELL, 1935b, pl. 22, fig. 21), Miquel Collection H 13, UM, Montpellier]. Holotype of type species is a distorted, poorly preserved, complete exoskeleton. Apparently totally effaced, apart from cephalic and pygidial border furrows; borders narrow but distinct. *Middle Cambrian:* France, *Paradoxides* beds.——FIG. 238,*5.* **G. geminus,* France (Coulouma, Hérault); holotype, exoskeleton, UM Miquel Collection H13, ×7 (new).

Glaberagnostus ROMANENKO, 1985, p. 57 [**G. altaicus;* OD; holotype (ROMANENKO, 1985, pl. 5, fig. 5), 1160/4, ZSGU, Novokuznetsk]. Cephalon smooth, lacking a border, and mostly effaced, with
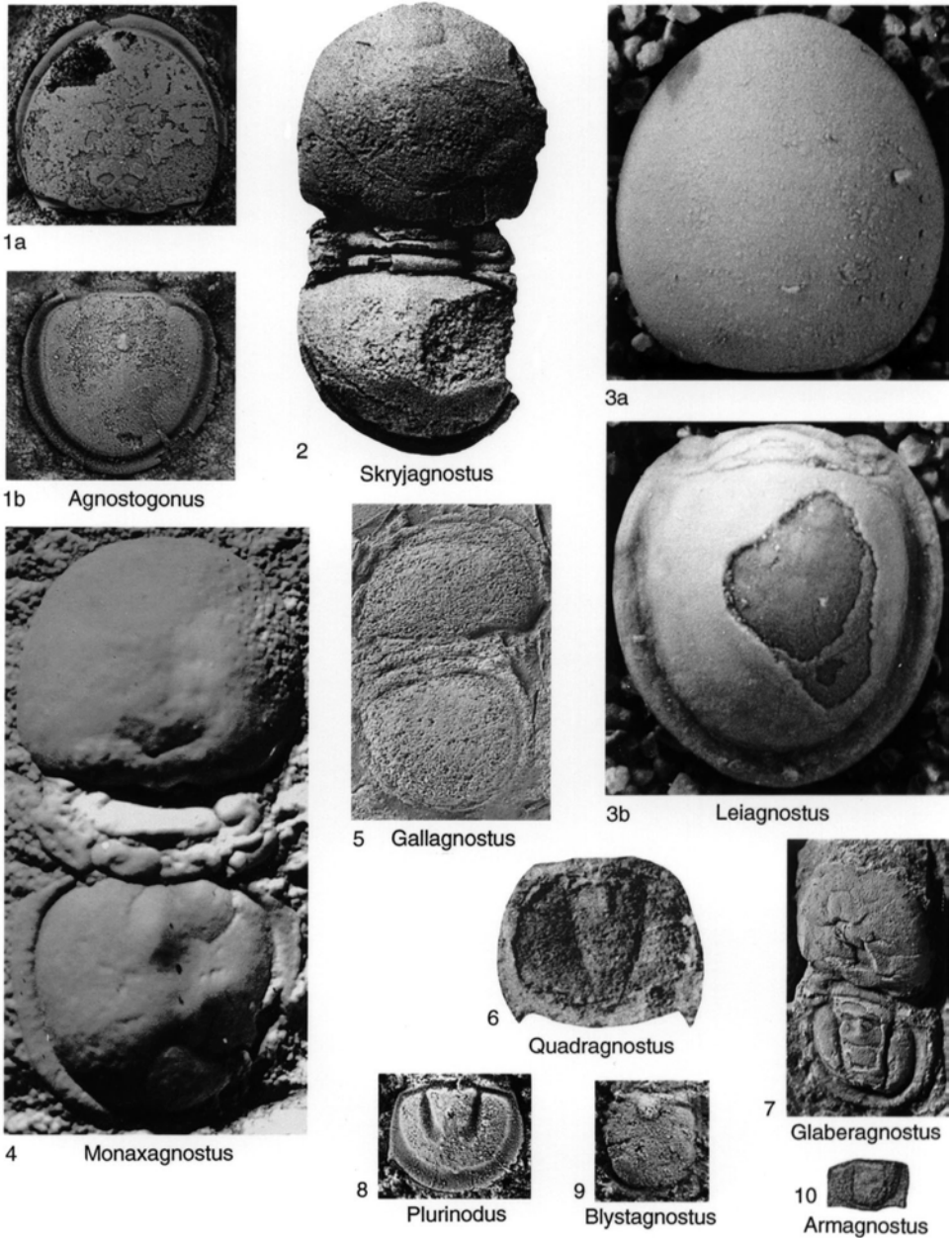
Fig. 238. Family Uncertain (p. 377–381)

bella defined only posteriorly; basal lobes small. Pygidium smooth; smaller than cephalon, with well-developed border and wide border furrow; axis defined laterally, posteriorly indistinct; axial node indistinct; marginal spines small or absent. *lower Upper Cambrian:* Russia (Altay Mountains), *G. reticulatus* Zone.——Fig. 238,*7.* **G. altaicus,* Upper Cambrian (Sakian, *Glyptagnostus*

reticulatus Zone), Russia (Altay Mountains, Siberia); holotype, exoskeleton, ZSGU 1160/4, ×4 (Romanenko, 1985, pl. 5, fig. 5).

Grandagnostus HOWELL, 1935a, p. 221 [**G. vermontensis;* OD; holotype (HOWELL, 1935a, pl. 22, fig. 8), 9736, YPM(PU), New Haven]. Generic name confined to the very poorly preserved holotype cephalon of the type species by ROBISON ex-
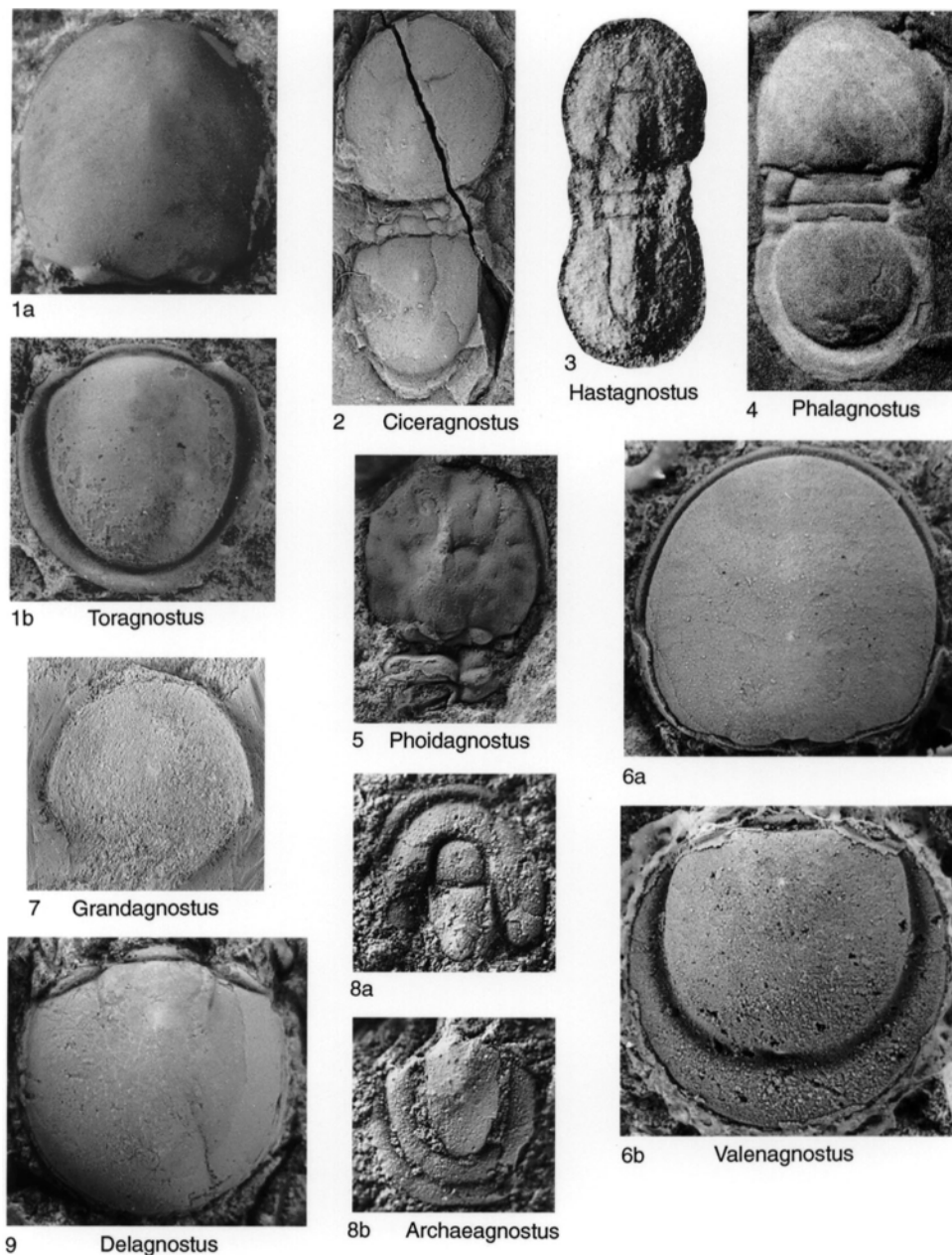
FIG. 239. Family Uncertain (p. 377–381)

(1988). Almost completely effaced; cephalic border extremely narrow (sag.) or absent; glabellar node advanced. *upper Middle Cambrian:* USA (Vermont).——FIG. 239,*7.* **G. vermontensis,* upper Middle Cambrian, USA (St. Albans, Vermont); holotype, cephalon, YPM(PU) 9736, ×3 (Robison, 1988, fig. 12.7).

Hastagnostus HOWELL, 1937, p. 1165 [**H. angustus;* OD; holotype (HOWELL, 1937, pl. 3, fig. 4), 9795, YPM(PU), New Haven]. The type species of this genus is based on a very poorly preserved, complete exoskeleton, which is difficult to interpret. *upper Middle Cambrian:* USA (Vermont), *Centropleura vermontensis* beds.——FIG. 239,*3. H. angustus,*

USA (St. Albans, Vermont); holotype, exoskeleton, YPM(PU) 9795, ×4 (Howell, 1937, pl. 3, fig. 4).

Leiagnostus JAEKEL, 1909, p. 401 [**L. erraticus;* OD; holotype (JAEKEL, 1909, fig. 23), K258, HMB, Berlin] [=*Phoidagnostoides* PILLET in CAPÈRA, COURTESSOLE, & PILLET, 1978, p. 78 (type, *L. migueli* SDZUY, 1958, p. 260, pl. 1, fig. 12–15)]. Cephalon and pygidium ovoid, effaced; cephalon lacking border, totally effaced except for advanced glabellar node; pygidium nonspinose, with weak axial node and relatively broad, flat border with nondeliquiate border furrow. *?uppermost Cambrian–Lower Ordovician:* Germany, Tremadoc–Arenig; Czech Republic, Tremadoc–Llanvirn; France, Wales, Tremadoc; Sweden, early Arenig; Argentina, Tremadoc (*N. argentina* Zone); China (Guizhou, ?Hunan, Gansu, Xinjiang), ?uppermost Cambrian–lower Llanvirn; ?Kazakhstan, *Rhadinopleura pyriforme* Zone.——FIG. 238,*3a,b.* **L. erraticus,* upper Lower Ordovician (?Kundan, upper Arenig–lower Llanvirn), Germany (glacial erratic in Neukölln, Berlin); *a,* cephalon of enrolled holotype, HMB K258, ×17 (Neben & Kreuger, 1971, pl. 11, fig. 37–38); *b,* pygidium of same specimen, HMB K258, ×17 (Ahlberg, 1988, fig. 2c).

Monaxagnostus LIU, 1982, p. 293 [**M. yongshunensis;* OD; holotype (LIU, 1982, pl. 209, fig. 8), HT 8123, HBG, Changsha]. Effaced exoskeleton; cephalon totally effaced except for traces of basal lobes, lacking border and border furrow; pygidium retaining indistinct axial node and rather broad border with nondeliquiate border furrow. *Middle Cambrian:* China (Hunan).——FIG. 238,*4.* **M. yongshunensis,* Middle Cambrian, China (Yongshun, Hunan); holotype, exoskeleton, HBG HT 8123, ×10 (Liu, 1982, pl. 209, fig. 8).

Phalagnostus HOWELL, 1955, p. 925 [*Battus nudus BEYRICH, 1845, p. 46; OD; neotype (BARRANDE, 1852, pl. 49, fig. 6; SD ŠNAJDR, 1958, p. 78), ČČ 229, No. 1017, NMP, Prague] [=*Phalacromina* KOBAYASHI, 1962, p. 29 (type, *Agnostus nudus ovalis* ILLING, 1916, p. 415, pl. 31, fig. 9–10)]. Almost totally effaced. Only glabellar culmination and small basal lobes weakly defined; otherwise cephalon totally effaced. Pygidial axis circular or ovate, defined by deep axial furrows; pygidial acrolobe undivided postaxially, forming posteriorly elongate pseudoborder, possibly with ventrally directed true border; anterolateral border furrow crossing pseudoborder and separating almost horizontal articulating facets; vestigial, elongate axial node present. *Middle Cambrian:* Sweden, *P. punctuosus* Zone; Denmark, *P. tessini* Zone; Wales, England, *H. parvifrons* Zone; France, *Paradoxides* beds; Czech Republic, *Eccaparadoxides pusillus* Zone; Russia (Bennett Island, Yakutia), Canada (Newfoundland), *P. davidis* Zone; ?Canada (Northwest Territories), *Cedaria minor* and *Olenaspella regularis* to *Proceratopyge rectispinata* Zones; ?USA (Vermont).——FIG. 239,*4.* **P. nudus* (BEYRICH); Middle Cambrian (*E. pusillus* Zone), Czech Republic (Týřovice, Bohemia); neotype, exoskeleton, NM ČČ 229, No. 1017, ×5 (Šnajdr, 1958, pl. 5, fig. 3).

Phaldagnostus IVSHIN in KHALFIN, 1960, p. 167 [**P. orbiformis;* OD; holotype (KHALFIN, 1960, p. 168, fig. 48), Por-1, ZSGU, Novokuznetsk]. Ivshin's type specimen has never been satisfactorily illustrated. The description does not permit distinction between this and other effaced genera. *Upper Cambrian:* Russia (Altay Mountains), Kazakhstan (Lesser Karatau Mountain Range), *G. reticulatus* to *P. curtare* Zones.

Phoidagnostus WHITEHOUSE, 1936, p. 93 [**P. limbatus;* OD; holotype (WHITEHOUSE, 1936, pl. 9, fig. 10), 3207, UQF, Brisbane]. Only cephalon known; acrolobe moderately convex, unconstricted, scrobiculate; border narrow; border furrow nondeliquiate; axial furrows anteriorly effaced, weakly developed posteriorly; median preglabellar furrow clearly developed; glabellar culmination rounded; elongate axial node at about cephalic midlength, flanked by subtriangular depressions; basal lobes short, transverse, tumid; prosopon smooth. *upper Middle Cambrian:* Australia (Queensland), *P. cassis* Zone.——FIG. 239,*5.* **P. limbatus,* upper Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Burke River area, western Queensland); holotype, cephalon, UQF 3207, ×6 (Whitehouse, 1936, pl. 9, fig. 10).

Plurinodus ÖPIK, 1967, p. 170 [**P. discretus;* OD; holotype (ÖPIK, 1967, pl. 60, fig. 17), CPC 5889, AGSO, Canberra]. Diminutive pygidia with broad borders, deliquiate border furrows, and unconstricted acrolobe; anteroaxis tapers rearward, defined by deep and wide axial furrows; F1, F2 effaced; completely effaced posterior lobe; terminal node situated at border furrow; retral marginal spines; agnostoid articulating device. Cephalon with depressed or effaced anterior glabellar lobe may be associated. [May belong to Pseudagnostinae.] *lower Upper Cambrian:* Australia (Queensland), *G. stolidotus* Zone.——FIG. 238,*8.* **P. discretus,* Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Duchess area, western Queensland); holotype, pygidium, CPC 5889, ×8 (new).

Quadragnostus HOWELL, 1935a, p. 219 [**Q. solus;* OD; holotype (HOWELL, 1935a, pl. 22, fig. 6), 9793, YPM(PU), New Haven]. The type species of this genus is based on a very poorly preserved holotype pygidium and an equally poorly preserved, fragmentary paratype cephalon, both of which are difficult to interpret. *upper Middle Cambrian:* USA (Vermont), *Centropleura vermontensis* beds.——FIG. 238,*6.* **Q. solus,* USA (St. Albans, Vermont); holotype, pygidium, YPM(PU) 9793, ×8.5 (Howell, 1935a, pl. 22, fig. 6).

Skryjagnostus ŠNAJDR, 1957, p. 236 [**S. pompeckji;* OD; holotype (ŠNAJDR, 1958, pl. 6, fig. 4), Šnajdr Collection, Br-191, NMP, Prague]. Exoskeleton almost totally effaced, except for a hint of axial furrows around rear of basal glabellar lobes and the presence of extremely narrow (sag.) border in both cephalon and pygidium. *Middle Cambrian:* Czech Republic, *E. pusillus* Zone; Russia (northwestern Siberia), *Pedinocephalus* or *Toxotis* Zone.——FIG. 238,*2.* **S. pompeckji,* Middle Cambrian (*Eccapara-*

doxides pusillus Zone), Czech Republic (Týřovice, Bohemia); holotype, exoskeleton, NM Br-191, ×12.5 (Horný & Bastl, 1970, pl. 1, fig. 3).

Toragnostus ROBISON, 1988, p. 52–53 [*Agnostus bituberculatus* ANGELIN, 1851, p. 6; OD; neotype proposed herein (HOLM & WESTERGÅRD, 1930, pl. 4, fig. 4), Ar 9563a, RM, Stockholm]. Almost completely effaced, lacking cephalic border and with wide pygidial border. Cephalon strongly convex; glabella outlined posteriorly, narrow, tapering forward, with broadly rounded or obtusely angular culmination; glabellar node elongate, well in front of cephalic midlength; basal lobes simple, bulbous, strongly transverse. Pygidial axis very broad, with M1 bounded by axial furrow; axial node weak, elongate. [The lectotype selected by ROZOVA (1964, p. 19) from the material illustrated by WESTERGÅRD (1946, pl. 14, fig. 10) is invalid because WESTERGÅRD's material was not part of ANGELIN's type lot.] *upper Middle Cambrian:* USA (Alaska); Denmark; China (Hunan); Sweden, *S. brachymetopa* Zone; Russia (Siberian Platform), *C. oriens* and *A. henrici* Zones, (Bennett Island), zone unknown; Kazakhstan (Tyan-Shan Range), Mayaian; northern Greenland, *L. laevigata* Zone.——FIG. 239,*1a,b.* *T. bituberculatus* (ANGELIN), upper Middle Cambrian (*Jincella brachymetopa* Zone), Sweden (Andrarum, Skåne); *a,* neotype, cephalon, RM Ar 9563a, ×7.7; *b,* topotype, pygidium, RM Ar 9563b, ×7.7 (new).

Valenagnostus JAGO, 1976, p. 144 [*Agnostus nudus* BEYRICH var. *marginata* BRÖGGER, 1878, p. 73; OD; holotype (BRÖGGER, 1878, pl. 6, fig. 3), not traced, PMO, Oslo]. Exoskeleton almost completely effaced; cephalic border and border furrow extremely narrow (sag.); pygidium with wide border, especially posteriorly, and deliquiate to subdeliquiate border furrow; unconstricted acrolobes. Cephalic axial furrows effaced, but axial glabellar node may be present retrally. Vestigial pygidial axial furrows may define long (sag.) axis extending to border furrow and bearing terminal node; axial node almost totally effaced; nonspinose; smooth. *upper Middle Cambrian–lower Upper Cambrian:* Norway, *P. rugulosus* Zone; Sweden, *Hyolithes* Limestone; Denmark, *P. davidis* Zone; Australia (Tasmania), *?P. punctuosus* to *L. laevigata* Zones, (Queensland), *D. notalibrae* to *E. eretes* Zones.——FIG. 239,*6a,b.* *V. marginatus* (BRÖGGER), upper Middle Cambrian (*Paradoxides forchhammeri* Zone), Norway (Aborrfallet, Ångermanland); *a,* figured specimen, cephalon, SGU 5018, ×8; *b,* figured specimen, pygidium, SGU 5022, ×8 (new)

Superfamily UNCERTAIN

Family PHALACROMIDAE
Hawle & Corda, 1847

[Phalacromidae HAWLE & CORDA, 1847, p. 42] [=Platagnostidae HOWELL, 1935b, p. 228]

Cephalon variably effaced; pygidium with long (sag.) and laterally expanded axis; py-

gidial axial node close to middle of axis, elongate; transverse groove or furrow present immediately behind axial node; variable border morphology and spinosity. *Middle Cambrian.*

Phalacroma HAWLE & CORDA, 1847, p. 43 [*Battus bibullatus* BARRANDE, 1846, p. 14; SD RAYMOND, 1913a, p. 139; lectotype (BARRANDE, 1852, pl. 49, fig. 6; SD ŠNAJDR, 1958, p. 74), ČC 244, NMP, Prague] [=*Platagnostus* HOWELL, 1935b, p. 228 (type, *P. immensus;* OD)]. Cephalon almost totally effaced, having barely perceptible border and axial furrows that are defined only posteriorly; basal lobes effaced. Pygidium with very wide (tr.) axis extending to narrow (sag.) posterior border; nonspinose. *Middle Cambrian:* Czech Republic, *Eccaparadoxides pusillus* Zone; France, *Paradoxides* beds; Russia (Siberia), *T. fissus* or *P. hicksi* to upper *P. davidis* Zones.——FIG. 240,*1.* *P. bibullatum* (BARRANDE); Middle Cambrian (*E. pusillus* Zone), Czech Republic (Týřovice, Bohemia); lectotype, exoskeleton, NM-ČC 244, No. 1027, ×8.7 (Horný & Bastl, 1970, pl. 1, fig. 1).

?Dignagnostus HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 111 [*D. grandis;* OD; holotype (REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 12, fig. 7–8), 483/218b, MMG, Tashkent]. With tendency to efface pygidial F1 and F2 furrows while retaining axial and border furrows. Pygidial axis pyriform, transversely expanded, long (sag.), reaching posterior border furrow; acrolobe unconstricted; pleural fields very narrow (tr.); borders of significant width; posterolaterally spinose. *Middle Cambrian:* Uzbekistan, *Sdzuyella-Aegunaspis* beds.——FIG. 240,*6.* *D. grandis;* holotype, pygidium, MMG 483/218b, ×10 (Repina, Petrunina, & Hajrullina, 1975, pl. 12, fig. 7–8).

Lisogoragnostus ROZOVA in LISOGOR, ROZOV, & ROZOVA, 1988, p. 64 [*L. kalisae;* OD; holotype (LISOGOR, ROZOV, & ROZOVA, 1988, pl. 5, fig. 9), 848/36, CSGM, Novosibirsk]. Cephalon partly effaced, with vestigial basal lobes and glabellar culmination; well-defined border furrows. Pygidium apparently lacking border or border furrows, with wide (tr.) short (sag.) axis bearing a low axial node anteriorly and lacking F1 and F2 furrows. *Middle Cambrian:* Kazakhstan, beds with *Peronopsis fallax;* Russia (Siberian Platform), *Tomagnostus fissus* Zone.——FIG. 240,*5.* *L. kalisae,* Middle Cambrian (Amgaian, beds with *Peronopsis fallax*), southern Kazakhstan (Kirshabakty River); holotype, exoskeleton, CSGM 848/36, ×12 (Lisogor, Rozov, & Rozova, 1988, pl. 5, fig. 9).

Family SPHAERAGNOSTIDAE
Kobayashi, 1939

[Sphaeragnostidae KOBAYASHI, 1939a, p. 177]

Agnostina with totally effaced cephalon, but retaining pygidial border, and short
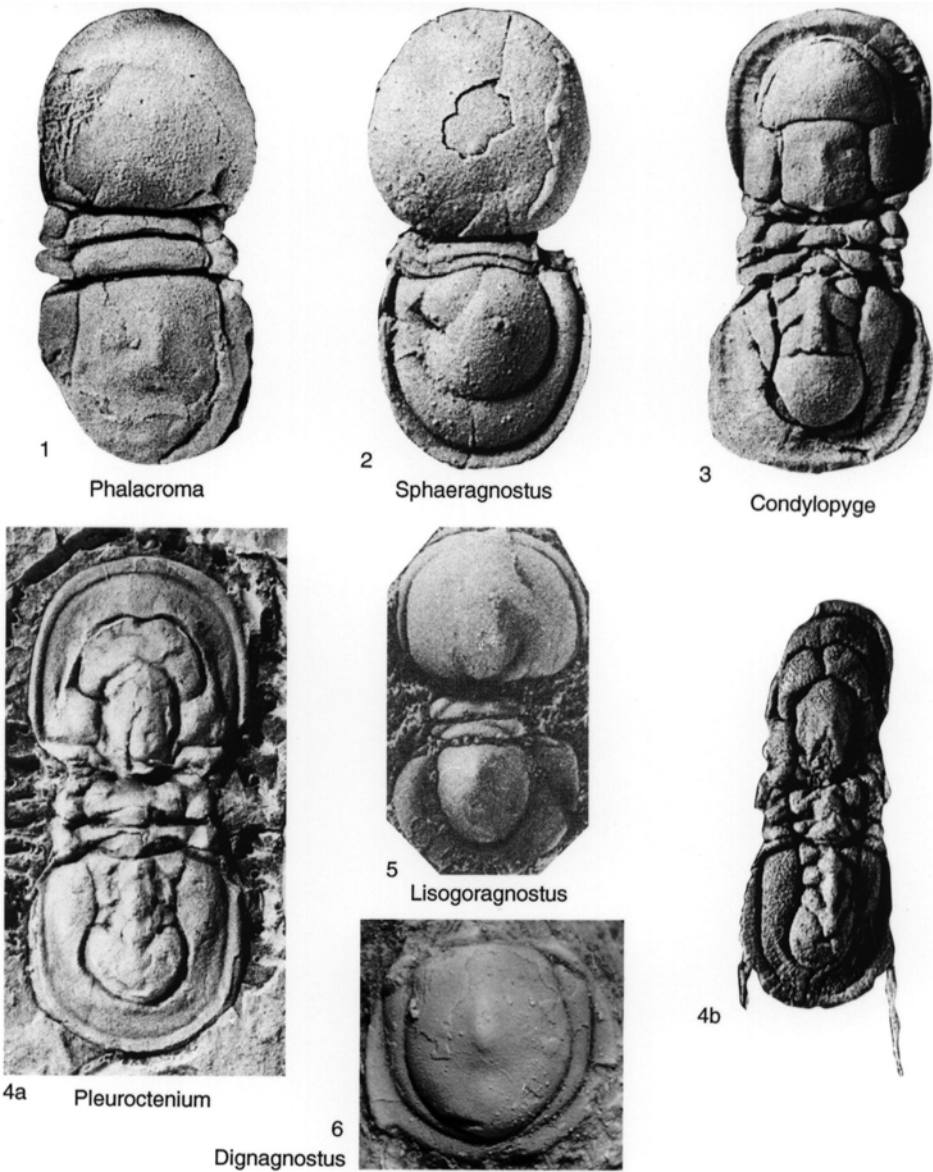
FIG. 240. Phalacromidae, Sphaeragnostidae, and Condylopygidae (p. 381–383).

(sag.), convex, subcircular pygidial axis. *Ordovician.*

Sphaeragnostus HOWELL & RESSER in COOPER & KINDLE, 1936, p. 361 [**Agnostus similaris* BARRANDE, 1872, p. 144; OD; holotype (BARRANDE, 1872, pl. 14, fig. 17–18), ČD 489 (see PEK, 1977, pl. 7, fig. 6), NMP, Prague]. Cephalon totally effaced, lacking traces of border furrows, axial furrows, and glabellar node externally. Pygidium with

well-defined, nondeliquiate border furrows, narrow border, and axial furrows defining short (sag.), broad (tr.), convex (tr., sag.), subcircular, unfurrowed axis bearing both axial and terminal nodes; acrolobe unconstricted, convex, lacking median postaxial furrow; posterolateral spines minute or absent. Pleural regions of thoracic segments extremely restricted (tr.); axial portions short (sag.), very wide (tr.). *Ordovician:* Czech Republic, Llandeilo; Wales, Llandeilo–Ashgill; Denmark,

Sweden, Poland, Ashgill; Ireland, lower Ashgill; Kazakhstan, upper Tremadoc, Caradoc; Turkestan Mountain Range, Ashgill; China (Jiangxi, Zhejiang, Nei Monggol, Jiangsu), Ashgill, (Hunan), Llandeilo; Canada (Quebec), middle Ashgill.——Fig. 240,2. *S. similaris* (Barrande), Middle Ordovician (Llandeilo), Czech Republic (Svatá Dobrotivá, Bohemia); holotype, exoskeleton, NM-ČD 489 (L16944), ×13.5 (Horný & Bastl, 1970, pl. 1, fig. 7).

Superfamily CONDYLOPYGOIDEA Raymond, 1913

[Condylopygoidea Raymond, 1913a, p. 139] [*nom. transl.* Shergold, Laurie, & Sun, *ex* Condylopygidae Raymond, 1913a, p. 139, *partim*]

Agnostina with transverse basal glabellar lobes separated by a median plate rather than joined by connective band bearing median tubercle or spine; anterior glabellar lobe laterally expanded. Pygidial axis with triannulate anteroaxis and posteriorly rounded posteroaxis. *Lower Cambrian–Middle Cambrian.*

Family CONDYLOPYGIDAE Raymond, 1913

[Condylopygidae Raymond, 1913a, p. 139]

With characteristics of superfamily. *Lower Cambrian–Middle Cambrian.*

Condylopyge Hawle & Corda, 1847, p. 50 [**Battus rex* Barrande, 1846, p. 17; M; lectotype (Barrande, 1852, pl. 49, fig. 5; SD Šnajdr, 1958, p. 52), ČC 237, NMP, Prague] [=*Paragnostus* Jaekel, 1909, p. 396 (type, *Battus rex* Barrande, 1846, p. 17); *Fallagnostus* Howell, 1935b, p. 230 (type, *F. blayaci;* OD)]. En grande tenue; cephalon and pygidium with strongly deliquiate border furrows; anterior glabellar lobe very large, approximately semicircular; posterior lobe cylindrical, with retral axial node; pygidial axis bearing elongate keel formed by fusion of axial nodes anteriorly; spines, where developed, short; prosopon smooth. *upper Lower Cambrian–Middle Cambrian:* Czech Republic, *Eccaparadoxides pusillus* Zone; England, *Protolenus* to *P. atavus* or *T. fissus* Zones; Wales, *B. oelandicus* Zone; Sweden, *A. insularis* to *P. punctuosus* Zones; France, *Paradoxides* beds; Germany, *P. insularis* to *P. paradoxissimus* Zones; Spain, *P. paradoxissimus* Zone; Canada (Newfoundland, New Brunswick), *P. hicksi* to *P. davidis* Zones; USA (Massachusetts); Russia (northern Siberia), Amgaian, *Oryctocara* to *Kounamkites* Zones, (southeastern Siberia), Mayaian Stage, *T. fissus* Zone.——Fig. 240,3. **C. rex* (Barrande), Middle Cambrian (*E. pusillus* Zone), Czech Republic (Týřovice, Bohe-

mia); lectotype, exoskeleton, NM-ČC 237, No. 1034, ×5 (Horný & Bastl, 1970, pl. 1, fig. 2).

Pleuroctenium Hawle & Corda, 1847, p. 116 [**Battus granulatus* Barrande, 1846, p. 15; M; lectotype (Barrande, 1852, pl. 49, fig. 5–7; SD Šnajdr, 1958, p. 56), ČC 250, No. 1008, NMP, Prague] [=*Dichagnostus* Jaekel, 1909, p. 396 (type, *Battus granulatus* Barrande, 1846, p. 15)]. En grande tenue; cephalon and pygidium with narrow borders and border furrows and weakly constricted acrolobes; anterior glabellar lobe crescentic, wrapped around posterior glabellar lobe, and commonly bisected by median sulcus; long cephalic and posterolateral pygidial spines commonly developed; discrete spines developed from axial pygidial nodes; lateral and posterior margins frequently bearing fringe of small spines; prosopon granular. *Middle Cambrian:* Czech Republic, *E. pusillus* Zone; England, *P. aurora* to *P. punctuosus* Zones; Wales, Sweden, *H. parvifrons* Zone; France, *Paradoxides* beds; Canada (Newfoundland, New Brunswick), *P. hicksi* to *P. davidis* Zones.——Fig. 240,4a. *P. granulatum scanense*, Middle Cambrian (*Hypagnostus parvifrons* Zone), England (Nuneaton district, Warwickshire); exoskeleton, BGS IGS Zs 4571, ×6 (Rushton, 1979, fig. 2j).——Fig. 240,4b. **P. granulatum* (Barrande), Middle Cambrian (*Eccaparadoxides pusillus* Zone), Czech Republic (Týřovice, Bohemia); lectotype, exoskeleton, NM-ČC 250, No. 1008, ×10.8 (Horný & Bastl, 1970, pl. 1, fig. 6).

NOMINA NUDA

Cenagnostus Whittard, 1940, p. 157.
Clavagnostotes Lu & Lin, 1981, p. 118.
Kitatagnostus Ergaliev, 1965, p. 24.
Munagnostus Ivshin in Khalfin, 1960, p. 17.
Parapseudagnostus Petrunina, 1966, p. 8.
Pseudagnostella Koroleva, 1982, p. 35.

REJECTED GENERA

Discagnostus Öpik, 1963, p. 55 [Eodiscida; Shergold, Laurie, & Sun, 1990, p. 8].
Gallagnostoides Kobayashi, 1939b, p. 580 [=*Microparia (Microparia)* Hawle & Corda, 1847, p. 52; Fortey & Owens, 1987, p. 172].
Mallagnostus Howell, 1935b, p. 228 [Eodiscida; Rushton, 1966, p. 10; Rasetti & Theokritoff, 1967, p. 190].
Pseudotrinodus Kobayashi & Hamada, 1971, p. 399 [Aulacopleurinae; Thomas & Owens, 1978, p. 74].

Suborder EODISCINA Kobayashi, 1939

[*nom. correct.* Moore, 1959, p. 187, *pro* Eodiscidi Kobayashi, 1939a, p. 74]

With or without eye, facial suture proparian when present; two or three thoracic segments, articulating half ring on anterior segment; pygidium with axis usually

extending close to border, pleural region segmented in some species. Protaspis calcified (known in few taxa). *Lower Cambrian–Middle Cambrian.*

INTRODUCTION TO SUBORDER EODISCINA

P. A. Jell

Origin and Phylogeny

Eodiscoids are generally considered to have evolved from polymerid trilobites by paedomorphosis (Stubblefield, 1936; Jell, 1975a; Fortey, 1990a; Shergold, 1991). Fortey (1990a, p. 556) suggested that *Sinodiscus changyangensis* S. Zhang, 1980 (in W. Zhang, Lu, & others) might be the most primitive eodiscoid. Another candidate could be the oldest genus known, *Tsunydiscus* W. Chang, 1966. Evaluation of *Tsunydiscus* begins by comparison with *Dipharus clarki* Korobov, 1980. That species may represent an immature redlichioid rather than an eodiscoid because of the dominant palpebro-ocular ridges, extremely long librigenae, and free pleural tips on the pygidium of variable numbers of segments. Furthermore, it occurs with several species of the redlichioid *Bulaiaspis* Lermontova, 1956 (in Tchernysheva & others), to any one of which it may belong. Glabellae of *D. clarki* and *Tsunydiscus* are extremely similar and distinct from all other eodiscoids, prompting separation of *Tsunydiscus* at the family level in the classification below. Among the species of *Tsunydiscus* are to be found those features (well-defined dorsal furrows and eye ridges and short preglabellar field) thought by Fortey (1990a) to characterize the primitive eodiscoid along with long librigenae as a redlichioid legacy; reduction in length of librigenae is evident on all eodiscoid lineages.

The phylogenetic scheme of Jell (1975a), which recognized three major lineages within the superfamily, is adopted here and is essentially unchanged except for reallocation and reassessment of several genera, identification of the Tsunydiscidae as the prob-
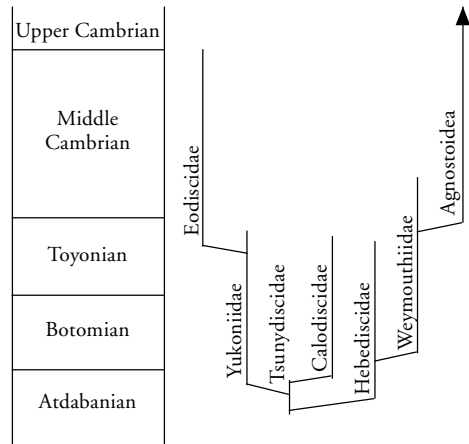
Fig. 241. Phylogenetical diagram of order with approximate relationships between superfamilies and families within Eodiscoidea.

able ancestor to all three lineages, and separation of the three lineages at family level (Fig. 241).

Descendants

The possibility that the Agnostina descended from the Eodiscoidea has been extensively debated, with Fortey (1990a) outlining the case for and Shergold (1991) the case against this possibility. Fortey (1990a, fig. 14) listed derived characters of Agnostida as: (1) reduction in number of thoracic segments to three or fewer, (2) loss of calcification of rostral plate, (3) an occipital width greatly exceeding width of preoccipital glabella, (4) broad, rolled cephalic border, (5) long cephalic shield (with maximum width in front of posterior margin in most species), (6) reduced or absent genal spines, and (7) fulcrate articulation. He identified the derived character of the Agnostina out of this group as the cephalothoracic aperture. Modifications to the occipital structure in miomerids (which bounds this aperture anteriorly) produce significant derived features; the trend in the Weymouthiidae to shortening and obliteration of the occipital ring is carried on in the Agnostina with the occipital ring divided into basal lobes as had evolved already in the eodiscoids *Chelediscus*

and *Tannudiscus. Tannudiscus* has been advanced as the eodiscoid closest to the ancestor of the Agnostina, with its bilobed glabella, basal glabellar lobes, both glabella and pygidial axis isolated from border furrow, and undivided pygidial axis. Although Shergold (1991) acknowledged *Tannudiscus* as a good candidate for the ancestor of Agnostina, he argued against such ancestry on the basis of stratigraphic difficulties and poor quality of Lower Cambrian materials involved. These negative arguments are not accepted here. Rasetti (1945b, 1948a, 1952a) championed the major distinction between eodiscoids and Agnostina, and Shergold regarded his discussion (1991) as supporting Rasetti's views. Rasetti (1972), however, had already rescinded his opinion on this matter, acknowledged the close relationship between the two groups, stated that the Agnostina were almost certainly derived from eodiscoids, and considered that the two groups together formed the Miomera.

Lack of a calcified protaspis in Agnostina had been employed as negative evidence for a relationship between eodiscoids and Agnostina, prior to the discovery of such a protaspis in *Neocobboldia chinlinica* by X. Zhang (1989) and *Pagetia ocellata* by Shergold (1991). Shergold (1991) used this discovery to separate eodiscoids and Agnostina, although protaspides are unknown in the Weymouthiidae, the eodiscoids thought to be ancestral to Agnostina. This is despite the record of a calcified protaspis in *Pseudagnostus benxiensis* Qian, 1982 (this record is questioned herein by Chatterton and Speyer, p. 213) and the argument of Fortey (1990a) that secondary loss of calcification in protaspides of Agnostina should be expected in light of their other specializations. Arguments based on the lack of this ontogenetic feature are surely premature in light of Qian's (1982) possible discovery and the need to search in more detail for protaspides of Agnostina.

Müller and Walossek (1987) argued for isolation of the Agnostina because the appendages of *Agnostus pisiformis* are entirely distinct from any other trilobite, but this argument must be set aside until appendages of eodiscoids are known; miomerids are specialized trilobites, with Agnostina the more specialized within the group, so appendages of Agnostina would be expected to be distinct from most other trilobites that are not so specialized.

Descent of Agnostina from Eodiscoidea has not been established beyond doubt. A large body of accepted inferential evidence makes it distinctly likely, but more research is needed.

History of Classification

During the last century almost all eodiscoid species were assigned to *Microdiscus* (Emmons, 1855), despite the fact that the type of that genus was known to be a juvenile of a post-Cambrian trilobite and not an eodiscoid. Matthew's (1896) subdivision of that genus into four sections was the first attempt at classification within the group. Kobayashi (1944a) thought the most significant subdivision should be based on whether there are two or three thoracic segments, with the next level of classification based on presence or absence of eyes and effacement of dorsal furrows. On this basis he arranged fifteen genera into five families, although from his table 4 showing phylogenetical relationships among the genera it is clear that he did not consider the Eodiscidae, one of his five families, a phylogenetic group.

Rasetti (1952a) repeated the observation that number of thoracic segments and presence or absence of eyes were the best characters for subdivision of the group. He recognized, however, that the number of thoracic segments could not be used at the family level. Moreover, he clearly acknowledged the likelihood that eyes and sutures had been independently lost in several lineages. Nevertheless, he proposed a classification into two families based solely on the presence or absence of eyes and facial sutures, stressing that this was a matter of expedience in view of the incomplete knowledge of the group and not necessarily relevant to phylogeny.

This classification was employed by Moore (in Harrington & others, 1959) and has been the basis of almost all classificatory schemes developed for or applied to the group since that date (including S. Zhang in W. Zhang, Lu, & others, 1980; Korobov, 1980; Repina & Romanenko, 1978).

A phenetic approach to classification (Jell, 1975a) showed that presence or absence of eyes and sutures was not a major discriminator, and the three lineages identified during that study each contained blind and sighted genera. By 1975 the range of morphology in the 34 genera was sufficient to start piecing together lineages with the intention of establishing a classification from the phylogeny. This was not entirely successful, and the resulting two families have not been universally accepted despite the fact that this classification is demonstrably closer to phylogeny than any previous scheme. Öpik (1975a) also recognized the inappropriateness of Rasetti's utilitarian classification and proposed three families that correspond roughly to the lineages identified by Jell (1975a). Öpik's tabulation of the features of the group indicated a mosaic pattern of morphology without clearcut family indicators.

Present Classification

There are now more than 50 genera. Some are intermediate between earlier established genera, but others exhibit entirely new phylogenetic branches, sometimes clarifying and sometimes complicating our understanding of the group. In the present classification the findings of Jell (1975a) and Öpik (1975a) are employed. These findings, along with the many new taxa described since 1976, lead to a classification into six families based on all available features, but the structure of the glabella and, in particular, modifications of the occipital area are key features. If the group evolved by neoteny from the Redlichioidea, as discussed above, the primitive structure of the eodiscoid occipital ring would be that seen in the Hebediscidae and Calodiscidae where SO is transverse and of more or less uniform depth and where LO is of uniform length, usually the same as L1, and may have a posterior spine; this is the primitive occipital structure. The Calodiscidae have the apomorphy of a reduced number of segments in the pygidial axis, although this feature is not exclusive to that family. The Yukoniidae plus Eodiscidae have the unique feature of the expansion of the rear of the glabella (mostly L1) into a long, slender posteromedian spine that lies over and disrupts the occipital ring. The Eodiscidae have the further distinction of scrobicules developed on the anterior border. (These may be secondarily effaced on some species.) The Weymouthiidae are all blind and include forms with the rear of the glabella roundly expanded over the occipital ring or vertically spinose, forms with the occipital ring obliterated by general glabellar expansion, and forms with primitive occipital structure but greatly increased numbers of axial segments.

Eodiscoid phylogeny is still incompletely understood, and assignment of some genera to higher taxa will remain a difficult task because of the great variety of glabellar modifications, progression to effacement in numerous lineages, and demonstrated parallel evolution of certain features (e.g., border nodes in the Calodiscidae and Serrodiscidae). The suprageneric classification cannot yet be considered stable because the phylogenetic relationships between all genera are far from clear, and the evolutionary pathways of several lineages are uncertain, particularly near their origins.

Superfamily EODISCOIDEA Raymond, 1913

[*nom. transl.* Jell, 1975a, p. 26, *ex* Eodiscidae Raymond, 1913b, p. 102]
[=Eodiscidea Richter, 1932, p. 852, *partim*; Dawsoniidea Kobayashi, 1943, p. 38; Eodiscoidae Hupé, 1953a, p. 108]

Glabella usually well defined, and subcylindrical, tapered forward, or narrowed, or expanded near midlength; LO may be simple ring of uniform length (sag.), may be almost obliterated by enlargement posteriorly of L1 portion of glabella into

large, posterior spine overlying LO, may be shortened by rounded posteromedial expansion of the L1 portion of the glabella, or may be divided into basal lobes by such expansion. Genae elevated laterally, depressed in front of glabella. Cephalic border may be smooth or have marginal spines, tubercles, or radial grooves (scrobicules). Eye small and abathochroal, may be present in the absence of facial sutures, or may be only an eye tubercle. Thorax with second or third segment bearing posteromedian spine in some. Pygidial axis of 3 to 12 simple, unmodified rings or with ring furrows effaced; usually prominent, with axial spine or spines in some. Pleural fields furrowed or not. Border narrow, with denticulate or spinose margin. Doublure narrow. *Lower Cambrian–Middle Cambrian.*

Family TSUNYDISCIDAE
S. Zhang, 1980

[*nom. transl.* JELL, herein, *ex* Tsunydiscinae S. ZHANG in W. ZHANG, LU, & others, 1980, p. 40]

Glabella extremely narrow, lateral glabellar furrows usually obscure, with rounded and expanded frontal glabellar lobe. SO transverse, complete; LO at least as long as L1, usually expanded laterally, may bear sharp, posteriorly directed spine. Long, curved posterior fixigenal spine may be present. Librigena long. Pygidium with narrow, multisegmented axis (six or more segments). *Lower Cambrian.*

Tsunydiscus W. CHANG, 1966, p. 150 [**Hebediscus niutitangensis* W. ZHANG, 1964, p. 3; OD; holotype (W. ZHANG, LU, & others, 1980, pl. 5, fig. 3), 21470, NIGP, Nanjing] [=*Mianxiandiscus* S. ZHANG & ZHU in W. ZHANG, LU, & others, 1980, p. 44 (type, *M. armatus;* OD; NIGP 37389); *Liangshandiscus* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 46 (type, *L. liangshanensis;* OD; NIGP 37400); *Emeidiscus* S. LI, 1980, p. 44 (type, *E. planilimbatus;* OD; CIGMR st279); *Hupeidiscus* W. CHANG in LU & others, 1974, p. 83 (type, *Hebediscus orientalis* W. ZHANG, 1953, pl. 1, fig. 1; OD; NIGP 7033); *Shizhudiscus* S. ZHANG & ZHU in W. ZHANG, LU, & others, 1980, p. 51 (type, *S. longquanensis;* OD; NIGP 37431); *Guizhoudiscus* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 55 (type, *G. kaiyangensis;* OD; NIGP 37460; =*Eodiscus chintingshanensis* LU, 1942, p. 180)]. Glabella conical, slightly expanded in frontal lobe; S1 and S2 usually

Tsunyidiscus

FIG. 242. Tsunydiscidae (p. 387)

evident but variable; SO variable but may be well impressed; border smooth or with epiborder furrow, row of nodes, or median expansion. Thorax with three segments. Pygidium with extremely narrow axis reaching close to posterior border furrow; axis multisegmented, with 6 to 10 axial rings; pleural areas with or without pleural furrows; border narrow, with or without marginal nodes. *lower Lower Cambrian–middle Lower Cambrian:* China (Hubei, Guizhou, Sichuan, Shaanxi, Yunnan).——FIG. 242. **T. niutitangensis,* lower Lower Cambrian (Shuijingtuo Formation), Guizhou (near Zhun Yi City); holotype, ×20 (W. Zhang, Lu, & others, 1980).

Family HEBEDISCIDAE
Kobayashi, 1944

[*nom. transl.* JELL, herein, *ex* Hebediscinae KOBAYASHI, 1944a, p. 45] [=Delgadoiinae KOBAYASHI, 1943, p. 40; Pagetiellinae S. ZHANG in W. ZHANG, LU, & others, 1980, p. 23; Dicerodiscinae S. ZHANG in W. ZHANG, LU, & others, 1980, p. 21]

Glabella wide at base, usually without lateral furrows, tapering forward or parallel sided, separating fixigenae anteriorly. SO transverse, complete; occipital ring as long as L1, rarely spinose or bluntly expanded. Pygidium with anteriorly wide, tapering axis of four or more rings plus terminus. *Lower Cambrian–lower Middle Cambrian.*

Hebediscus WHITEHOUSE, 1936, p. 80 [**Ptychoparia attleborensis* SHALER & FOERSTE, 1888; OD; holotype (SHALER & FOERSTE, 1888, pl. 2, fig. 14), 18332, USNM, Washington, D.C.]. Glabella straight sided, anteriorly truncated; LO poorly
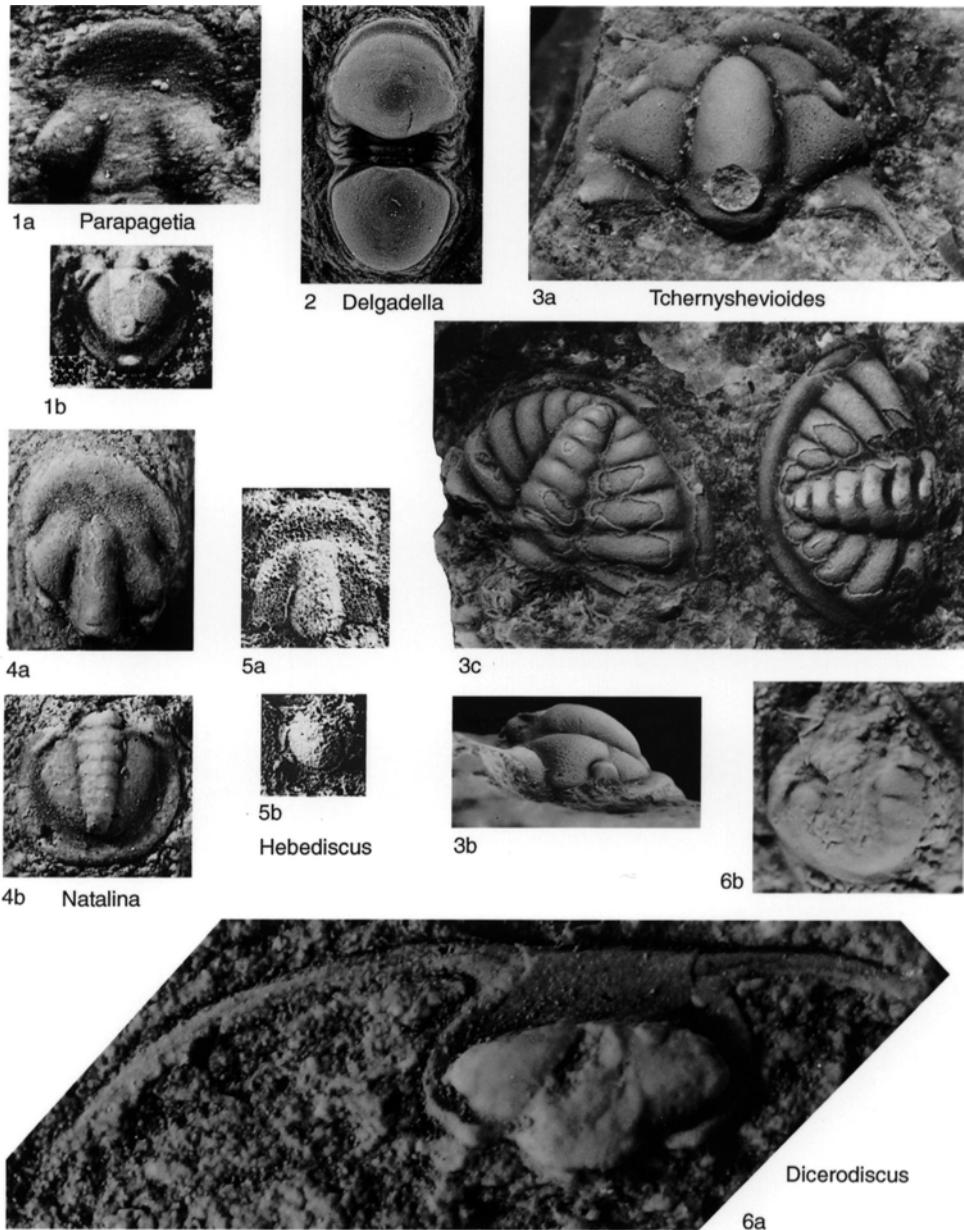
FIG. 243. Hebediscidae (p. 388–390)

defined if at all; anterior border furrow elongate; border short, flat; palpebral lobe long, usually without palpebral furrow; librigena large for family. Thorax with three segments. Pygidium semielliptical; axis reaching border furrow posteriorly, with seven or more rings plus small terminus; pleural area narrow, with or without furrows; border narrow, smooth or with marginal denticles. *Lower Cambrian:* USA (Massachusetts), Canada (Newfoundland), England, Spain, Russia (Siberian Platform, Altay), Mongolia, Morocco.——FIG. 243,5*a,b.* **H. attleborensis,* Lower Cambrian, Hoppin Slate, Massachusetts (North Attleboro); *a,* cranidium, ×8; *b,* pygidium, ×8 (Shaw, 1950).

Delgadella WALCOTT, 1912c, p. 560 [**Lingulepis lusitanica* DELGADO, 1904, p. 365; OD; type not

traced] [=*Alemtejoia* KOBAYASHI, 1943, p. 40 (type, *Microdiscus souzai* DELGADO, 1904, p. 351; SD KOBAYASHI, 1944a, p. 68); *Delgadoia* VOGDES, 1917, p. 27 (type, *Microdiscus caudatus* DELGADO, 1904, p. 349); *Delgadodiscus* KOBAYASHI, 1935, p. 112 (type, *Microdiscus caudatus* DELGADO, 1904, p. 349; OD); *Pagetiellus* LERMONTOVA, 1940, p. 119 (type, *Microdiscus lenaicus* TOLL, 1899, p. 23; OD); *Pentagonalia* GEYER, 1988, p. 109 (type, *P. amouslekensis*; OD; SMF 41767)]. Cephalon convex; axial furrow almost obsolete, particularly on external surface; glabellar furrows absent; border furrow and narrow border distinct; palpebral lobe poorly defined; librigena long. Thorax with three segments. Pygidium with long axis of 10 rings; axial furrow almost obsolete; pleural area usually smooth; border and border furrow narrow. *Lower Cambrian:* Russia (Siberian Platform, Mt. Altay), Mongolia, Spain, Sardinia, Portugal, Morocco, Canada (Newfoundland).——FIG. 243,*2. D. lenaicus* (TOLL), Lower Cambrian (Botomian), Siberian Platform (Lena River, Yakutia); lectotype, ×3.5 (Lermontova, 1951a).

Dicerodiscus W. ZHANG, 1964, p. 3 [**D. tsunyiensis;* OD; holotype (W. ZHANG, LU, & others, 1980, pl. 1, fig. 5), 37305, NIGP, Nanjing]. Glabella conical, unfurrowed; LO usually with small spine; pair of long, anterior fixigenal spines running laterally from anterior border then curving posteriorly; border long between spines, narrow laterally; facial suture lacking; eye lobe indistinct on lateral part of cheek elevation. Thorax unknown. Pygidium convex; parallel-sided axis not reaching border furrow; three pairs of pleural furrows; border narrow. *Lower Cambrian (Qiongzhusian–Canglangpuan):* China (Guizhou, Sichuan).——FIG. 243,*6a.* **D. tsunyiensis,* Lower Cambrian (Canglangpuan), Guizhou; holotype, cephalon, ×20.——FIG. 243,*6b. D. pertenus,* Lower Cambrian (Qiongzhusian), Sichuan; pygidium, ×15 (W. Zhang, Lu, & others, 1980).

Luvsanodiscus KOROBOV, 1980, p. 72 [**L. gammatus;* OD; holotype (KOROBOV, 1980, pl. 4, fig. 16), 66, coll. 4251, PIN, Moscow]. Glabella with straight, parallel to slightly tapering sides, with truncated anterior, weak or no lateral glabellar furrows; LO poorly defined, with median tubercle; palpebral lobe overhanging border laterally; palpebral furrow shallow, exsagittal. Pygidium with axis of seven rings; ring and pleural furrows poorly impressed; border extremely narrow, with short marginal spines. *Lower Cambrian (Atdabanian):* Mongolia.——FIG. 244,*1a,b.* **L. gammatus,* Lower Cambrian (Atdabanian, Egyngolskaya Suite), northwestern Mongolia; *a,* holotype, cranidium, ×11; *b,* pygidium, ×11 (Korobov, 1980).

Natalina E. ROMANENKO in REPINA & ROMANENKO, 1978, p. 128 [**N. incita;* OD; holotype (REPINA & ROMANENKO, 1978, pl. 6, fig. 15), 1811/80, ZSGU, Novokuznetsk] [=*Limbadiscus* KOROBOV, 1980, p. 66 (type, *L. dilatum*; OD; PIN 58, coll. 4251)]. Glabella parallel sided, anteriorly rounded, unfurrowed, without posterior spine; border furrow long; border flat to gently convex, tapering laterally;

Luvsanodiscus
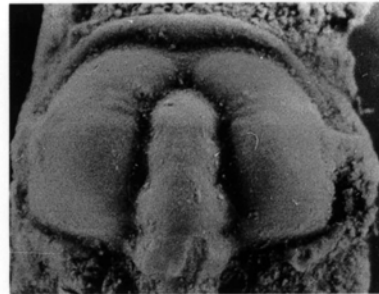
Neopagetina

FIG. 244. Hebediscidae (p. 389–390)

palpebral lobe projecting from fixigenal elevation; palpebral furrow distinct; librigena small, longer than wide. Pygidium with almost parallel-sided axis of six rings plus terminus reaching into posterior border furrow; pleural area narrow, smooth; border furrow wide; border rimlike, of uniform width. *Lower Cambrian (Botomian):* Russia (Altay, Gorno-Altayskaya).——FIG. 243,*4a,b.* **N. incita,* Lower Cambrian (Sanashtykgol), Gorno-Altayskaya (Sema River); *a,* holotype, cranidium, ×10; *b,* pygidium, ×10 (Repina & Romanenko, 1978).

Neopagetina POKROVSKAYA, 1960, p. 56, *nom. nov. pro Pagetina* LERMONTOVA, 1940, p. 121, *non* BARNARD,

1931 [*Pagetina rjonsnitzkii* LERMONTOVA, 1940, p. 121; OD; holotype (LERMONTOVA, 1951a, pl. 3, fig. 7a), 34/5156, TsGM, St. Petersburg]. Glabella tapering forward to rounded anterior; preglabellar median furrow short, wide, depressed; anterior border extremely short, smooth, may be medially elongate; eye ridge anteriorly convex; librigena extremely short; LO simple, may have short occipital spine. Pygidial axis of six rings plus terminus, not reaching border furrow; pleural field with well-impressed pleural furrows; border narrow, smooth. *Lower Cambrian (Botomian, Toyonian):* Russia (Siberian Platform, Mt. Altay), Mongolia, Greenland.——FIG. 244,*2a,b.* *N. rjonsnitzkii,* Botomian, Kutorgina Formation, Siberia (Peleduy River); *a,* lectotype, cranidium, ×12; *b,* pygidium, ×7 (Lermontova, 1940).

Parapagetia REPINA in REPINA & others, 1964, p. 258 [*P. limbata;* OD; holotype (REPINA in REPINA & others, 1964, pl. 38, fig. 1), 253/1, CSGM, Novosibirsk] [=*Planodiscus* KOROBOV, 1980, p. 65 (type, *P. patulus;* OD; PIN 54, coll. 4251)]. Glabella parallel sided, relatively short; occipital spine absent or short; preglabellar field long; anterior border poorly defined, usually slightly elongate medially. Pygidium with short axis of four rings plus terminus; border and border furrow together wide, with poor definition between them; border sometimes elongate posteromedially. *Lower Cambrian (Botomian):* Russia (Gorno-Altayskaya, Tuva), Mongolia.——FIG. 243,*1a.* *P. limbata,* Lower Cambrian (Sanashtykgol), Gorno-Altayskaya (River Katun); holotype, cranidium, ×15.——FIG. 243,*1b. P. plana* E. ROMANENKO, Lower Cambrian (Sanashtykgol), Gorno-Altayskaya (River Ul'men'); pygidium, ×15 (Repina & others, 1964).

Tchernyshevioides HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 100 [*T. ninae;* OD; holotype (REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 7, fig. 1–2), 483/160, MMG, Tashkent]. Glabella long, reaching anterior border furrow; SO well impressed; occipital ring with long posterodorsal spine; palpebral lobe short, prominent, and situated well forward; librigena tiny. Pygidium with axis of five rings plus terminus; pleural furrows impressed; border narrow, smooth. *Middle Cambrian (Amgaian):* Asia (Tian-Shan), Morocco.——FIG. 243,*3a–c.* *T. ninae,* Amgaian (*Pseudanomocarina* Zone), Tian-Shan (Sulyukta region); *a,* holotype, cranidium, ×8; *b,* lateral view of cranidium, ×8; *c,* pygidia, ×8 (Repina, Petrunina, & Hajrullina, 1975).

Family CALODISCIDAE
Kobayashi, 1943

[*nom transl.* ÖPIK, 1975a, p. 25, *ex* Calodiscinae KOBAYASHI, 1943, p. 38] [=Brevidiscinae KOBAYASHI, 1943, p. 39; Neocobboldinae S. ZHANG in W. ZHANG, LU, & others, 1980, p. 30]

Glabella parallel sided or tapering forward, may be rounded and expanded anteriorly and may be divided by transverse glabel-

lar furrows. SO transverse, complete; LO simple, at least as long as L1 or reduced, not spinose or expanded. Palpebral lobes short and prominent when present. Pygidium with wide, tapering axis of fewer than six segments. *Lower Cambrian–lower Middle Cambrian.*

Calodiscus HOWELL, 1935b, p. 224, *nom. nov. pro Goniodiscus* RAYMOND, 1913b, p. 101, *non* MÜLLER & TROSCHEL, 1842 [*Agnostus lobatus* HALL, 1847, p. 258; OD; syntypes (RASETTI, 1952a, pl. 51, fig. 8–11), 210, AMNH, New York] [=*Brevidiscus* KOBAYASHI, 1943, p. 39 (type, *B. lunulatus;* OD; USNM 15393)]. Glabella parallel sided, with two, shallow transglabellar furrows; glabellar anterior reaching border furrow; border narrow laterally, smooth or with a few tubercles laterally; eyes and facial sutures absent. Pygidial axis of few rings (four or five), wide, reaching border furrow or close to it; border narrow, with smooth or serrated margin. *Lower Cambrian (Atdabanian, Botomian):* Sweden, England, Germany, Morocco, Siberia (Mt. Altay), USA (Massachusetts, New York, Alaska), Canada (Newfoundland), Greenland.——FIG. 245,*4a,b.* *C. lobatus* (HALL), Botomian (West Castleton Formation), New York (Troy); *a,* syntype, cephalon, ×12; *b,* syntype, pygidium, ×12 (Rasetti, 1952a).

Chelediscus RUSHTON, 1966, p. 18 [*C. acifer;* OD; holotype (RUSHTON, 1966, pl. 2, fig. 26a–e), A.57104, SM, Cambridge]. Glabella conical, bilobed (anterior lobe much smaller in type); LO depressed, forming basal lobes; median preglabellar furrow present; border furrow with line of pits; border with pair of marginal spines laterally and pair of genal spines. Thorax with two segments. Pygidium strongly convex; axis wide, tapering strongly in posterior half, of five or six rings; pleural areas with rudimentary furrows; border narrow. *Lower Cambrian (Botomian):* England, USA (New York), Canada (Newfoundland), Russia (Siberian Platform).——FIG. 245,*1a–c.* *C. acifer,* upper *Protolenus* Zone, Purley Shale, England (Warwickshire); *a,* paratype, cephalon, ×8; *b,c,* enrolled holotype in pygidial and lateral views, ×8 (Rushton, 1966).

Korobovia JELL in BENGTSON & others, 1990, p. 263 [*K. ocellata;* OD; holotype (JELL in BENGTSON & others, 1990, fig. 177c,f), 112656, NMVP, Melbourne]. Glabella may be subconical, reaching border furrow, with vague transverse furrow about one-third length from anterior; eye ridge convex forward, leading to small palpebral lobe situated well forward and low on fixigenal elevation; border short, rimlike, with two small nodes just behind small librigena. Pygidium transverse; axis broad, of 3 rings plus terminus, each with high, spinelike tubercle; pleural furrows impressed; border narrow, with or without marginal spines. *Lower Cambrian (Botomian):* South Australia, Mongolia, Russia (Gorno-Altayskaya).——FIG. 245,*3a–c.* *K. ocel-*
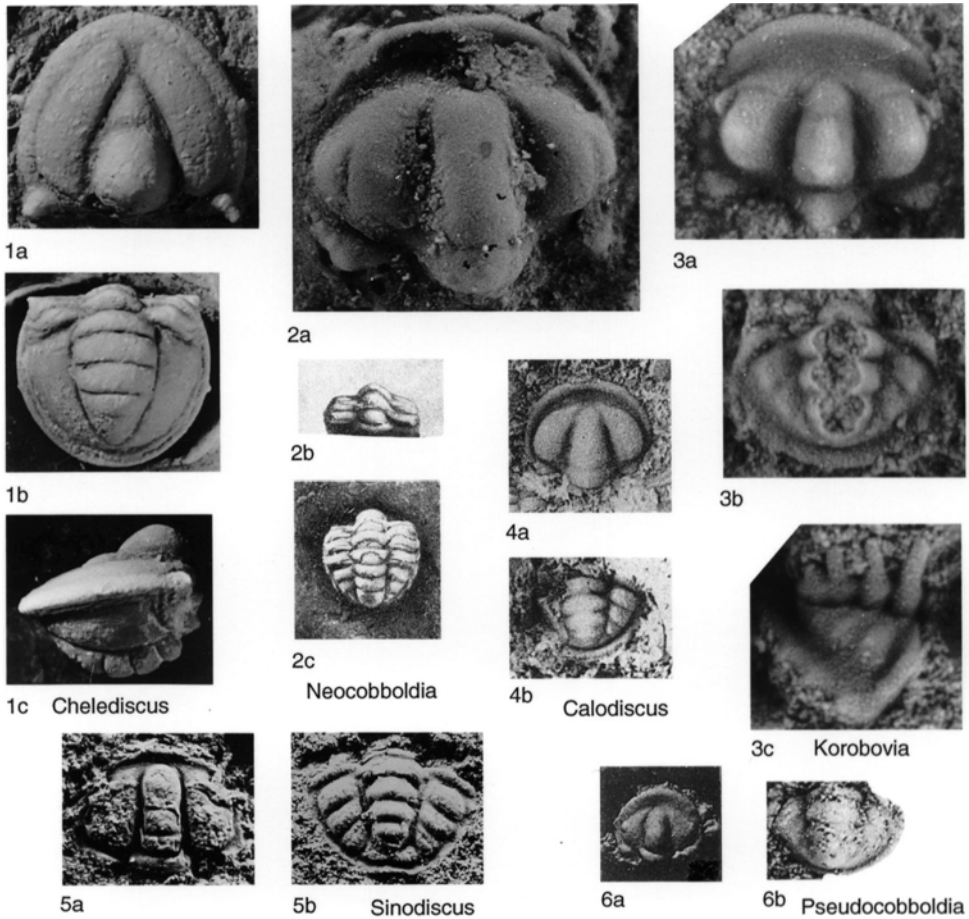
FIG. 245. Calodiscidae (p. 390–392)

lata, Pararaia janeae Zone, Oraparinna Shale, South Australia (Flinders Range); *a,* holotype, cranidium, ×15; *b,* pygidium, ×15; *c,* lateral view of pygidium, ×15 (Bengtson & others, 1990).

Neocobboldia RASETTI, 1952a, p. 438, *nom. nov. pro Cobboldia* LERMONTOVA, 1940, p. 120, *non* BRAUER, 1887; *nec* LEIPER, 1910 [**Cobboldia dentata* LERMONTOVA, 1940, p. 120; OD; holotype (LERMONTOVA, 1951a, pl. 3, fig. 2) 23/5156, TsGM, St. Petersburg] [=*Margodiscus* KOROBOV, 1980, p. 54 (type, *M. rackovskii* KOROBOV, 1980, p. 55; OD; PIN 18, coll. 4251)]. Glabella parallel sided, anteriorly rounded at border furrow, unfurrowed except for well-impressed, transverse SO; fixigenae narrow, separated anteriorly by short, depressed median preglabellar field; border furrow usually longer than border; anterior border short, convex, tapering only slightly laterally; palpebral furrow slitlike, exsagittal, short. Pygidium transverse; axis wide, of 3 or 4 rings plus terminus, finishing at border furrow;

pleural areas usually with well-impressed pleural furrows; border narrow, denticulate. *Lower Cambrian (Botomian):* Russia (Siberian Platform, Gorno-Altayskaya), Mongolia.——FIG. 245,*2a–c.* **N. dentata,* Lower Cambrian (*Protolenus* Zone), Siberia (Lena River, Yakutia); *a,* holotype, cranidium, ×6.5; *b,c,* thorax and pygidium, ×6.5 (Lermontova, 1951a).

Pseudocobboldia HUPÉ in BOUDDA, CHOUBERT, & FAURE-MURET, 1979, p. 73 [**Cobboldia(?) pulchra* HUPÉ, 1953a, p. 113; OD; holotype (HUPÉ, 1953a, pl. 11, fig. 21), not traced]. Glabella subconical, anteriorly rounded at border furrow, unfurrowed except for well-impressed SO; border smooth, short, and flat; prominent eye tubercle situated laterally above narrowest part of border; eye ridge running from axial furrow behind glabellar anterior to eye. Pygidium transverse; axis wide, consisting of three rings plus terminus that does not reach border furrow; pleural area narrow, with shallow pleural

furrows; border narrow, tapering posteriorly, weakly denticulate. *lower Middle Cambrian:* Morocco.——Fig. 245,*6a,b.* **P. pulchra* (Hupé), lower Middle Cambrian (Jbel Wawrmast Formation), Morocco (Anti-Atlas Mountains); *a,* holotype, cranidium, ×4 (Hupé, 1953a); *b,* pygidium, ×14 (Geyer, 1988).

Sinodiscus W. Chang in Lu & others, 1974, p. 83 [**S. shipaiensis;* OD; holotype (W. Chang in Lu & others, 1974, pl. 31, fig. 5), 37350, NIGP, Nanjing] [=*Tologoja* Korobov, 1980, p. 81 (type, *T. subquadrata;* OD; PIN 99, coll. 4251)]. Glabella cylindrical except for gently expanded and rounded anterior lobe and wide LO, reaching anterior border furrow, with 2 transglabellar furrows variably impressed; LO wide, as long as L1, nonspinose; border short, upturned, uniform; palpebral lobe short, level with anterior glabellar lobe, defined by well-impressed palpebral furrow; librigena small. Thorax with three segments. Pygidial axis wide, of two to five rings plus posteriorly rounded terminus isolated from border furrow; pleural furrows well impressed; border narrow, uniform, without marginal spines. *Lower Cambrian (Botomian, upper Qiongzhusian):* Mongolia, China (Hubei, Guizhou).——Fig. 245,*5a,b.* **S. shipaiensis,* upper Qiongzhusian (Shipai Formation), western Hubei; *a,* holotype, cranidium, ×6; *b,* pygidium, ×6 (Lu & others, 1974).

Family WEYMOUTHIIDAE
Kobayashi, 1943

[Weymouthiidae Kobayashi, 1943, p. 40, *emend.* Jell, 1975a, p. 27]
[=Ladadiscinae Soloviev, 1964, p. 34]

Most taxa in this family are large for the superfamily. Glabella wide at base, normally parallel sided but may taper gently or expand medially, usually without glabellar furrow but, if present, furrow may be incomplete or transglabellar and deeply impressed. Fixigenae normally confluent in front of glabella. SO often not impressed but dorsally complete when evident; LO simple or shortened by posterodorsal expansion of rounded L1. Without eyes. Pygidium with long, strongly tapering axis; axis with 10 or more rings (when segmentation is evident); segmentation commonly effaced. *Lower Cambrian–Middle Cambrian.*

Weymouthia Raymond, 1913b, p. 102 [*Agnostus nobilis Ford, 1872, p. 421; OD; types not traced, reported lost by Walcott, 1890b]. Cephalon effaced except for border furrow; border narrow, bearing tubercles laterally. Thorax with three segments. Pygidium effaced except for border furrow; border narrow. *Lower Cambrian:* USA (Massachusetts). ——Fig. 246,*6.* **W. nobilis* (Ford), Lower Cam-

brian (Hoppin Slate), Massachusetts (North Attleboro); articulated specimen, ×5 (Shaw, 1950).

Abakolia Bognibova in Tchernysheva, 1971, p. 205 [**A. pauca;* OD; holotype (Tchernysheva, 1971, pl. 24, fig. 3), P-1056a-3, CSGM, Novosibirsk] [=*Costadiscus* Babcock, 1994a, p. 115 (type, *C. minutus;* OD; MGUH 21.322)]. Cephalon semicircular; glabella with S1 as small pits laterally, with depressed preglabellar median furrow; border elongate anteriorly, tapering laterally; eye ridge, palpebral lobe, and eye absent. Pygidium semicircular; axis narrow, of six rings and terminal portion, not reaching border furrow; each pleural area crossed by at least six pleural furrows, and with one or two short, almost longitudinal pleural ribs at rear, partly behind axis; border extremely narrow. *Lower Cambrian (Botomian):* Mongolia. *Middle Cambrian:* Russia (Mt. Altay), Greenland.——Fig. 247,*6a,b.* **A. pauca,* Middle Cambrian (lower Amgaian, Abakolskaya Suite), Altay (western Sayan Mountains); *a,* holotype, cranidium, ×8; *b,* pygidium, ×10 (Tchernysheva, 1971).

Acidiscus Rasetti, 1966a, p. 11 [**A. birdi;* OD; holotype (Rasetti, 1966a, pl. 6, fig. 11–12), 145987, USNM, Washington, D.C.]. Cephalic border with one or two pairs of marginal spines; glabella isolated from border furrow, with two short, pitlike pairs of lateral furrows; occipital and genal spines present. Pygidium like *Serrodiscus;* axis with ten rings; pleurae smooth; doublure may be extended into short spines. *upper Lower Cambrian:* USA (New York), Canada (Newfoundland), England.——Fig. 248,*7a,b.* **A. birdi,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a,* holotype, cranidium, ×2; *b,* paratype, pygidium, ×2 (Rasetti, 1966a).

Acimetopus Rasetti, 1966a, p. 13 [**A. bilobatus;* OD; holotype (Rasetti, 1966a, pl. 4, fig. 1–4), 145991, USNM, Washington, D.C.]. Cephalic border strongly convex, with a pair of marginal spines laterally; glabella strongly divided by deep furrow (S1 plus S2) with large anterior lobe isolated from border furrow, with L2 as a pair of small, separated, subtriangular lobes, and with L1 large and inflated posterodorsally into a cranidial spine; LO short and low behind L1; genal spines present. Pygidial axis of type with nine rings, strongly inflated, with vertical spine on second ring; border furrow deep; border narrow, without spines. *upper Lower Cambrian:* USA (New York), England.——Fig. 246,*1a–d.* **A. bilobatus,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a,* holotype, cranidium, ×5; *b,* same in lateral view, ×5; *c,* paratype, pygidium, ×5; *d,* paratype, pygidium in lateral view, ×5 (Rasetti, 1966a).

Analox Rasetti, 1966a, p. 15 [**A. bipunctata;* OD; holotype (Rasetti, 1966a, pl. 6, fig. 1–3), 145993, USNM, Washington, D.C.]. Glabella extending forward into merged axial and border furrows; S1 long but not deep; L1 large, drawn out posterodorsally into glabellar spine; anterior lobe wider than anterior portion of L1; LO indistinct beneath

glabellar spine. Anterior border swollen medially, defined by furrows running anterolaterally from axial furrow at front of glabella, ending in a pit; border absent laterally; posterior border furrow fading out a little in front of genal angle. Pygidium with long axis (eight rings in type); border narrow, defined by equally narrow border furrow; doublure forming vertical face without spines. *upper Lower Cambrian:* USA (New York).——FIG. 247,*1a–c.* *A. bipunctata,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a,* holotype, cranidium, ×6; *b,* lateral view of same, ×6; *c,* paratype, pygidium, ×6 (Rasetti, 1966a).

Bathydiscus RASETTI, 1966a, p. 16 [*B. dolichometopus;* OD; holotype (RASETTI, 1966a, pl. 9, fig. 1–3), 145995, USNM, Washington, D.C.]. Glabella wide, convex, unfurrowed except for faint occipital furrow; median part of border gently arched in anterior view; posterior border with pair of erect spines close to axial furrow as in *Oodiscus.* Pygidial axis wide, tapering, unfurrowed; border furrow wider posteriorly; border narrow, depressed posteriorly; doublure vertical and high laterally (i.e., not reflexed parallel to dorsal exoskeleton), much lower posteriorly. *upper Lower Cambrian:* USA (New York), Canada (Newfoundland).——FIG. 247,*5a–c.* *B. dolichometopus,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a,* holotype, cranidium, ×4; *b,* paratype, pygidium, ×3; *c,* paratype, pygidium, ×4 (Rasetti, 1966a).

Bolboparia RASETTI, 1966a, p. 18 [*B. superba;* OD; holotype (RASETTI, 1966a, pl. 5, fig. 1–4), 145998, USNM, Washington, D.C.]. Glabella anteriorly pointed, extended posterodorsally into a spine, with poorly defined lateral furrows; LO short, behind glabellar spine; cheeks inflated anterolaterally, hanging over border; preglabellar field depressed as broad furrow; anterior border expanded medially, with a pair of marginal spines laterally and near the genal angle one or more pairs of tubercles in front of transverse furrow running from border furrow to margin; genal spines present. Pygidial axis of ten rings, spine on second ring; narrow border extended into ventrally directed spines. Surface densely granulose in three known species. *upper Lower Cambrian:* USA (New York), Canada (Quebec). ——FIG. 246,*2a,b.* *B. superba,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a,* holotype, cranidium, ×4; *b,* lateral oblique view of same, ×4 (Rasetti, 1966a). ——FIG. 246,*2c,d. B. elongata,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *c,* paratype, pygidium, ×4; *d,* lateral view of same, ×4 (Rasetti, 1966a).

Cephalopyge GEYER, 1988, p. 123 [*C. notabilis;* OD; holotype (GEYER, 1988, fig. 61), 41781, SMF, Frankfurt am Main]. Cephalon subcircular except for straight posterior; externally smooth, convex, and hanging over extremely narrow border; glabella evident on internal mold, conical, with SO being only furrow evident; LO short, hanging over poste-

rior margin. Thorax with three segments. Pygidium externally smooth, convex; internal mold showing conical axis extending to posterior margin; border not present. *upper Lower Cambrian:* Morocco.——FIG. 248,*2. *C. notabilis,* upper Lower Cambrian (Jbel Wawrmast Formation), Morocco (Anti-Atlas Mountains); holotype, ×4 (Geyer, 1988).

Cobboldites KOBAYASHI, 1943, p. 38 [*Microdiscus comleyensis* COBBOLD, 1910, p. 21; OD; lectotype (COBBOLD, 1910, pl. 3, fig. 2), A18.478, SM, Cambridge]. Glabella conical, broadly rounded anteriorly at border furrow, unfurrowed; border flat, narrowing laterally. Pygidium with seven axial rings (usually not evident on exterior surface) tapering posteriorly to the border furrow; border narrow, tapering posteriorly, without spines or tubercles. *upper Lower Cambrian:* England, Morocco. *?Middle Cambrian:* England.——FIG. 247,*4a,b. *C. comleyensis,* upper Lower Cambrian (Comley Series, *Protolenus* Limestone), England (Shropshire); *a,* syntype, cranidium, ×5; *b,* syntype, pygidium, ×5 (Cobbold, 1910).

Jinghediscus XIANG & ZHANG, 1985, p. 92 [*J. nummularius;* OD; holotype (XIANG & ZHANG, 1985, pl. 1, fig. 1), T1348, CAGC, Beijing]. Like *Mallagnostus,* with bilobed glabella divided by transverse furrow and posteriorly inflated. [Questionably a synonym of *Mallagnostus.*] *lower Middle Cambrian:* China (Xinjiang), ?Australia (Queensland).——FIG. 246,*4a,b. *J. nummularius,* lower Middle Cambrian (*Xystridura* Zone), Xinjiang; *a,* holotype, cranidium, ×8; *b,* pygidium, ×10 (Xiang & Zhang, 1985).

Leptochilodiscus RASETTI, 1966a, p. 25 [*L. punctulatus*; OD; holotype (RASETTI, 1966a, pl. 11, fig. 1–3), 146009, USNM, Washington, D.C.] [=*Kerberodiscus* BASSETT, OWENS, & RUSHTON, 1976, p. 630 (type, *K. succinctus;* OD; NMW 75.5G.7)]. Glabella long, narrow, tapering to pointed anterior, and not reaching border furrow; SO well impressed; LO short; border extremely narrow. Pygidial axis with ten axial rings, almost effaced, reaching posterior border furrow; border extremely narrow, extended ventrally with series of short spines; margin arched over median line in posterior view. *upper Lower Cambrian:* USA (New York), Canada (Quebec), Wales.——FIG. 248,*5a–c.* *L. punctulatus,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a,* holotype, cephalon, ×7.5; *b,c,* pygidium, posterior and dorsal views, respectively, ×5 (Rasetti, 1966a).

Litometopus RASETTI, 1966a, p. 26 [*L. longispinus;* OD; holotype (RASETTI, 1966a, pl. 8, fig. 1–3), 146012, USNM, Washington, D.C.]. Cephalon almost semicircular; glabella tapering forward to border furrow, unfurrowed; border convex, with pair of small marginal spines laterally and large genal spines. Pygidium same shape as cephalon; axis tapering posteriorly to border furrow, unfurrowed to very faintly furrowed; border flat, wide, with doublure sloping adaxially, and with serrated margin. [Questionably a synonym of *Cobboldites.*]
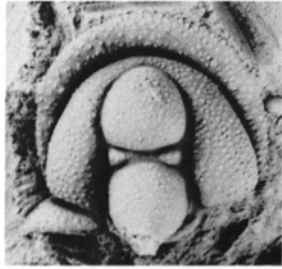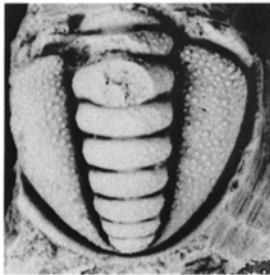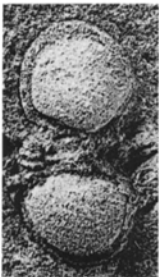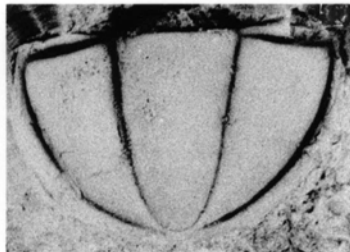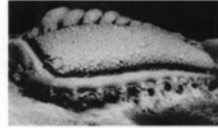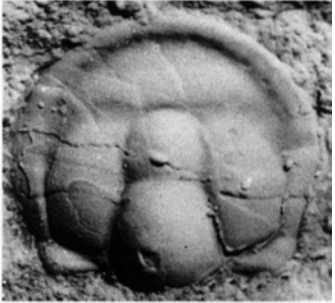
FIG. 246. Weymouthiidae (p. 392–398)
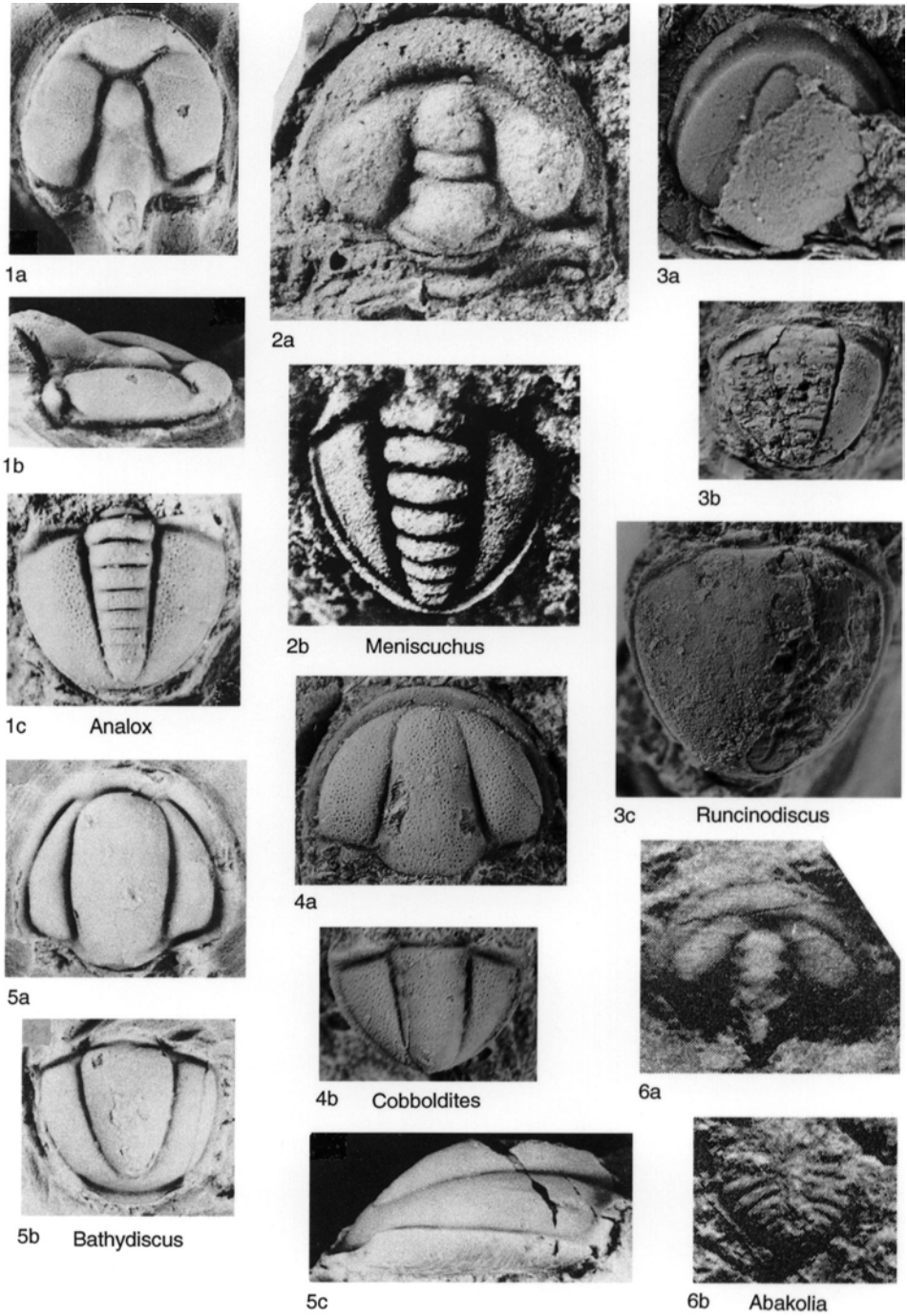
FIG. 247. Weymouthiidae (p. 392–398)
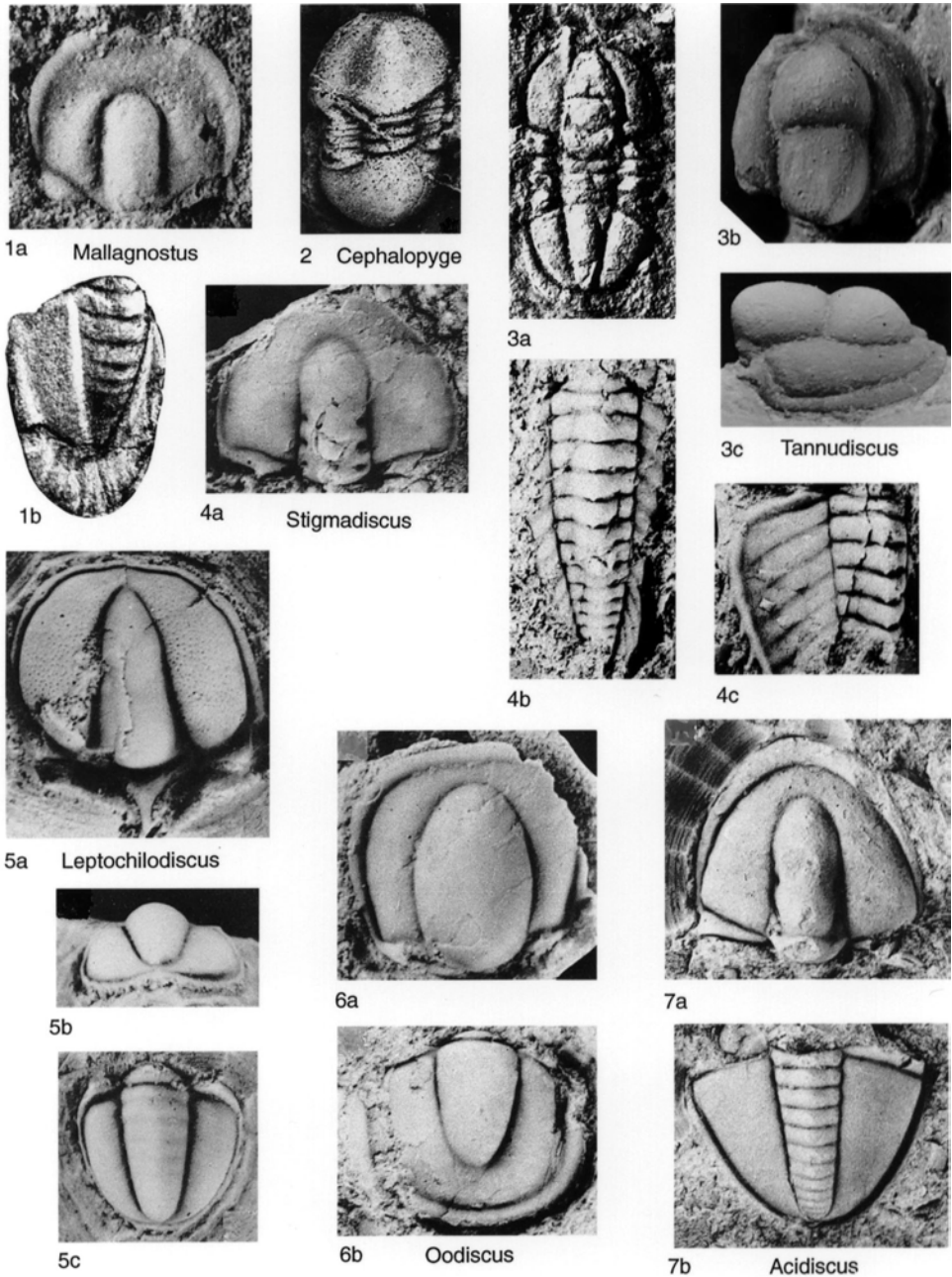
FIG. 248. Weymouthiidae (p. 392–398)

upper Lower Cambrian: USA (New York).——FIG. 246,5a,b. *L. longispinus,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Taconic, Griswold Farm); *a,* holotype, cephalon, ×3; *b,* pygidium, ×3 (Rasetti, 1966a).

Mallagnostus HOWELL, 1935b, p. 228 [**Agnostus desideratus* WALCOTT, 1890b, p. 629; OD; holotype (RASETTI & THEOKRITOFF, 1967, pl. 20, fig. 31), 18327, USNM, Washington, D.C.] [=*Ladadiscus* POKROVSKAYA, 1959, p. 167 (type, *L. limbatus*; OD;

VNIGNI 3536/85)]. Cephalon semielliptical; glabella unfurrowed (pits situated laterally indicate furrows in one species), finishing well behind broad border furrow; LO short, ill-defined, not spinose; anterior border long, only gently convex, tapering laterally; border furrow running to margin just anterior to genal angle. Thorax with three segments. Pygidium same shape as cephalon, with conical axis of eight or more rings, not reaching to posterior border furrow; pleural areas smooth. *upper Lower Cambrian:* USA (New York), Canada (Newfoundland), Spain, England, Russia (Tuva, Gorno-Altayskaya), Mongolia. *Middle Cambrian:* China (Tian Shan), Russia (Yakutia).——Fig. 248,*1a.* *M. desideratus* (Walcott), upper Lower Cambrian, New York; holotype, cranidium, ×10 (Rasetti & Theokritoff, 1967).——Fig. 248,*1b.* M. llarenai, upper Lower Cambrian (*serratus*-Band), Herrerias-Mergel Formation, Spain (Cala); holotype, pygidium, ×4 (Richter & Richter, 1941a).

Meniscuchus Öpik, 1975a, p. 28 [*M. menetus*; OD; holotype (Öpik, 1975a, pl. 4, fig. 1–2), CPC 13171, AGSO, Canberra]. Glabella rounded anteriorly at border furrow, strongly divided by complete S2 and S3; L3 of variable length (lateral lobes only in some species), posteriorly inflated and widened; LO short, low behind inflation of glabella; anterior border elongate, strongly convex, tapering laterally. Pygidium relatively narrow; axis tapering and reaching border furrow posteriorly, deeply segmented (with 4 to 10 axial rings); pleural areas unfurrowed; border uniformly narrow; doublure wide and almost vertical. *Lower Cambrian (Botomian):* USA (Alaska, New York), Canada (Newfoundland, Quebec), Russia (Siberian Platform, Gorno-Altayskaya), Australia (New South Wales).——Fig. 247,*2a,b.* *M. menetus,* Lower Cambrian (Cymbric Vale Formation), New South Wales; *a,* holotype, cranidium, ×8; *b,* pygidium, ×11 (Öpik, 1975a).

Ninadiscus Korobov, 1980, p. 101 [*N. strobulatus;* OD; holotype (Korobov, 1980, pl. 9, fig. 3), 139, coll. 4251, PIN, Moscow]. Glabella tapering gently forward to sharply rounded anterior at border furrow, with L1 expanded posterodorsally into well-rounded protrusion; S1 and S2 well impressed; L2 shorter than frontal lobe, which is shorter than L1; LO short and lower than L1; border furrow uniform throughout, may swing gently to posterior in midline; border narrow laterally, elongate sagittally, may bear up to three symmetrically arranged tubercles anteriorly. Pygidium with long, narrow axis of 10 rings reaching almost to posterior border; pleural areas smooth; border extremely narrow. *Lower Cambrian (Botomian):* Mongolia, USA (New York).——Fig. 249,*1a,b.* *N. strobulatus,* Lower Cambrian (Egyngolskaya Suite), northwestern Mongolia; *a,* holotype, cranidium, ×15; *b,* pygidium, ×10 (Korobov, 1980).

Oodiscus Rasetti, 1966a, p. 28 [*O. subgranulatus;* OD; holotype (Rasetti, 1966a, pl. 10, fig. 1–3), 146014, USNM, Washington, D.C.]. Cephalon tending towards subquadrate outline; glabella wide

Fig. 249. Weymouthiidae (p. 397–398)

(one-third cephalic width), strongly convex, completely unfurrowed except for shallow lateral depressions posteriorly as occipital furrow; preglabellar field short; border with 1 or 2 pairs of marginal spines laterally and a pair of small spines posteriorly (one species has a pair of tubercles anteriorly). Pygidium same shape as cephalon; axis tapered, unfurrowed, not reaching posterior border; border virtually flat, usually slightly wider laterally than long posteriorly. *upper Lower Cambrian:* USA (New York), Canada (Newfoundland).——Fig. 248,*6a,b.* *O. subgranulatus,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold

Farm); *a,* holotype, cephalon, ×5; *b,* paratype, pygidium, ×3 (Rasetti, 1966a).

Runcinodiscus Rushton in Bassett, Owens, & Rushton, 1976, p. 635 [**R. index;* OD; holotype (Cobbold, 1931, pl. 38, fig. 17–18), 15360, SM, Cambridge]. Externally effaced; cephalon semielliptical; glabella long, tapering forward; border tuberculate, flat. Pygidium with long, conical axis of nine or more rings plus terminus; border distinct, level, short posteriorly, with ventral swellings or spines. [Questionably a synonym of *Serrodiscus.*] *upper Lower Cambrian:* England, Norway.——Fig. 247,*3a–c.* **R. index, Protolenus* Zone, Comley Series (*Protolenus* Limestone), England (Shropshire); *a,* partly exfoliated holotype cranidium, ×10; *b,* mostly exfoliated pygidium, ×6; *c,* pygidium, ×6 (new).

Semadiscus E. V. Romanenko in Repina & Romanenko, 1978, p. 109 [**S. sollennis;* OD; holotype (E. V. Romanenko in Repina & Romanenko, 1978, pl. 3, fig. 1), 1811/12, ZSGU, Novokuznetsk]. Glabella short, undivided except for well-impressed SO; long occipital spine present; border narrow throughout but tapering laterally. Pygidium unknown. [Questionably a synonym of *Serrodiscus.*] *Lower Cambrian (Botomian):* Russia (Siberia, Gorno-Altayskaya), USA (New York), Canada (Newfoundland).——Fig. 246,*3.* **S. sollennis,* Lower Cambrian (lower Botomian), Gorno-Altayskaya (Sema River); holotype, cranidium, ×11 (Repina & Romanenko, 1978).

Serrodiscus Richter & Richter, 1941a, p. 23 [**Eodiscus (Serrodiscus) serratus;* OD; holotype (Richter & Richter, 1941a, pl. 1, fig. 1), 1234, SMF, Frankfurt am Main] [=*Paradiscus* Kobayashi, 1943, p. 38 (type, *Microdiscus speciosus* Ford, 1873, p. 137; OD; lectotype, NYSM 4588)]. Cephalon semielliptical; glabella long, conical or parallel sided, usually weakly furrowed or unfurrowed (but S2 and S3 may be better impressed); LO generally short, with or without a spine; cheeks joined anteriorly in short preglabellar field or separated by a depression; border convex, with up to eight pairs of tubercles laterally. Thorax with three segments. Pygidium with wide, subconical axis of more than eight rings; pleural area unfurrowed or extremely weakly furrowed on internal mold; border narrowing posteriorly, usually with ventral spines. *Lower Cambrian:* USA (New York, Massachusetts, Alaska), Canada (Newfoundland, New Brunswick, Northwest Territories), Greenland, Spitsbergen, England, Wales, Spain, Germany, Poland, Morocco, Russia (Mt. Altay), China (Gansu), Australia (South Australia, New South Wales).——Fig. 249,*2a,b.* **S. serratus,* Herrerias-Mergel Formation (*serratus*-Band), Spain (Cala); *a,* cephalon, ×2; b, holotype, pygidium, ×2.5 (Richter & Richter, 1941a).

Stigmadiscus Rasetti, 1966a, p. 35 [**S. stenometopus;* OD; holotype (Rasetti, 1966a, pl. 12, fig. 1–2), 146029, USNM, Washington, D.C.]. Cephalon semielliptical; glabella parallel sided, anteriorly pointed; S1 and S2 as deep pits close to the axial furrow in the posterior half of the glabella with area

adaxial from them considerably inflated; SO with pair of deep pits laterally; LO bearing a spine or node; border narrow, with pair of small spines posteriorly. Assigned pygidium semielliptical, of low convexity; axis tapering, with 12 axial rings, the first ring shorter medially than laterally; pleural areas bearing well-impressed, oblique pleural furrows; border narrow, with five pairs of downwardly directed marginal spines. [Assignment of the pygidium (Rasetti, 1967, p. 53) is not certain due to difference in outline from that of the cephalon, lower convexity of shield, and style of furrows on axis.] *upper Lower Cambrian:* USA (New York), Canada (Newfoundland), Russia (Gorno-Altayskaya).——Fig. 248,*4a–c.* **S. stenometopus,* upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a,* holotype, cranidium, ×3 (Rasetti, 1966a); *b,* partial pygidium, ×3 (Rasetti, 1967); *c,* partial pygidium, ×3 (Rasetti, 1967).

Tannudiscus Pokrovskaya, 1959, p. 177 [**T. tannuolaicus;* OD; holotype (Pokrovskaya, 1959, pl. 11, fig. 20), 3536/98, VNIGNI, Moscow]. Glabella long, wide, bilobed; posterior lobe lacking furrow or spine but may be roundly inflated posteriorly; LO short, low at rear of inflated rear of glabella; border convex, moderately wide, elongate sagittally and extending back to anterior of glabella in some species. Thorax with three segments. Pygidial axis conical, of seven or eight rings, may or may not reach posterior border furrow; ring furrows indistinct or obsolete; border almost flat, similar in width to cephalic border. *Lower Cambrian (Toyonian):* England, Canada (Newfoundland), Russia (Gorno-Altayskaya, Tuva), China (Gansu).——Fig. 248,*3a.* **T. tannuolaicus,* Toyonian (Shivelikskaya Suite), Tuva (Shivelik-Khem River, eastern Tannu-Ola Mountains); holotype, ×10 (Pokrovskaya, 1959).——Fig. 248,*3b,c. T. balanus* Rushton, 1966, Lower Cambrian (Purley Shales), England (Warwickshire); holotype, cranidium in dorsal and lateral views, ×12 (Rushton, 1966).

Family YUKONIIDAE S. Zhang, 1980

[*nom. transl. et emend.* Jell, herein, *ex* Yukoniinae S. Zhang in W. Zhang, Lu, & others, 1980, p. 21]

Glabella narrow, usually parallel sided and anteriorly rounded. SO a pair of pits low on sides of glabella and angling back beneath median cranidial spine; LO extremely short, overridden by cranidial spine. Large spine arising from L1 medially and directed back almost horizontally to pointed tip. Preglabellar area usually long, with smooth anterior border. Pygidium variable with axis of three to seven rings. *Lower Cambrian–Middle Cambrian.*

Yukonia Palmer, 1968, p. 38 [**Y. intermedia;* OD; holotype (Palmer, 1968, pl. 2, fig. 14), 146674,
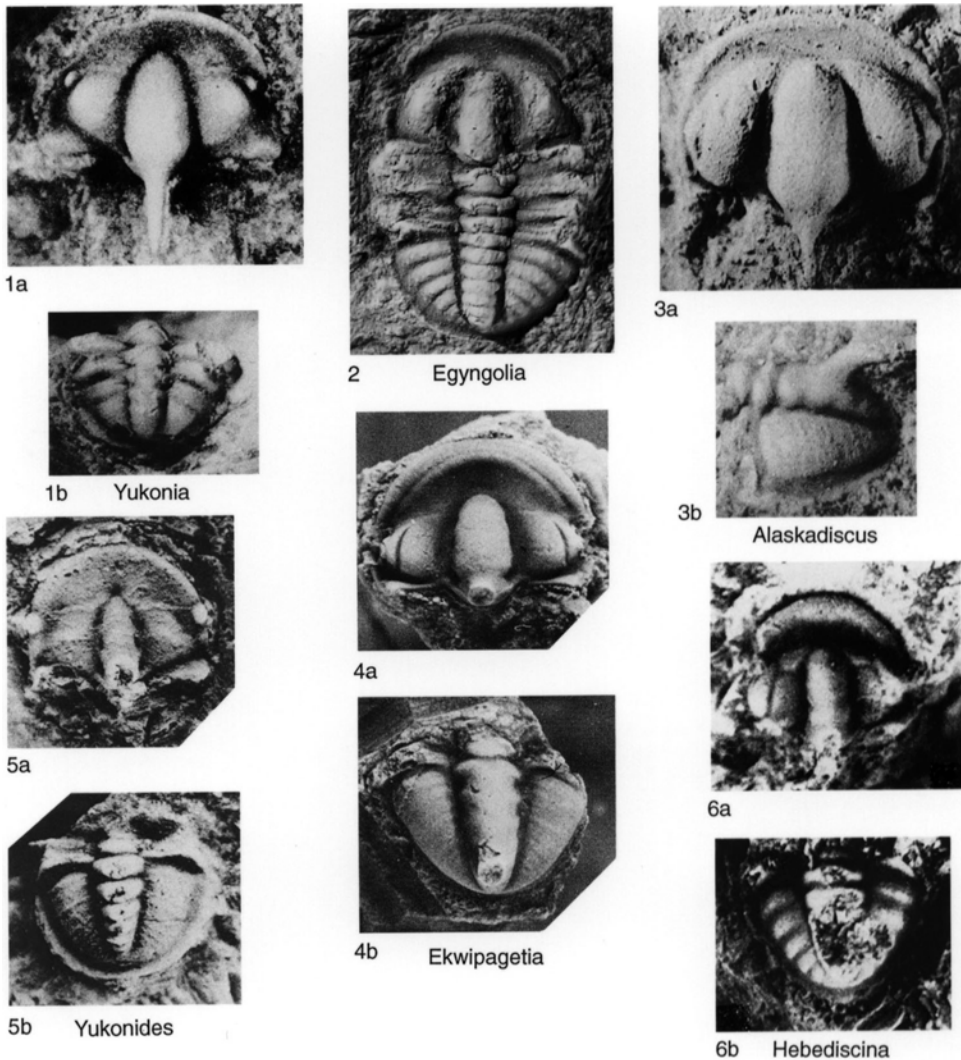
FIG. 250. Yukoniidae (p. 398–400)

USNM, Washington, D.C.]. Glabella relatively wide, unfurrowed, strongly tapered into cranidial spine; eye tubercles situated laterally just above the border furrow. Thorax with three segments. Pygidium transverse, with narrow, poorly segmented axis; border narrow, with irregular (possibly weakly spinose) margin. *Lower Cambrian:* USA (Alaska).——FIG. 250,*1a,b.* **Y. intermedia,* Lower Cambrian (Adams Argillite), Alaska (Water Level area, Yukon River); *a,* holotype, cranidium, ×20; *b,* paratype, pygidium, ×15 (Palmer, 1968).

Alaskadiscus S. ZHANG in W. ZHANG, LU, & others, 1980, p. 31 [**Neocobboldia spinosa* PALMER, 1968, p. 34; OD; holotype (PALMER, 1968, pl. 2, fig. 9–10), 146670, USNM, Washington, D.C.]. Glabella

unfurrowed except for SO low on sides at rear, reaching rear of long border furrow; SO running up to cranidial spine just behind greatest tapering of the cranidial spine; LO short, overlain by slender, horizontal cranidial spine (much narrower than glabella); border uniformly short; palpebral furrows well impressed; librigena short, small. Thorax with two segments. Pygidium transverse; axis of five or six rings, with large geniculate spine on third and fourth; border narrow, with several pairs of marginal spines. *Lower Cambrian:* USA (Alaska).——FIG. 250,*3a,b.* **A. spinosa* (PALMER), middle Lower Cambrian (Adams Argillite), Alaska (Yukon River); *a,* holotype, cranidium, ×15; *b,* left lateral view of pygidium, ×15 (Palmer, 1968).

Egyngolia KOROBOV, 1980, p. 83 [*E. obtusa;* OD; holotype (KOROBOV, 1980, pl. 7, fig. 1), 102, coll. 4251, PIN, Moscow] [=*Mongolodiscus* KOROBOV, 1980, p. 99 (type, *M. zaicevi;* OD; PIN 137, coll. 4251]. Glabella wide; SO to S3 impressed as deep circular pits isolated or almost isolated from axial furrow; S1 and S2 may continue faintly across the axis; palpebral lobes short but prominently raised; librigena tiny; anterior border usually a short rim marginal to long border furrow. Thorax with three segments. Pygidium with axis of six or seven rings and tiny terminal portion, with small tubercle on each ring, and no terminal spine; pleural areas usually with pleural furrows; border narrow, usually with six pairs of small marginal tubercles. *Lower Cambrian (Atdabanian):* Russia (Siberian Platform, Dzhagdy Mountains), Mongolia, South Australia.——FIG. 250,*2.* *E. obtusa,* Lower Cambrian (Botomian, Egyngolskaya Suite), northwestern Mongolia; holotype, ×7.5 (Korobov, 1980).

Ekwipagetia FRITZ, 1973, p. 9 [*E. plicofimbria* FRITZ, 1973; OD; holotype (FRITZ, 1973, pl. 6, fig. 7–9), 33214, GSC, Ottawa]. Large; glabella relatively short, wide, with much narrower occipital spine; anterior border bearing epiborder furrow; palpebral furrows well impressed. Pygidium with narrow, poorly furrowed axis bearing posterodorsally directed spine towards its posterior; border thin, with fine marginal spines. *Lower Cambrian:* USA (New York), Canada (Northwest Territories), Greenland, "Nevadella" Zone.——FIG. 250,*4a,b.* *E. plicofimbria,* "Nevadella" Zone, Sekwi Formation, Northwest Territories (Mackenzie Mountains); a, holotype, cranidium, ×7.8; b, paratype, pygidium, ×7.8 (Fritz, 1973).

Hebediscina RASETTI, 1972, p. 46 [*H. sardoa;* OD; holotype (RASETTI, 1972, pl. 7, fig. 5–6), 69, SG, Rome] [=*Szechuanaspis* CHIEN & YAO in LU & others, 1974, p. 84 (type, *S. longispinus;* OD; NIGP 20456); *Zhenbadiscus* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 36 (type, *Z. typicalis;* OD; NIGP 37336)]. Preglabellar field usually depressed, particularly at glabellar anterior; cranidial spine short, often slender; anterior border convex in section, without radial markings; palpebral lobes large; palpebral furrows well impressed. Pygidium with axis of four to seven rings tapering posteriorly almost to border furrow; pleural furrows variable but generally impressed; border narrow, with several (commonly five) pairs of marginal or dorsomarginal spines. *Lower Cambrian:* Sardinia, Mongolia, China (Sichuan), South Australia.——FIG. 250,*6a,b.* *H. sardoa,* Lower Cambrian (Nebida Formation), Sardinia (Monte Cuccurinu); a, holotype, cranidium, ×12; b, paratype, pygidium, ×12 (Rasetti, 1972).

Lenadiscus REPINA in KHOMENTOVSKII & REPINA, 1965, p. 109 [*L. unicus;* OD; holotype (KHOMENTOVSKII & REPINA, 1965, pl. 1, fig. 9), 265/1269, CSGM, Novosibirsk]. Glabella narrowed near anterior just behind eye ridges; eye ridges prominent, palpebral lobes teardrop-shaped. Frontal area long

and flat, with prominent caecal network in some specimens. Pygidium subsemicircular; wide axis of three rings plus terminal portion. Pair of long, slender posterolateral marginal spines; four prominent ridges on pleural lobe occurring intersegmentally at the axis and converging on base of marginal spines. *Lower Cambrian (Botomian):* Russia (Siberian Platform), Mongolia.——FIG. 251*a–d.* *L. unicus,* Lower Cambrian (Botomian), Siberia (Lena River); a, cranidium, ×20; b, partial cranidium, ×20; c, holotype, pygidium, ×10; d, pygidium, ×20 (Repina & Pereladov, 1988).

Yukonides FRITZ, 1972, p. 10 [*Y. lacrinus;* OD; holotype (FRITZ, 1972, pl. 8, fig. 1–2), 27278, GSC, Ottawa]. Glabella narrow; with marked preglabellar depression; eye ridge, when elevated, extending to eye tubercles on lateral margin; librigenae absent. Pygidium with axis of five to seven rings; border bearing inconspicuous marginal spines or nodes. *middle Lower Cambrian:* USA (New York), Canada (Northwest Territories), Russia (Siberian Platform).——FIG. 250,*5a,b.* *Y. lacrinus,* "Nevadella" Zone, Sekwi Formation, Northwest Territories (Mackenzie Mountains); a, holotype, cranidium, ×8.7; b, pygidium, ×10.8 (Fritz, 1972).

Family EODISCIDAE Raymond, 1913

[Eodiscidae RAYMOND, 1913b, p. 102, *emend.* JELL, 1975a, p. 29 and herein] [=Dawsoniidae RESSER, 1937, p. 9; Pagetidae KOBAYASHI, 1935, p. 112; Aulacodiscidae HUPÉ, 1954, p. 59; Opsidiscidae HUPÉ, 1953b, p. 170; Pagetiellinae S. ZHANG in W. ZHANG, LU, & others, 1980, p. 23]

Same as Yukoniidae, but anterior border scrobiculate. Pygidial axis of four to ten rings. *upper Lower Cambrian–Middle Cambrian.*

Eodiscus HARTT in WALCOTT, 1884b, p. 24 [*E. pulchellus;* OD; syntypes (RASETTI, 1952a, pl. 54, fig. 10–11), 3794, CU, Ithaca; =*Microdiscus scanicus* LINNARSSON, 1883, p. 29; lectotype (LINNARSSON, 1883, pl. 4, fig. 17), 5602, SGU, Uppsala] [=*Spinodiscus* KOBAYASHI, 1943, p. 39 (type, *Microdiscus punctatus* SALTER, 1864c, p. 237; OD; lectotype BMNH 42646); *Deltadiscus* KOBAYASHI, 1943, p. 39 (type, *Microdiscus punctatus precursor* MATTHEW, 1886, p. 75; OD; ROM 47; =*Microdiscus scanicus* LINNARSSON, 1883, p. 29)]. Glabella may be anteriorly acuminate; S1 and S2 discontinuous lateral indentations only; frontal area relatively long, with median preglabellar furrow; border short, uniform; scrobicules may be effaced; eyes and facial sutures absent. Thorax with three segments. Pygidium with long, narrow axis of 10 or more rings; border narrow. Surface ornament variable between species. *Middle Cambrian:* Canada (Newfoundland, New Brunswick), Sweden, Spain, Wales, England, Norway, Russia (Siberian Platform).——FIG. 252,*1a–c.* *E. scanicus* (LINNARSSON)*,* Middle Cambrian (*Ptychagnostus atavus* Zone), Sweden; a, whole specimen, ×6; b, lectotype, cranidium, SGU 5602, ×6; c, cranidium, ×6 (Westergård, 1946).

Dawsonia Hartt in Dawson, 1868, p. 655 [*Microdiscus dawsoni;* OD; types not traced] [=*Aculeodiscus* Šnajdr, 1950, p. 201 (type, *A. bohemicus;* OD; NMP 32028); *Metadiscus* Kobayashi, 1943, p. 39 (type, *Microdiscus sculptus* Hicks in Harkness & Hicks, 1871, p. 400; OD; SM A1088)]. Coarsely granulose; glabella poorly furrowed laterally; anterior border convex; blind. Thorax with two segments. Pygidium with axis of six rings plus terminus; pleural furrows deeply incised; border extremely narrow. *Middle Cambrian:* Canada (Newfoundland, New Brunswick), Sweden, Wales, Czechoslovakia, Russia (Siberian Platform).——Fig. 253,*2.* *D. dawsoni,* Middle Cambrian (Fossil Brook Formation), New Brunswick (Fossil Brook); latex cast of whole specimen, ×8 (Rasetti, 1952a).

Helepagetia Jell, 1975a, p. 82 [*H. bitruncula;* OD; holotype (Jell, 1975a, pl. 29, fig. 1), 27793, ANU, Canberra]. Small species; like *Pagetia* except that eyes are present and facial sutures are absent. Pygidium with few axial rings and a terminal or subterminal axial spine. Ornament of dense, fine pustules with larger granules sparsely interspersed. *Middle Cambrian:* Australia (Queensland, Tasmania), *P. punctuosus* to *L. laevigata* Zones.——Fig. 252,*5a,b.* *H. bitruncula,* Middle Cambrian (Currant Bush Limestone), western Queensland; *a,* holotype, cephalon, ×15.6; *b,* paratype, pygidium, ×12.5 (Jell, 1975a).

Kiskinella Romanenko & Romanenko, 1962, p. 24 [*K. cristata;* OD; holotype (Romanenko & Romanenko, 1962, pl. 3, fig. 3), 1328/1958, ZSGU, Novokuznetsk]. Glabella not reaching border furrow, unfurrowed except for SO; median preglabellar furrow separating fixigenae; librigenae extremely small; palpebral lobe small, low on side of fixigenal elevation. Pygidium with parallel-sided axis of four rings (plus terminal portion) finishing well before border furrow; pleural furrows deep; border extremely narrow. *Middle Cambrian (Amgaian):* Russia (Gorno-Altyskaya).——Fig. 252,*6a,b.* *K. cristata,* Middle Cambrian (Amgaian), Gorno-Altayskaya (Kiska River); *a,* holotype, cranidium, ×9; *b,* pygidium, ×9 (Romanenko & Romanenko, 1962).

Macannaia Jell, 1975a, p. 71 [*Pagetia maladensis* Resser, 1939, p. 25; OD; holotype (Resser, 1939, pl. 2, fig. 5, right), 98491a, USNM, Washington, D.C.]. Small; similar to *Pagetia;* glabella narrow, occupying small part of cranidium, may be anteriorly truncated; preglabellar field short, depressed immediately in front of glabella; palpebral lobes usually highly elevated. Thorax with two segments, with geniculate spine on axis of second segment. Pygidial axis narrow, reaching posterior border furrow, usually expanded dorsally at rear, with spine varying from minute node to long horizontal spine; border widest in midlength of pygidium. *Middle Cambrian:* Spain; USA (Idaho), *Glossopleura* Zone; Australia (New South Wales), *Peronopsis longinqua* Zone; Russia (Siberian Platform), upper Toyonian–

Lenadiscus
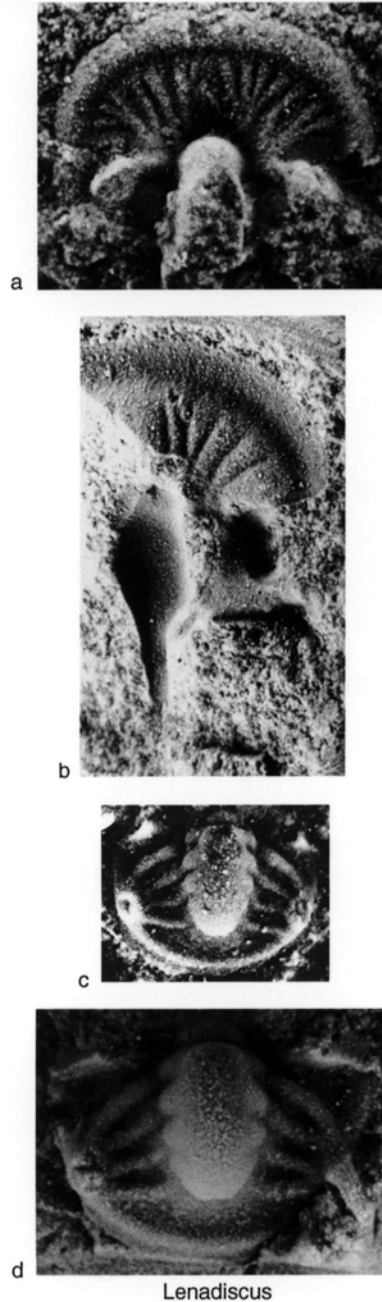
Fig. 251. Yukoniidae (p. 400)

Amgaian.——Fig. 252,*3a,b.* *M. maladensis* (Resser), Middle Cambrian (Langston Limestone), Idaho; *a,* holotype, cranidium, ×12; *b,* pygidium, ×12 (Rasetti, 1966b).
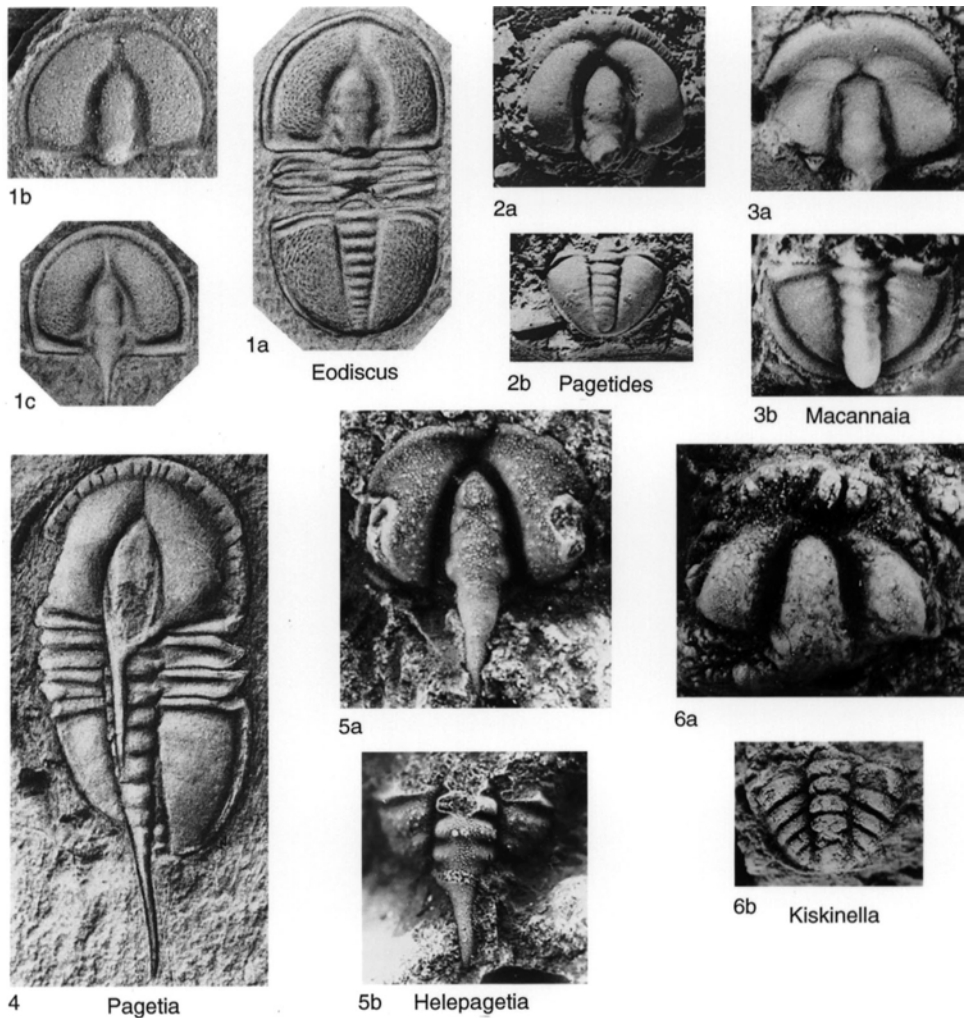
Fig. 252. Eodiscidae (p. 400–403)

Opsidiscus Westergård, 1950b, p. 606, *nom. nov. pro Aulacodiscus* Westergård, 1946, p. 26, *non* Douvillé, 1921 [*Aulacodiscus bilobatus* Westergård, 1946, p. 26; OD; holotype (Westergård, 1946, pl. 1, fig. 21), 4702, SGU, Uppsala]. Small species; like *Pagetia,* but has small abathochroal eye and fused facial suture. Thorax with two segments, the second segment bearing small, geniculate median spine. Pygidium with axis of two to six rings plus terminal portion but no terminal spine. *upper Middle Cambrian:* Sweden, Russia (Siberian Platform, Gorno-Altayskaya), Australia (Queensland, Tasmania), India, Antarctica.——Fig. 253,*1a,b.* **O. bilobatus,* upper Middle Cambrian (*Lejopyge laevigata* Zone), Sweden; *a,* holotype, cranidium, Östergotland, ×8;

b, pygidium, Västergotland, ×8 (Westergård, 1946).

Pagetia Walcott, 1916b, p. 407 [**P. bootes;* OD; syntypes (Walcott, 1916b, pl. 67, fig. 1), 62855–62861, USNM, Washington, D.C.] [=*Eopagetia* Kobayashi, 1943, p. 40 (type, *Microdiscus significans* Etheridge, 1902, p. 3; OD; lectotype chosen Whitehouse, 1936, p. 83, AMF 9138A); *Mesopagetia* Kobayashi, 1943, p. 40 (type, *Pagetia clytia* Walcott, 1916b, p. 408; OD; syntypes USNM 62862–62867)]. Glabella may taper forward, usually with furrows poorly impressed laterally; preglabellar field of variable length, usually depressed; border tapering laterally; abathochroal eye present; facial suture proparian. Thorax with two or

three segments, with geniculate, posteriorly directed median spine on second. Pygidium with axis of three to six rings plus terminal portion bearing spine of variable length; axis not reaching border furrow. *upper Lower Cambrian:* USA (New York), Canada (Yukon Territory). *Middle Cambrian:* USA (Idaho, New York), Canada (Quebec, British Columbia), India, Russia (Siberian Platform), Korea, China (Guizhou, Yunnan), Antarctica, Australia (Queensland, New South Wales, Northern Territory, South Australia).——FIG. 252,*4. *P. bootes, Bathyuriscus-Elrathina* Zone, Burgess Shale, British Columbia; articulated syntype, ×8 (Rasetti, 1966b).

Pagetides RASETTI, 1945b, p. 311 [**P. elegans;* OD; holotype (RASETTI, 1945b, pl. 1, fig. 1), 304a, LU, Montreal] [=*Discomesites* ÖPIK, 1975b, p. 32 (type, *D. fragum;* OD; AGSO 13177)]. Like *Pagetia,* but with well-developed palpebral furrows. Pygidium without axial spine. *upper Lower Cambrian:* Scotland, USA (Alaska, New York, Vermont), Canada (Northwest Territories, Quebec), Russia (Siberian Platform), Australia (New South Wales), Antarctica. *lower Middle Cambrian:* Canada (Newfoundland).——FIG. 252,*2a,b. *P. elegans,* upper Lower Cambrian (Sillery Formation), Quebec (Levis); *a,* holotype, cranidium, ×6; *b,* pygidium, ×6 (Rasetti, 1945b).

Sinopagetia W. ZHANG & YUAN, 1981, p. 162 [**S. neimengguensis;* OD; holotype (W. ZHANG & YUAN, 1981, pl. 2, fig. 1), 62248, NIGP, Nanjing; =*Pagetia jinnanensis* LIN & WU in W. ZHANG, LIN, & others, 1980, p. 47; holotype (W. ZHANG, LIN, & others, 1980, pl. 1, fig. 1), 51075, NIGP, Nanjing]. Glabella wide at base, tapering forward; L1 expanded posteriorly but not spinose; anterior border elongate medially; librigena subquadrate; palpebral furrow not impressed. Pygidial axis of five rings and terminal portion, lacking posterior spine, not reaching posterior border furrow; ring furrows not well impressed; border extremely narrow, smooth. *lower Middle Cambrian:* Inner Mongolia, China (Shaanxi).——FIG. 253,*3a,b. *S. jinnanensis,* lower Middle Cambrian (Hsuchuang Formation), Inner Mongolia (Gangdeershan); *a,* holotype, cranidium, ×20; *b,* pygidium, ×18 (W. Zhang & Yuan, 1981).

GENERA PREVIOUSLY ASSIGNED TO EODISCOIDEA BUT HERE CONSIDERED DOUBTFUL OR EXCLUDED

Dipharus CLARK, 1923a, p. 478 [**D. insperatus;* OD; holotype (SHAW, 1950, pl. 79, fig. 18), 1693, MCZ, Cambridge] [=*Pseudodipharus* KOROBOV, 1980, p. 91 (type, *P. privus;* OD; PIN 128, coll. 4251)]. Glabella subconical, narrow, extending to anterior border furrow, with slightly expanded frontal lobe and up to three pairs of poorly impressed lateral glabellar furrows; LO medially elongate, without a spine; fixigenae with a prominent tubercle behind eye
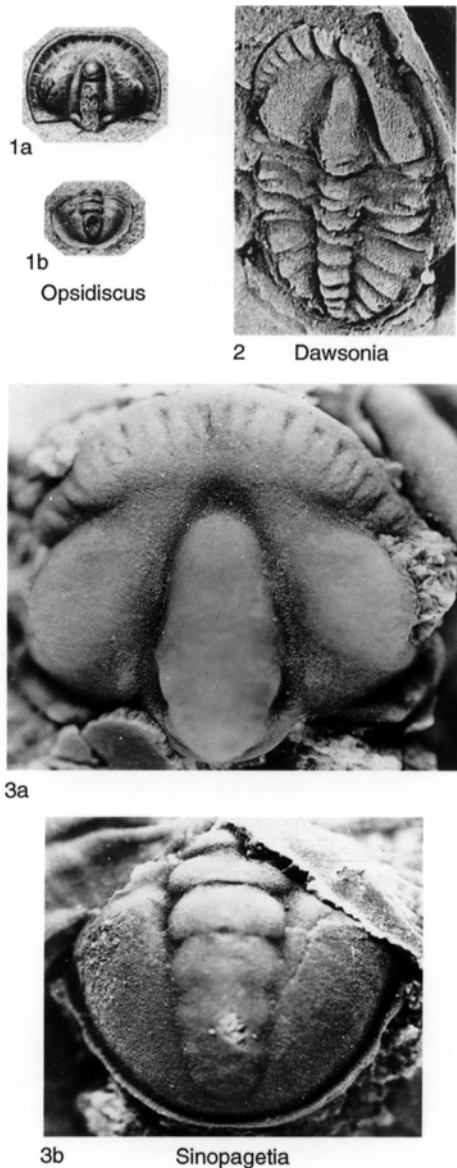
FIG. 253. Eodiscidae (p. 400–403)

ridge; palpebral lobe long, curved, defined by well-impressed palpebral furrow, and continuing into eye ridge and meeting axial furrow at level of anterior of glabella; border extremely short; librigena long and narrow. Pygidium with posteriorly tapering axis of six rings plus terminal portion, finishing just forward of border furrow; pleural areas with pleural and interpleural furrows extending across border area so that pleural ribs extend into

exsagittal marginal spines. [Probably the juvenile form of a Redlichiida; too imperfectly known.] *Lower Cambrian:* USA (Massachusetts), Mongolia.

Discagnostus ÖPIK, 1963, p. 55 [**D. spectator;* OD; holotype (ÖPIK, 1963, pl. 2, fig. 14–15), CPC 4262, AGSO, Canberra]. Glabella short, with continuous glabellar furrow dividing short anterior glabellar lobe, with rear of glabella roundly expanded posterodorsally; border with closely spaced, radial scrobicules; two pairs of prominent genal tubercles situated anteriorly and posteriorly. [SHERGOLD and others (1990) assigned this genus to the Eodiscoidea. If this genus is a derivative of the *Pagetia-Opsidiscus* lineage, one of the pairs of genal tubercles would be a new feature; if it is an Agnostina, both pairs of tubercles are new features. Its assignment, which is doubtful, must await further knowledge, particularly of the cephalothoracic area and pygidium.] *Upper Cambrian:* Australia (Queensland), *Glyptagnostus stolidotus* Zone.

Glabrella LERMONTOVA, 1940, p. 120 [**G. ventrosa;* OD; syntypes (LERMONTOVA, 1940, pl. 35, fig. 9, 9a–d), 64, 74, 77, TsGM, St. Petersburg]. Probably belongs to Kingstoniidae or Corynexochida. *Middle Cambrian (Amgaian):* Russia (Tian-Shan, southern Fergama).

Mendodiscus RUSCONI, 1950a, p. 74 [**M. tuberculatus;* OD; holotype (RUSCONI, 1956, fig. 4), 2644, MHN, Mendoza]. The holotype and only figured specimen is a trilobite pygidium, probably belonging to the Corynexochidae; it is not an eodiscoid, much less a cranidium. *lower Middle Cambrian:* Argentina.

Miraculaspis ROMANENKO in ROMANENKO & ROMANENKO, 1967, p. 72 [**M. picta;* OD; holotype (REPINA & ROMANENKO, 1978, pl. 7, fig. 14–15), 1329/18, ZSGU, Novokuznetsk]. Cephalon unknown. Pygidium subquadrate; axis wide, parallel sided to slightly narrowed at rear of first ring, bluntly rounded posteriorly at border furrow, with 3 pairs of pits laterally but isolated from axial furrow; pleural areas narrow, shorter than axis, with widely spaced tubercles; border furrow and border forming wide flange tapering forward and crossed by numerous dividing radial ridges. [Style of furrows laterally on axis and caecal network suggest a cephalon, but structure of the transverse margin, particularly the oblique lateral sections, suggest a pygidium. Similar furrows on the pygidial axis are known on pygidia of the Condylopygidae (Agnostina). Moreover, an expanded border region is common in the Condylopygidae. Assignment of this genus must await a cephalon.] *Lower Cambrian (Botomian):* Russia (Gorno-Altayskaya).

Shivelicus POKROVSKAYA, 1959, p. 180 [**S. parvus;* OD; holotype (POKROVSKAYA, 1959, pl. 10, fig. 15), 3536/99, VNIGNI, Moscow]. Probably belongs to Corynexochida. *Lower Cambrian (Botomian):* Russia (Tuva, Transbaikal, Gorno-Altayskaya, western Sayan, Kuznetsk Altay).

Triangulaspis LERMONTOVA, 1940, p. 120 [**Ptychoparia meglitzkii* TOLL, 1899, p. 22; OD; holotype (LER-

MONTOVA, 1940, pl. 35, fig. 5), 21/5156, TsGM, St. Petersburg) [=*Angusteva* HUPÉ, 1953a, p. 114 (type, *Ptychoparia? annio* COBBOLD, 1910, p. 24; OD; syntypes Cobbold Nos. 401–403); *Acutaspis* REPINA in REPINA, BELYAEVA, & SOBOLEV, 1976, p. 151 (type, *A. facilis;* OD; IGGN 509/51)]. Pygidium not known with certainy as markedly different forms have been assigned to different species apart from the type. [Probably belongs to Ellipsocephaloidea, especially after SDZUY (1962b) showed the Spanish species *T. fusca* (pl. 22, fig. 13) with at least five thoracic segments.] *Lower Cambrian (Atdabanian, Botomian):* Russia (Siberian Platform), England, Spain, Morocco, Canada (Newfoundland).

Triangullina REPINA in KHOMENTOVSKII & REPINA, 1965, p. 107 [**T. parvula;* OD; holotype (KHOMENTOVSKII & REPINA, 1965, pl. 1, fig. 11), 265/1608, CSGM, Novosibirsk) [=*Plenudiscus* KOROBOV, 1980, p. 74 (type, *P. crassus;* OD; PIN 71, coll. 4251)]. Probably belongs to Ellipsocephaloidea; closely related to *Triangulaspis. Lower Cambrian (Atdabanian):* Russia (Siberian Platform), Mongolia.

Order REDLICHIIDA
Richter, 1932

Ocular lobe attached to glabella in front of S3, prominent throughout development; eye ridge may be subdivided. Many-segmented thorax, with pleural spines; may be subdivided into prothorax and opisthothorax. *Lower Cambrian–Middle Cambrian.*

The systematic arrangement of this section follows recent practice, but these views were questioned by GEYER (1996), who gave arguments for placing the Fallotaspidoidea in Suborder Redlichiina.

Suborder OLENELLINA
Walcott, 1890b

No facial suture; wide (tr.) rostral plate extending between genal angles, perrostral suture. Hypostome probably conterminant in holaspides in which preglabellar area was

short (sag.) or absent (Fig. 30.1). Thorax nonfulcrate. Pygidium narrow (tr.), with few segments. Calcified protaspis unknown; earliest meraspis with segmented interocular area. *Lower Cambrian.*

INTRODUCTION TO SUBORDER OLENELLINA

A. R. PALMER and L. N. REPINA

Olenellina are a morphologically varied and highly diverse group of generally micropygous trilobites that share a primary absence of facial sutures, the presence of a well-developed ocular lobe at all developmental stages, and an ontogeny in which the first mineralized stages are already early meraspids (PALMER, 1957). They are restricted to and characteristic of rocks of later Early Cambrian age and constitute a major suborder within the order Redlichiida (MOORE, 1959). More than 50 genera or subgenera and their associated higher taxa are recognizable (PALMER & REPINA, 1993). These taxa form the principal basis for biostratigraphic subdivisions (Fig. 254) of the later Lower Cambrian rocks of Laurentia (North America exclusive of the eastern seaboard from Newfoundland to Florida and including Spitsbergen and northwestern Scotland) and are major indices for the later Lower Cambrian biostratigraphy of Baltica (northern Europe exclusive of the British Isles), Avalonia (England, Wales, eastern Newfoundland, Nova Scotia, eastern New England, USA), Siberia, and the Moroccan sector of Gondwana (including Spain).

Ancestry of the Olenellina can only be speculative. They first appear as fully developed and morphologically diverse trilobites in the early, but not earliest, part of the shelly fossil record and are the oldest trilobites known. The principal phylogenetic trend within the Olenellina involves the relationship between the ocular lobe and the frontal (anterior) lobe (LA) of the glabella (REPINA, 1990a). In all of the earliest Olenellina, which include forms from Siberia, Laurentia, and the Moroccan sector of Gondwana, the glabella has parallel sides or tapers forward, LA is short, and the ocular lobe is attached along the entire margin of LA (Fallotaspidinae, Daguinaspidinae). In later genera, LA first becomes elongate, so that the ocular lobes connect only to its posterior part (Judomiidae, Nevadiidae), and then generally expands laterally, and the glabella as a whole expands anteriorly from the level of S1 (Olenellidae, Holmiidae). LA in these genera is also commonly inflated. Accompanying this modification, the distal parts of L3 extend laterally and posterolaterally and encroach on L2, often isolating the S2 furrows (Fig. 255), and L3 takes on a broad M-shape.

This phylogenetic trend underlies the proposed classification of the superfamilies. Within the Fallotaspidoidea, all Fallotaspididae, the earliest family of the Olenellina, have the ocular lobe attached along the entire margin of LA and an unmodified L3, and the anterior end of LA does not project forward of a line tangent to the anterolateral margin of the ocular lobe. In the remaining, generally younger families of the Fallotaspidoidea (Archaeaspididae, Judomiidae, Neltneriidae, Nevadiidae), the anterior end of LA projects forward of the junction with the anterior margin of the ocular lobe, but L3 remains unmodified. All Olenelloidea, which includes the youngest Olenellina, have the ocular lobe attached to the posterior part of LA and have a modified L3.

Within the superfamilies of the Olenellina, morphological changes of taxonomic value at the family level follow different patterns. The principal character distinguishing the two families in the Olenelloidea is the relationship between the extraocular area and the interocular area. The Holmiidae all have a narrow extraocular area that is less than twice the width of the interocular area. With minor exceptions (*Olenelloides* and some undescribed Laurentian forms), the Olenellidae have a wide extraocular area that is more than twice the width of the interocular area. In the Fallotaspidoidea, the relationship between the ocular lobe and LA, the shape of the glabella (parallel sided versus tapered),
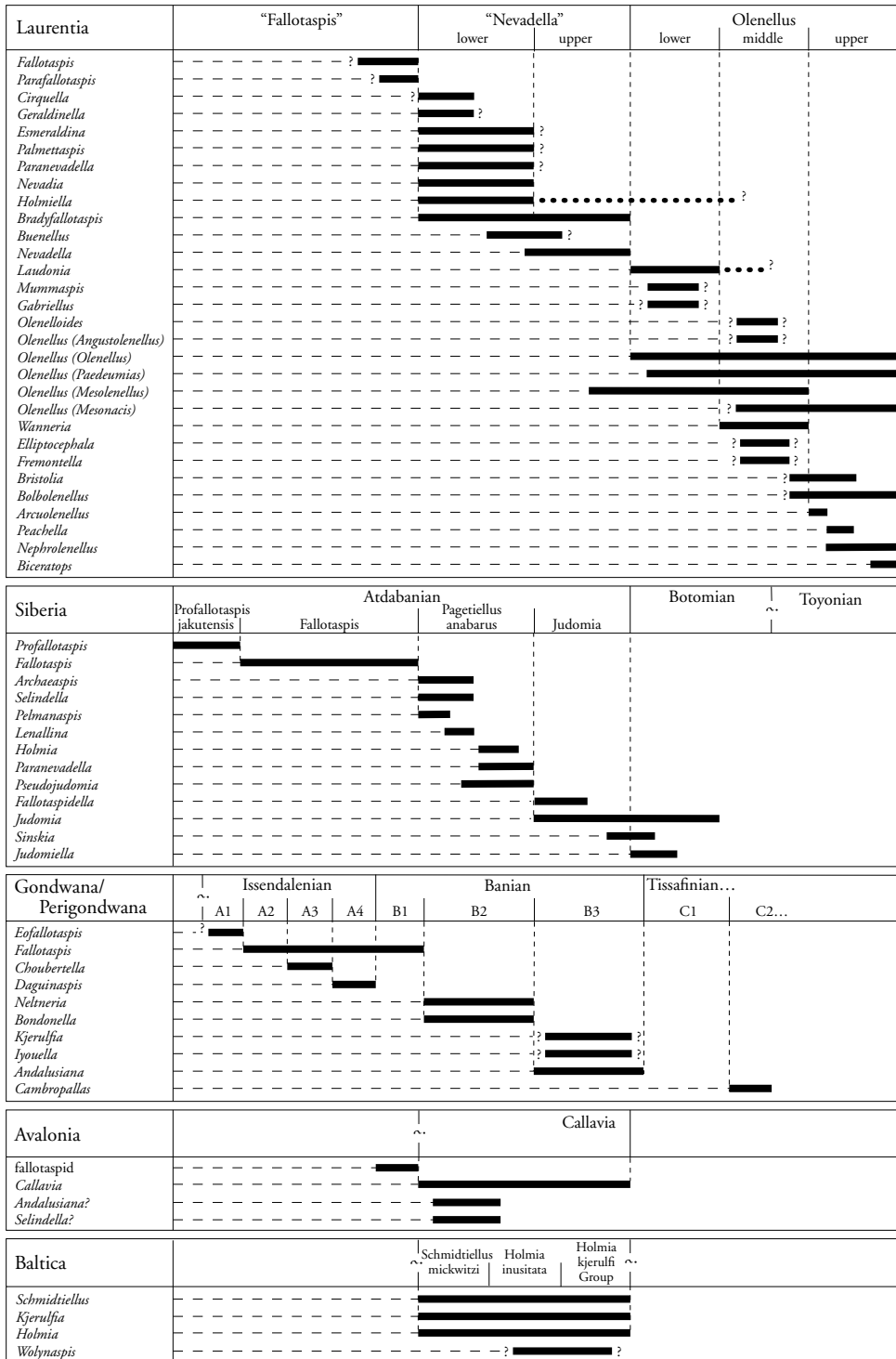
FIG. 254. Ranges of Olenellina within the principal paleogeographic regions of the Early Cambrian world (adapted from Palmer & Repina, 1993).

and the outline of the cephalon distinguish families.

Subfamilies of the Olenellidae are discriminated by the shape of the glabella and form of the thorax. Subfamilies of the Holmiidae are discriminated by general form of the thorax, by presence or absence of a preglabellar field, and by relative positions of the genal and intergenal spines. Subfamilies of the Fallotaspididae are discriminated by presence or absence of genal spines.

At the generic and subgeneric level, all taxonomically useful characters represent parts of continuous trends, including exsagittal shortening of the ocular lobes, changes in width of the interocular area, modification in sagittal length of the preglabellar field, position of the genal spines relative to the posterior cephalic margin, elaboration of the third thoracic segment, loss of genal spines, and position and degree of development of the intergenal spines. These characters are thus difficult to characterize precisely. Nevertheless, within-population variability in these characters is low (Riccio, 1952; Cowie & McNamara, 1978; McNamara, 1978), and their various combinations generally distinguish groups of species.

One of the many mysteries regarding the Olenellina is their complete absence from Lower Cambrian rocks of the Asiatic sector of Gondwana/peri-Gondwana (Australia, Antarctica, India, and southeastern Asia), where the characteristic Early Cambrian trilobites are Redlichiina. This has been traditionally expressed in an Early Cambrian biogeography that has recognized an olenellid realm or province and a redlichiid realm or province (e.g., Richter & Richter, 1941b; Cowie, 1971; W. Zhang, 1989). Olenellina and Redlichiina coexisted in the Moroccan sector of Gondwana, in the epicontinental seas of southern Siberia, and in areas now included in some central Asian orogens. In these areas of coexistence, the earliest Olenellina may be direct ancestors of the earliest Redlichiina (Repina, 1990a). Perhaps their subsequent geographic segregation resulted from some kind of environmental or competitive control of dispersal to the more peripheral parts of the Cambrian world.

Superfamily OLENELLOIDEA
Walcott, 1890

[Olenellidiae Walcott, 1890b, p. 635] [=Olenelloidea Richter & Richter, 1941a, p. 33, *partim;* Olenellacea Henningsmoen, 1951, p. 184, *partim;* Bergström, 1973b, p. 284, *partim;* Olenelloidae Hupé, 1953a, p. 116, *partim;* Olenelloidea Suvorova in Tchernysheva, 1960, p. 62, *partim;* Repina, 1979, p. 27, *partim;* Whittington, 1989, p. 113, *partim;* Palmer & Repina, 1993, p. 21]

LA usually enlarged; glabella narrowest at L2 or S1. L3 usually modified distally with posterolateral part bending backward and encroaching on L2. Ocular lobe connected only to posterolateral part of LA. *Lower Cambrian.*

Family OLENELLIDAE Walcott, 1890

[Olenellidiae Walcott, 1890b, p. 635, *sensu* Repina, 1979, p. 20] [=Mesonacidiae Walcott, 1890b, p. 635; Walcott, 1910, p. 236, *partim;* Olenellidae Hupé, 1953a, p. 124, *partim;* Poulsen in Moore, 1959, p. 191, *partim;* Suvorova in Tchernysheva, 1960, p. 62, *partim;* Bergström, 1973b, p. 312, *partim;* Ahlberg, Bergström, & Johansson, 1986, p. 40; Palmer & Repina, 1993, p. 21]

Width (tr.) of interocular area generally half or less that of extraocular area. Third thoracic segment slightly to strongly macropleural. *Lower Cambrian.*

Subfamily OLENELLINAE
Walcott, 1890

[Olenellinae Walcott, 1890b, p. 635] [=Olenellinae Poulsen in Moore, 1959, p. 192, *partim;* Suvorova in Tchernysheva, 1960, p. 62, *partim;* Repina, 1979, p. 22, *partim;* Fremontiinae Repina, 1979, p. 22, *partim;* Palmer & Repina, 1993, p. 21]

Glabellar furrows weakly to moderately defined. Width (tr.) of anterior part of L1 equal to or only slightly less than width (tr.) of occipital ring. LA slightly to moderately expanded anteriorly. Posterior tip of ocular lobe ranging from opposite L2 to opposite posterior part of occipital ring. Posterior margin of cephalon nearly straight or slightly deflected forward distal to intergenal spine or swelling. Intergenal spine or distinct intergenal angle usually present. Prothorax, where known, with axis narrower than inner part of pleurae. Third thoracic segment weakly to moderately macropleural, with pleural spine not greatly elongated. Fifteenth thoracic segment with long axial spine. Opisthothorax with variable number of uniformly small segments, each bearing narrow

pleurae. Pygidium small, subquadrate, may have 1 or 2 pairs of short marginal spines. *Lower Cambrian.*

Olenellus HALL, 1861, p. 114 (for explanation of date of this name, see WHITTINGTON, 1989, p. 114) [*Olenus thompsoni* HALL, 1859, p. 59; SD WAL-COTT, 1886, p. 163; holotype (HALL, 1859, p. 59, fig. 1), 244, AMNH, New York (lost)]. External surface generally smooth or with faint Bertillon pattern of lirae, rarely granular or reticulate. Occipital ring smooth or with small node near posterior margin; occipital spine rare; genal spine angle opposite or posterior to L1; genal spine slender. *Lower Cambrian:* North America (including Greenland), northwestern Scotland, Spitsbergen, Argentina (San Juan area), *Olenellus* Zone; ?Novaya Zemlya, zone uncertain.

  O. (Olenellus). Genal spines at posterolateral cephalic corners or slightly advanced to position opposite L1; intergenal spines, if present, small, close to genal spines, and directed slightly posterolaterally. Preglabellar field absent or very short, length (sag.) usually less than twice length (sag.) of anterior border; ocular lobe curved, its posterior tip convergent toward glabella and situated opposite or posterior to posterior part of L1; S2 isolated from axial furrow, usually present as distinct transverse slit. *Lower Cambrian:* North America (including Greenland), *Olenellus* Zone; Spitsbergen, *?Olenellus* Zone; ?Novaya Zemlya, zone uncertain.——FIG. 255,*1. *O. (O.) thompsoni,* Vermont; topotype, complete individual, USNM 15418a, ×2 (Palmer & Repina, 1993, fig. 3.1).

  O. (Angustolenellus) PALMER & REPINA, 1993, p. 22 [*Olenellus hamoculus* COWIE & MCNAMARA, 1978, p. 627; OD; holotype (COWIE & MCNA-MARA, 1978, pl. 70, fig. 3), 13302, GSE, Edinburgh]. Posterior margin of cephalon directed slightly anterolaterally distal to intergenal spine; intergenal spine about midway between genal spine and axial furrow or closer to axial furrow. Length (sag.) of preglabellar field equal to or slightly greater than that of anterior border; posterior tip of ocular lobe directed nearly straight backward, situated opposite or anterior to midlength of L1. *Lower Cambrian:* northwestern Scotland, middle *Olenellus* Zone.——FIG. 255,*5. *O. (A.) hamoculus;* cephalon, holotype, ×3 (Cowie & McNamara, 1978, pl. 70, fig. 3).

  O. (Mesolenellus) PALMER & REPINA, 1993, p. 22 [*Holmia hyperborea* V. POULSEN, 1974, p. 84; OD; holotype (V. POULSEN, 1974, pl. 1, fig. 4), 13008, MMK, Copenhagen]. Posterior margin of cephalon directed slightly forward distal to intergenal spine or intergenal angle. Length (sag.) of preglabellar field equal to or slightly greater than length (sag.) of anterior border; intergenal spine or angle about midway between genal spine and axial furrow or closer to axial furrow; posterior tip of ocular lobe convergent towards glabella, situated opposite or posterior to occipital furrow. *Lower Cambrian:* USA (Nevada), Canada (southern Rocky Mountains, Devon Island), northern Greenland, Argentina (San Juan region), lower? and middle *Olenellus* Zone.——FIG. 255,*4. *O. (M.) hyperborea* (POULSEN), northern Greenland; topotype, complete individual, MGUH 13.945 from GGU 184219, ×4 (Palmer & Repina, 1993, fig. 3.7).

  O. (Mesonacis) WALCOTT, 1885, p. 328 [*Olenus vermontanus* HALL, 1859, p. 60; OD; holotype (HALL, 1859, p. 60, fig. 2), 230, AMNH, New York (lost)] [=*Fremontia* RAW, 1936, p. 243 (type, *Olenellus fremonti* WALCOTT, 1910, p. 320; SD HARRINGTON, 1956, p. 57), USNM 56819a]. Posterior margin of cephalon angled forward distal to intergenal angle. Preglabellar field absent or very short, with length (sag.) generally equal to or less than that of anterior border; posterior tip of ocular lobe directed nearly straight posteriorly; situated opposite of or anterior to medial part of L1; interocular area may be extended posteriorly as low, broad ridge. Most species with width (tr.) of inner part of macropleural third segment, exclusive of spine, less than 1.5 times width of axis. Pygidium, known only for type species, with 2 pairs of short marginal spines. *Lower Cambrian:* North America (all parts), northwestern Scotland, middle and upper *Olenellus* Zone.——FIG. 255,*2. *O. (M.) vermontanus* (HALL), Vermont; complete individual, topotype, USNM 15399a, ×1.3 (Palmer & Repina, 1993, fig. 3.2).

  O. (Paedeumias) WALCOTT, 1910, p. 304 [*Paedeumias transitans;* OD; lectotype (WAL-COTT, 1910, pl. 34, fig. 1; SD RESSER, 1928, p. 4), 56808b, USNM, Washington, D.C.]. Posterior margin of cephalon nearly straight or only slightly angled forward distal to position of intergenal spines; intergenal spine or swelling generally closer to genal spine than to axial furrow. Length (sag.) of preglabellar field greater than twice length (sag.) of anterior border; posterior tip of palpebral lobe convergent toward glabella, opposite or posterior to posterior part of L1. *Lower Cambrian:* North America (all parts), northwestern Scotland, *Olenellus* Zone.——FIG. 255,*3. *O. (P.) transitans* (WAL-COTT), Vermont; complete individual, lectotype, USNM 56808b, ×3 (Palmer & Repina, 1993, fig. 3.3).

Fremontella HARRINGTON, 1956, p. 58 [*Wanneria halli* WALCOTT, 1910, p. 301; OD; lectotype (WALCOTT, 1910, pl. 31, fig. 3; SD HARRINGTON, 1956, p. 58), 56806c, USNM, Washington, D.C.]. External surface smooth. Genal spine strongly advanced; genal spine angle anterior to S2; intergenal angle nearly a right angle. Preglabellar field absent; posterior tip of ocular lobe opposite anterior part of L1. *Lower Cambrian:* USA (Alabama), Argentina (San Juan area), *Olenellus* Zone.——FIG. 256,*2. *F. halli* (WALCOTT), Alabama; cephalon, lectotype, ×1.25 (Palmer & Repina, 1993, fig. 3.4).

Mummaspis Fritz, 1992, p. 17 [*Wanneria occidens* Walcott, 1913b, p. 314; OD; holotype (Walcott, 1913b, pl. 53, fig. 2), 60080, USNM, Washington, D.C.]. Parts of external surface reticulate. Posterior margin of cephalon nearly straight; intergenal swelling slightly distal to midlength of posterior margin. Preglabellar field absent or length (sag.) less than that of border; S3 deep, continuous across glabella; occipital spine may be present. Ocular furrow deep; outer band of ocular lobe narrower than inner band. Third thoracic segment generally only weakly macropleural. *Lower Cambrian:* Canada (southern Rocky Mountains), lower *Olenellus* Zone.——Fig. 256,*1a,b.* *M. occidens* (Walcott); *a,* complete individual, topotype, USNM 443745, ×4 (Fritz, 1992, pl. 9, fig. 2); *b,* cephalon and partial thorax, topotype, USNM 433750, ×1.7 (Fritz, 1992, pl. 10, fig. 2).

Subfamily BICERATOPSINAE
Pack & Gayle, 1971

[Biceratopsinae Pack & Gayle, 1971, p. 895] [=Olenellidae Bergström, 1973b, p. 312, *partim;* Ahlberg, Bergström, & Johansson, 1986, p. 40, *partim;* Biceratopsinae Repina, 1979, p. 22; Palmer & Repina, 1993, p. 23]

Glabella narrowest at midlength; glabellar furrows very poorly developed; width (tr.) of L1 less than width (tr.) of occipital ring; ocular lobe close to glabella, its posterior tip opposite or anterior to L1. Genal spine absent or opposite midlength of ocular lobe; intergenal spine absent; intergenal angle may be developed. Thorax divided into prothorax and opisthothorax; third segment strongly expanded distally; pleural spine extremely long, with tips posterior to body; fifteenth segment with long axial spine. *Lower Cambrian.*

Biceratops Pack & Gayle, 1971, p. 895 [*B. nevadensis;* OD; holotype (Pack & Gayle, 1971, pl. 102, fig. 2–3), 168225, USNM, Washington, D.C.]. Posterior margin of cephalon nearly straight; genal angle broadly rounded; genal and intergenal spines absent. Length (sag.) of preglabellar field equal to or less than that of anterior border; ocular lobe prominent, close to glabella, with posterior tip opposite S1 and elevated above top of glabella. Opisthothorax of at least 11 segments. *Lower Cambrian:* USA (Arizona, Nevada), upper *Olenellus* Zone.——Fig. 257,*1.* *B. nevadensis,* Nevada; complete individual, holotype, USNM 168225, ×3 (Pack & Gayle, 1971, pl. 102, fig. 2).

Peachella Walcott, 1910, p. 342 [*Olenellus iddingsi* Walcott, 1884b, p. 28; OD; holotype (Walcott, 1884b, pl. 9, fig. 12), 15407a, USNM, Washington, D.C.]. Posterior margin of cephalon nearly straight. Glabella extended to or nearly to border furrow; posterior tip of ocular lobe approximately opposite S1; genal spine at posterolateral corner or slightly advanced, strongly inflated. Opisthothorax of at least 10 segments. *Lower Cambrian:* USA (California, Nevada), upper *Olenellus* Zone.——Fig. 257,*2.* *P. iddingsi* (Walcott), California; nearly complete individual, LACMIP 11621, ×2 (Palmer & Repina, 1993, fig. 4.2).

Subfamily BRISTOLIINAE
Palmer & Repina, 1993

[Bristoliinae Palmer & Repina, 1993, p. 23] [=Olenellinae Poulsen in Moore, 1959, p. 162, *partim;* Olenellidae Bergström, 1973b, p. 312, *partim;* Ahlberg, Bergström, & Johansson, 1986, p. 40, *partim;* Fremontiinae Repina, 1979, p. 22, *partim*]

Glabella usually strongly constricted at S1 or L2; width (tr.) of anterior part of L1 usually distinctly narrower than occipital ring; glabellar furrows generally well developed. Preglabellar field shorter (sag.) than anterior border or absent. Posterior tip of ocular lobe opposite or anterior to L1. Third thoracic segment with inner part of pleural region strongly expanded distally; pleural spine may be extended posterior to end of thorax. Opisthothorax well developed. Pygidium not known. *Lower Cambrian.*

Bristolia Harrington, 1956, p. 59 [*Mesonacis bristolensis* Resser, 1928, p. 7; OD; lectotype (Resser, 1928, pl. 2, fig. 5–6; SD Harrington, 1956, p. 59), 78390, USNM, Washington, D.C.]. Cephalon subpentagonal to subquadrate in outline; genal spine originating opposite or anterior to L2; intergenal spine absent. Preglabellar field absent; posterior tip of ocular lobe opposite or anterior to L1. Fifteenth thoracic segment with long axial spine; opisthothorax of at least 17 segments. *Lower Cambrian:* USA (California, Nevada), Greenland (Inglefield Land), *Olenellus* Zone.——Fig. 258,*1.* *B. bristolensis,* California; nearly complete individual, UCR 10/7, ×1 (Palmer & Repina, 1993, fig. 4.5).

Arcuolenellus Palmer & Repina, 1993, p. 24 [*Olenellus arcuatus* Palmer in Palmer & Halley, 1979, p. 67; OD; holotype (Palmer & Halley, 1979, pl. 2, fig. 12), 177200, USNM, Washington, D.C.]. Posterior margin of cephalon strongly and evenly curved back distally; genal spine short, situated at posterolateral corner well behind level of occipital ring; intergenal spine absent. Preglabellar field short (sag.); width of interocular area about half width of glabella at L2; posterior tip of ocular lobe opposite L1. *Lower Cambrian:* USA (California), upper *Olenellus* Zone; Argentina (San Juan area), *Olenellus* Zone.——Fig. 258,*2.* *A. arcuatus* (Palmer), California; cephalon, holotype, USNM 177200, ×6 (Palmer & Halley, 1979, pl. 2, fig. 12).

Bolbolenellus Palmer & Repina, 1993, p. 24 [*Olenellus euryparia* Palmer in Palmer & Halley,
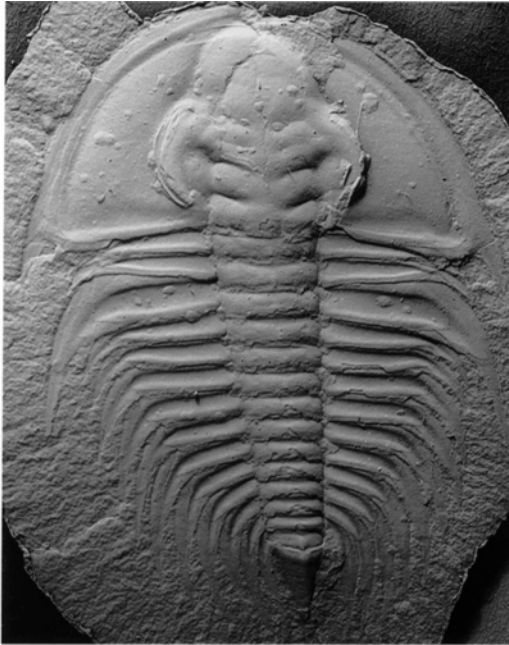
1   Olenellus

2   Mesonacis
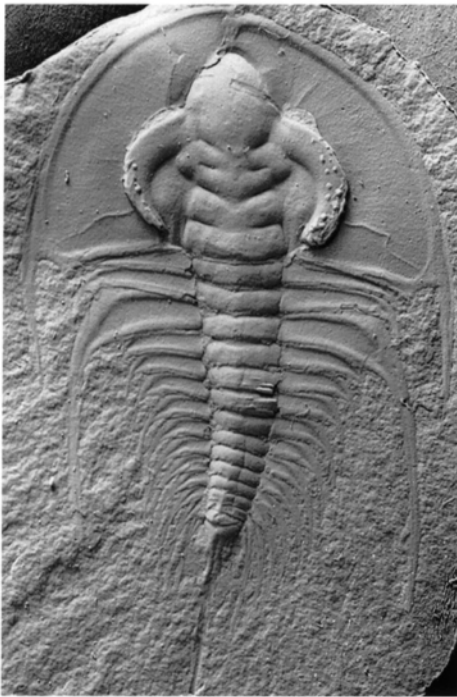
3   Paedeumias
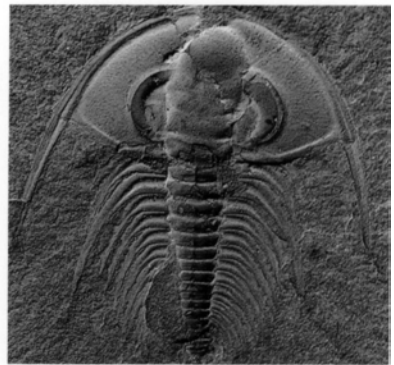
4   Mesolenellus

5   Angustolenellus

FIG. 255. Olenellidae (p. 408)
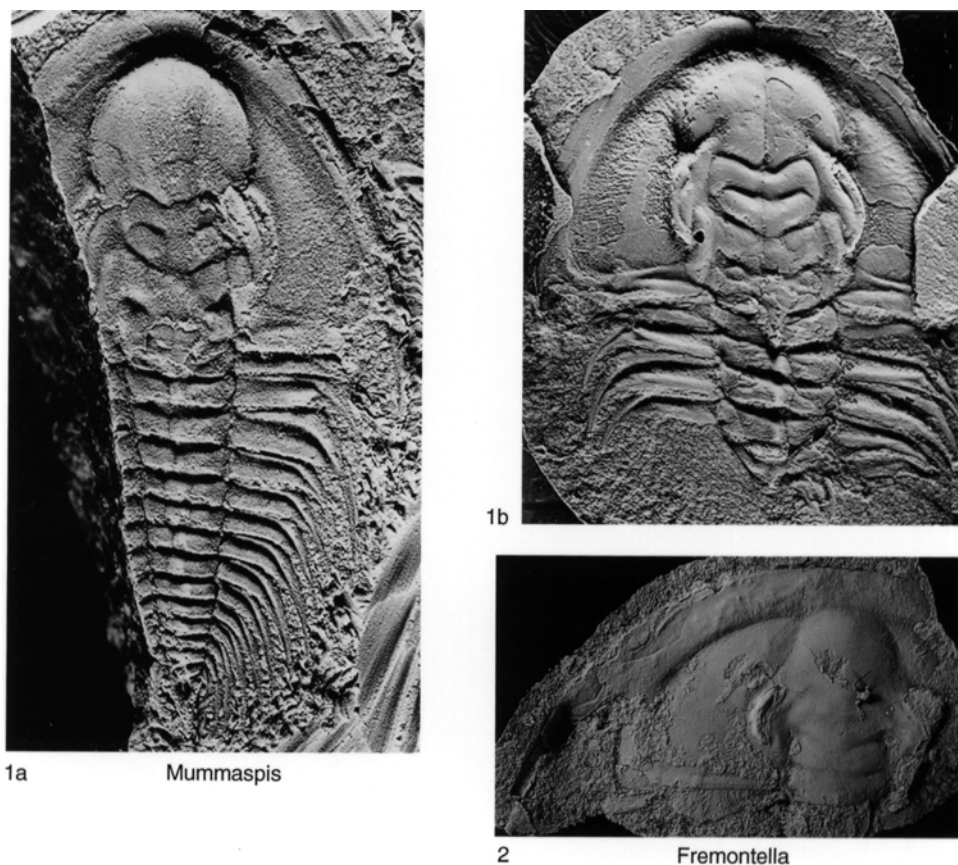
FIG. 256. Olenellidae (p. 408–409).

1979, p. 69; OD; holotype (PALMER & HALLEY, 1979, pl. 2, fig. 18), 177204, USNM, Washington, D.C.]. Posterior margin of cephalon nearly straight or deflected anterolaterally distal to intergenal spine or intergenal angle; genal spine originating opposite or posterior to L1; intergenal spine present on some species. LA prominent, subglobular, may overlap border in dorsal view; preglabellar field absent; posterior tip of ocular lobe approximately opposite occipital furrow. *Lower Cambrian:* USA (California, Nevada), Canada (Cordilleran region, Devon Island), ?northern Greenland, Mexico (Caborca), middle? and upper *Olenellus* Zone.——FIG. 258,*3.* **B. euryparia* (PALMER), California; cephalon, holotype, USNM 177204, ×2 (Palmer & Halley, 1979, pl. 2, fig. 18).

Nephrolenellus PALMER & REPINA, 1993, p. 24 [**Olenellus multinodus* PALMER in PALMER & HALLEY, 1979, p. 72; OD; holotype (PALMER & HALLEY, 1979, pl. 4, fig. 4), 177225, USNM, Washington, D.C.]. Posterior margin of cephalon directed slightly posterolaterally to intergenal spine or intergenal swelling that is situated near slightly advanced genal spine. Preglabellar field short (sag.);

width of interocular area approximately half or more width of glabella at L2; posterior tip of ocular lobe opposite L1. Third thoracic segment macropleural, having extremely long pleural spine with tip posterior to end of thorax; prothorax of 13 segments; opisthothorax of at least 17 segments; 15th segment lacking strong axial spine. *Lower Cambrian:* USA (California, Nevada); Canada (southern Rocky Mountains), upper *Olenellus* Zone.——FIG. 258,*4a.* **N. multinodus* (PALMER), California; cephalon, holotype, USNM 177225, ×5 (Palmer & Halley, 1979, pl. 4, fig. 4).——FIG. 258,*4b. Nephrolenellus* sp., Nevada; nearly complete individual, USNM 466536, ×3 (Palmer & Repina, 1993, fig. 4.3).

Subfamily GABRIELLINAE
Palmer & Repina, 1993

[Gabriellinae PALMER & REPINA, 1993, p. 24]

Posterior margin of cephalon curved forward. Intergenal angle variably developed, situated slightly distal to midlength of
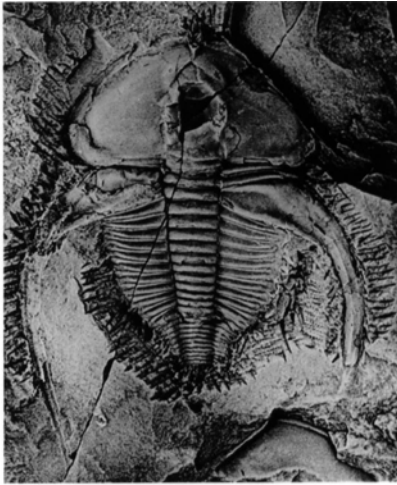
1 Biceratops
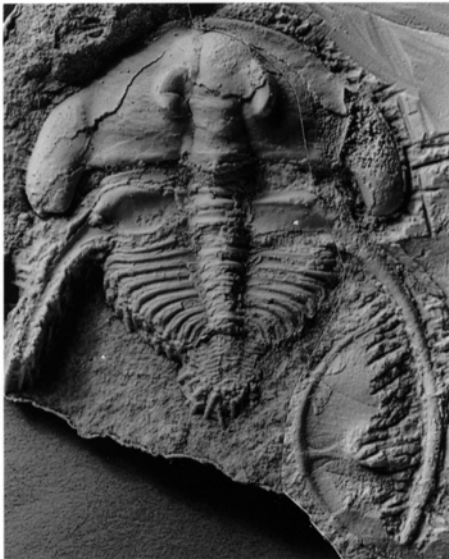
2 Peachella

Fig. 257. Olenellidae (p. 409)

posterior margin. Genal spine originating opposite or anterior to S1. Glabella bullet shaped. Ocular lobe close to glabella, its tip opposite or posterior to occipital furrow. Thorax with at least 17 segments; each segment with width (tr.) of thoracic axis greater than width of inner parts of pleural region; third thoracic segment not modified; fifteenth segment with long axial spine.

Opisthothorax not clearly differentiated. Pygidum elongate; sides convergent posteriorly; end bluntly pointed. *Lower Cambrian.*

Gabriellus Fritz, 1992, p. 20 [**G. lanceatus;* OD; holotype (Fritz, 1992, pl. 17, fig. 6), 443792, USNM, Washington, D.C.] Characters as for subfamily. *Lower Cambrian:* USA (Nevada), Canada (Cordilleran region), lower *Olenellus* Zone.——Fig. 259,*3. Gabriellus* sp.; complete individual, Canada, GSC 104195, ×1.7 (Palmer & Repina, 1993, fig. 4.9).

Subfamily LAUDONIINAE
Palmer & Repina, 1993

[Laudoniinae Palmer & Repina, 1993, p. 24]

Cephalon subquadrate to subhexagonal in outline. Genal spine strongly advanced, originating anterior to S1. Intergenal spine strongly developed in adult at posterolateral corner of cephalon. Width (tr.) of anterior part of L1 nearly equal to that of occipital ring. Thorax with third segment weakly macropleural; 15th segment lacking axial spine. Opisthothorax not clearly differentiated. Pygidium small, bilobate. *Lower Cambrian.*

Laudonia Harrington, 1956, p. 60 [**L. bispinata;* OD; holotype (Harrington, 1956, pl. 15, fig. 4), 9465T1, KUMIP, Lawrence]. Cephalon subquadrate to subpentagonal in outline; genal spine originating opposite or anterior to L3; procranidial spine not developed in adult; intergenal ridge distinct. Preglabellar field absent or shorter (sag.) than border; posterior tip of ocular lobe opposite or anterior to L1. Thorax of about 20 segments. External surface reticulate. *Lower Cambrian:* Canada (southern Rocky Mountains), USA (Nevada), Mexico (Caborca), lower *Olenellus* Zone.——Fig. 259,*2. L. amputata* Fritz; cephalon and partial thorax, Canada, USNM 443754, ×2 (Fritz, 1992, pl. 11, fig. 4).

?Olenelloides Peach, 1894, p. 668 [**Olenellus (Olenelloides) armatus* Peach, 1894, p. 669; OD; lectotype (Peach, 1894, pl. 32, fig. 4; SD McNamara, 1978, p. 637), 472, GSE, Edinburgh]. Cephalon subhexagonal in outline; prominent procranidial, genal, or intergenal spine at each angle of the hexagon; intergenal spine close to glabella; LA subglobular. Preglabellar field absent; width (tr.) of narrow interocular area about equal to width of equally narrow extraocular area opposite midlength of ocular lobe; posterior tip of ocular lobe opposite L2. Thorax with 9 segments; axis wider than inner part of pleural region exclusive of spines; third and sixth thoracic segments macropleural. *Lower Cambrian:* northwestern Scotland, middle *Olenellus* Zone.——Fig. 259,*1a,b. *O. armatus* (Peach); *a,*

1   Bristolia

2   Arcuolenellus

3   Bolbolenellus

4a
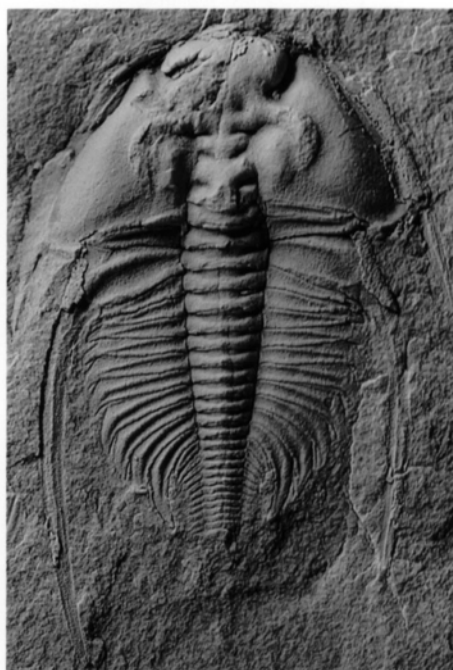
4b   Nephrolenellus

Fɪɢ. 258. Olenellidae (p. 409–411)

reconstruction of entire individual, ×5 (McNamara, 1978, fig. 1); *b,* cephalon, lectotype, GSE 472, ×8 (McNamara, 1978, pl. 71, fig. 1).

Subfamily WANNERIINAE Hupé, 1953

[Wanneriinae Hᴜᴘᴇ́, 1953a, p. 124] [=Olenellinae Sᴜᴠᴏʀᴏᴠᴀ in Tᴄʜᴇʀɴʏsʜᴇᴠᴀ, 1960, p. 62, *partim;* Holmiidae Bᴇʀɢsᴛʀöᴍ, 1973b, p. 285, *partim;* Wanneriidae Aʜʟʙᴇʀɢ, Bᴇʀɢsᴛʀöᴍ, & Jᴏʜᴀɴssᴏɴ, 1986, p. 40, *partim;* Wanneriinae Pᴀʟᴍᴇʀ & Rᴇᴘɪɴᴀ, 1993, p. 25]

LA enlarged. Posterior margin of cephalon straight or curved backward towards base of genal spine. Intergenal spine absent. Preglabellar field absent. Posterior tip of ocular lobe opposite or anterior to occipital furrow. Thorax with 17 segments, not divided into prothorax and opisthothorax; third segment unmodified; fifteenth segment bearing long axial spine. Pygidium small, subquadrate, with prominent median notch. External surface reticulate; polygons may have central granule; on well-preserved specimens

boundaries of polygons marked by rows of perforations on underside of exoskeleton. *Lower Cambrian.*

Wanneria Walcott, 1910, p. 296 [**Olenellus (Holmia) walcottanus* Wanner, 1901, p. 267; OD; lectotype (Wanner, 1901, pl. 31, fig. 1; SD Resser & Howell, 1938, p. 227, pl. 10, fig. 9), 56807a, USNM, Washington, D.C.]. Characters as for subfamily. *Lower Cambrian:* North America (widespread, including Greenland), middle *Olenellus* Zone.——Fig. 260. **W. walcottana* (Wanner), Pennsylvania; complete individual, topotype, USNM 85357, ×1 (Palmer & Repina, 1993, fig. 5).

Family HOLMIIDAE Hupé, 1953

[*nom. transl.* Bergström, 1973b, p. 285, *ex* Holmiinae Hupé, 1953a, p. 125] [=Holmiinae Hupé, 1953a, p. 125, *partim;* Poulsen in Moore, 1959, p. 194, *partim;* Suvorova in Tchernysheva, 1960, p. 62, *partim;* Holmiidae Bergström, 1973b, p. 285, *partim;* Repina, 1979, p. 20, *partim;* Ahlberg, Bergström, & Johansson, 1986, p. 43, *partim;* Palmer & Repina, 1993, p. 25; Callaviinae Poulsen in Moore, 1959, p. 192, *partim;* Bergström, 1973b, p. 309, *partim;* Callaviidae Ahlberg, Bergström, & Johansson, 1986, p. 40, *partim*]

Width (tr.) of interocular area more than half that of extraocular area. Third thoracic segment generally unmodified; prothorax and opisthothorax not differentiated. *Lower Cambrian.*

Subfamily HOLMIINAE Hupé, 1953

[Holmiinae Hupé, 1953a, p. 125] [=Holmiinae Poulsen in Moore, 1959, p. 194, *partim;* Suvorova in Tchernysheva, 1960, p. 62, *partim;* Repina, 1979, p. 20, *partim;* Palmer & Repina, 1993, p. 25; Holmiidae Ahlberg, Bergström, & Johansson, 1986, p. 43, *partim;* Elliptocephalinae Hupé, 1953a, p. 124, *partim;* Poulsen in Moore, 1959, p. 194, *partim;* Wanneriidae Ahlberg, Bergström, & Johansson, 1986, p. 40, *partim;* Callaviinae Bergström, 1973b, p. 309, *partim*]

Glabella expanded forward. Cephalic border generally convex in cross section. Inner pleural region of thorax narrower than axis. *Lower Cambrian–?lowest Middle Cambrian.*

Holmia Matthew, 1890, p. 160 [**Paradoxides kjerulfi* Linnarsson, 1873, p. 790; OD; lectotype (Linnarsson, 1873, pl. 16, fig. 1; SD Palmer & Repina, 1993, p. 25), 5329a,b, SGU, Uppsala]. Intergenal spine generally well developed at or slightly proximal to midlength of posterior cephalic margin. Glabella expanded anteriorly, L3 modified; posterior tip of ocular lobe opposite or posterior to L1. Thorax narrow, with 16 or 17 segments; pleural spines thornlike; each segment with axial spine. Pygidium small, subquadrate, nonspinose; posterior margin nearly straight (tr.). *Lower Cambrian:* Sweden, Norway, Poland, *Schmidtiellus mickwitzi* to *Holmia kjerulfi* group Zones; Russia (Siberian Platform), upper *Pagetiellus anabarus* Zone.——Fig. 261,*1. *H. kjerulfi* (Linnarsson);

cephalon, partial thorax, pygidium, Norway, paratype, PMO 61378, ×3 (Whittington, 1990, fig. 13).

Andalusiana Sdzuy, 1961, p. 246 [**A. cornuta;* OD; holotype (Sdzuy, 1961, pl. 3, fig. 4), L3072, UMU, Münster]. Posterior cephalic margin nearly straight; intergenal spine not apparent. Glabella expanded anteriorly; LA with distinct lateral projections situated in front of ocular lobe and segregated by shallow longitudinal furrow; preglabellar field narrow; posterior tip of ocular lobe opposite posterior part of L1. Thorax narrow; each segment with axial node and short (exsag.) pleural spine not constricted at base; number of segments not known. *Lower Cambrian:* Spain (Guadalcanal), Marianian stage; United Kingdom (Comley, Shropshire), *Callavia* Zone; Morocco (Anti-Atlas), *Sectigena* Zone; ?Norway (Oslo Region), *Holmia kjerulfi* group Zone.——Fig. 261,*3. Andalusiana* sp.; cephalon, Morocco, IGR 19613, ×2 (Palmer & Repina, 1993, fig. 6.3).

Cambropallas Geyer, 1993, p. 76 [**C. telesto;* OD; holotype (Geyer, 1993, fig. 4; pl. 1, fig. 1–2; pl. 4, fig. 2–3), 93VII1, PIW, Würzburg]. Posterior cephalic margin arcuate, intergenal spine not apparent. Glabella slightly expanded anteriorly, extended onto inner part of broad anterior border; posterior tip of ocular lobe opposite anterior part of L1; genal spine broad based. Thorax with 15 or 16 segments, each with axial node; pleural spine short (exsag.), not constricted at base. Pygidium small, with short, blunt posterolateral spine. *?lowest Middle Cambrian:* Morocco (Anti-Atlas), *Cephalopyge notabilis* Zone.——Fig. 261,*4. *C. telesto;* complete individual, Morocco, holotype, ×0.5 (Geyer, 1993, pl. 1, fig. 1).

Elliptocephala Emmons, 1844, p. 21 [**E. asaphoides;* OD; neotype (Walcott, 1910, pl. 24, fig. 1; SD Palmer & Repina, 1993, p. 26), 18350a, USNM, Washington, D.C.]. Posterior margin of cephalon straight or slightly angled forward distal to intergenal swelling; intergenal spine absent. Posterior tip of ocular lobe opposite or slightly anterior to occipital furrow. Length (sag.) of preglabellar field equal to or slightly greater than that of anterior border. Thorax moderately wide, consisting of 18 segments; pleural regions of adults lacking macropleurae; 15th through 18th segments with strong axial spine. Pygidium small, subquadrate, with single pair of short anterolateral spines. External surface with some reticulate areas. *Lower Cambrian:* USA (New York), Canada (Quebec), *Olenellus* Zone.——Fig. 262,*4. *E. asaphoides;* cephalon and partial thorax, New York, NYSM 4598, ×5 (Palmer & Repina, 1993, fig. 6.7).

Esmeraldina Resser & Howell, 1938, p. 228 [**Holmia rowei* Walcott, 1910, p. 292; OD; lectotype (Walcott, 1910, pl. 29, fig. 3; Fritz, 1995, p. 714), 568011c, USNM, Washington, D.C.]. Intergenal spine generally well developed at or slightly proximal to midlength of posterior cephalic margin. Glabella slightly expanded anteriorly; L3 not modified; posterior tip of ocular lobe opposite
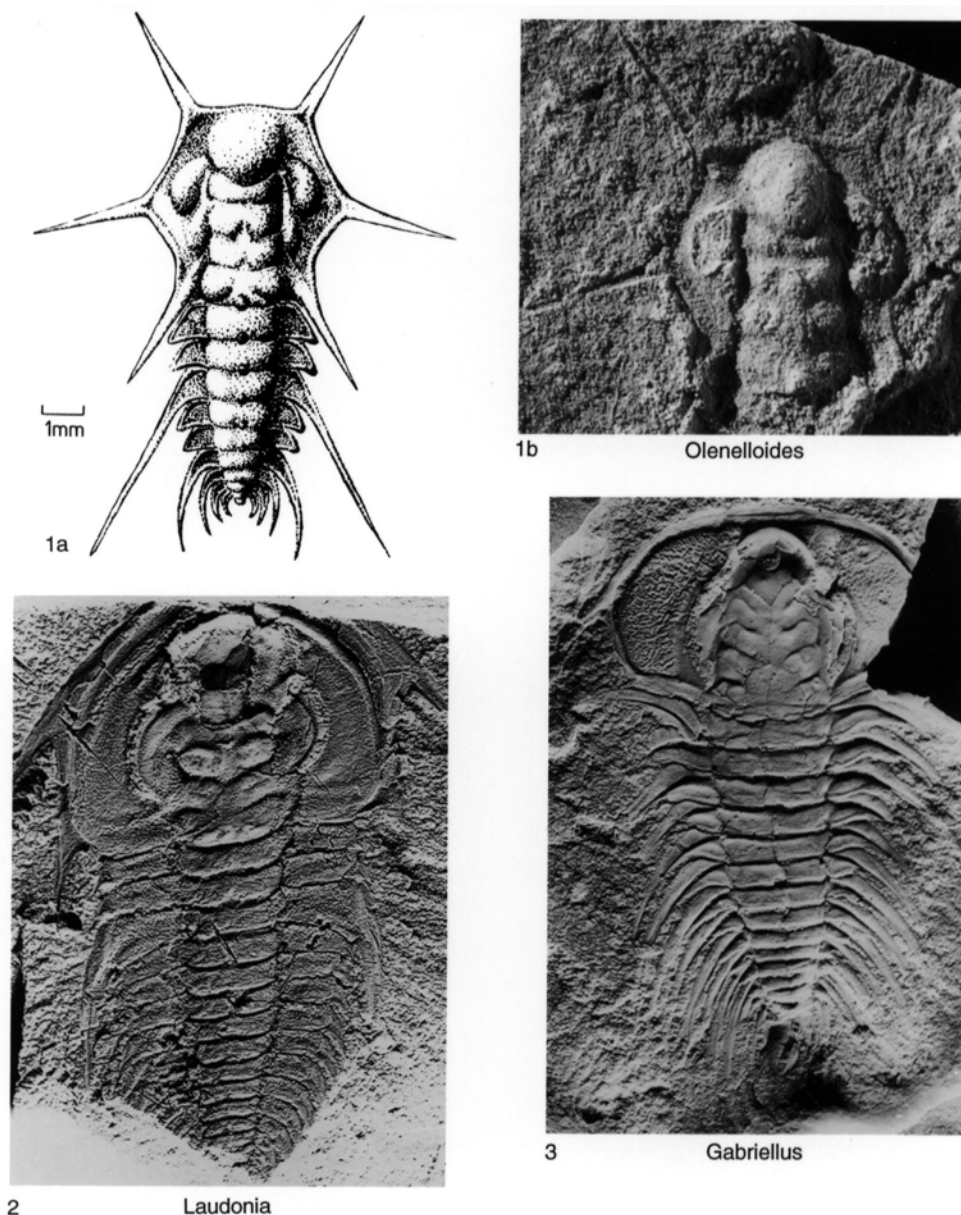
FIG. 259. Olenellidae (p. 412–413)

L1. Thorax narrow, with 17 segments; pleural spines chelate; each segment with axial spine. Pygidium small, expanded posteriorly; posterior margin spinose. External surface granular. *Lower Cambrian:* USA (Nevada), lower *"Nevadella"* Zone.——FIG. 262,*1a,b.* **E. rowei* (WALCOTT); *a,* cephalon, ICS 3642, ×1.6 (new); *b,* cephalon and partial thorax, ICS 3643, ×0.8 (new).

Holmiella FRITZ, 1972, p. 25 [**H. preancora;* OD; holotype (FRITZ, 1972, pl. 4, fig. 4–6), 27241, GSC, Ottawa]. Outline of cephalon subpentagonal; genal spine prominent, originating opposite or anterior to S3; short intergenal spine or node located at or on axial side of intergenal angle. Glabella expanded anteriorly; posterior tip of ocular lobe opposite or posterior to L1. Pygidium large, wider
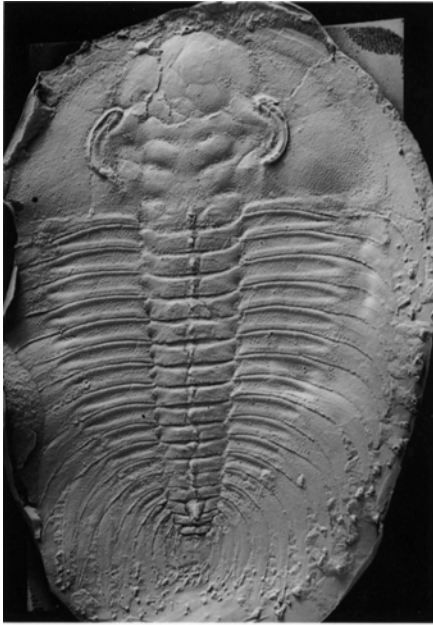
Wanneria

Fig. 260. Olenellidae (p. 414)

than long, of at least three segments; anterior two segments extended into short border spines. *Lower Cambrian:* USA (Nevada), Canada (Mackenzie Mountains), *"Nevadella"* Zone.——Fig. 262,*2a,b.* **H. preancora,* Canada; *a,* cephalon, paratype, GSC 27240, ×4 (Fritz, 1972, pl. 4, fig. 1); *b,* pygidium, holotype, GSC 27241, ×5 (Fritz, 1972, pl. 4, fig. 6).

Iyouella Geyer & Palmer, 1995, p. 470 [**I. contracta;* OD; holotype (Geyer & Palmer, 1995, fig. 6.9–6.10), 52260b, SMF, Frankfurt am Main]. Glabella slightly tapered forward, reaching onto anterior border. Ocular lobe long, posterior tip opposite occipital furrow. Genal spine slightly advanced; intergenal spine small, midway between axial furrow and genal spine. *Lower Cambrian:* Morocco (Anti-Atlas), *Sectigena* Zone.——Fig. 262,*3.* **I. contracta;* incomplete cephalon, holotype, ×4.5 (Geyer & Palmer, 1995, fig. 6.9).

Palmettaspis Fritz, 1995, p. 718 [**P. consorta* Fritz, 1995, p. 720; OD; holotype (Fritz, 1995, fig. 8.4), 476024, USNM, Washington, D.C.]. Intergenal spine generally well developed at or slightly proximal to midlength of posterior cephalic margin. Glabella parallel sided or slightly expanded anteriorly; L3 not modified. Posterior tip of ocular lobe opposite L1 or occipital furrow. Thorax narrow; pleural spines chelate or sentate; each segment with axial spine or node. Pygidium unknown. *Lower Cambrian:* USA (Nevada), lower *"Nevadella"* Zone.

——Fig. 262,*5.* **P. consorta;* cephalon, paratype, USNM 476021, ×5 (Fritz, 1995, fig. 8.2).

Schmidtiellus Moberg in Moberg & Segerberg, 1906, p. 35 (footnote) [**Olenellus mickwitzi* Schmidt, 1888, p. 13; types not designated, original specimens missing (diagnosis based on *S. mickwitzi torelli* Moberg, 1899, redescribed by Bergström, 1973b, p. 296–301)]. Posterior margin of cephalon nearly straight; intergenal spine not developed. Glabella with prominent axial spine on anterior margin of occipital ring and encroaching on occipital furrow; posterior tip of ocular lobe opposite or posterior to L1. Thorax narrow; each segment with short (exsag.) pleural spine not constricted at base; at least 1 posterior segment bearing strong, posteriorly directed axial spine. Pygidium small, subquadrate. *Lower Cambrian:* Sweden (Scania), Estonia, *Schmidtiellus mickwitzi* Zone.——Fig. 261,*2. S. reetae;* cephalon and partial thorax, holotype, GIT 2590a, ×1.4 (Bergström, 1973b, fig. 15a).

Subfamily CALLAVIINAE Poulsen in Moore, 1959

[Callaviinae Poulsen in Moore, 1959, p. 192, *partim*] [=Callaviinae Bergström, 1973b, p. 309, *partim;* Repina, 1979, p. 20, *partim;* Palmer & Repina, 1993, p. 26; Callaviidae Ahlberg, Bergström, & Johansson, 1986, p. 40, *partim;* Holmiinae Hupé, 1953a, p. 125, *partim;* Suvorova in Tchernysheva, 1960, p. 62, *partim;* Holmiidae Repina, 1979, p. 20, *partim;* Ahlberg, Bergström, & Johansson, 1986, p. 43, *partim;* Neltneriinae Bergström, 1973b, p. 309, *partim*]

Glabella subcylindrical in outline or slightly expanded anteriorly; LA extended onto inner part of border. Preglabellar field absent. Border broad. Posterior tip of ocular lobe opposite or posterior to midlength of L1. Thorax broad, with 16 to 18 segments; not clearly differentiated into prothorax and opisthothorax. Pleural regions lack macropleurae. Pleural spines elongate. Pygidium small, subquadrate. *Lower Cambrian.*

Callavia Matthew, 1897, p. 397 [**Olenellus (Mesonacis) broeggeri* Walcott, 1890a, p. 41; SD Walcott, 1910, p. 275; lectotype (Walcott, 1890b, pl. 92, fig. 1, part; SD Hutchinson, 1962, p. 119), 18331, USNM, Washington, D.C.]. Intergenal spine well developed, adjacent to genal spine; intergenal ridge usually present. *Lower Cambrian:* United Kingdom (Comley, Shropshire), Canada (Avalon Peninsula), USA (eastern Massachusetts), *Callavia* Zone.——Fig. 263,*1a. *C. broeggeri* (Walcott), Canada; cephalon, topotype, USNM 462671, ×1 (Palmer & Repina, 1993, fig. 6.8).——Fig. 263,*1b. C. crosbyi,* eastern Massachusetts; complete individual, paratype, USNM 56798g, ×4 (Palmer & Repina, 1993, fig. 6.5).

Kjerulfia Kiaer, 1917, p. 71 [**K. lata;* OD; lectotype (Kiaer, 1917, pl. 10, fig. 1; SD Nikolaisen &
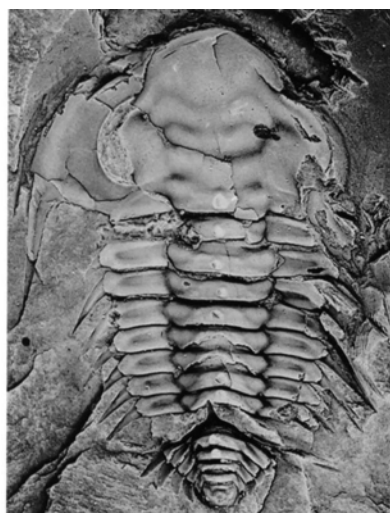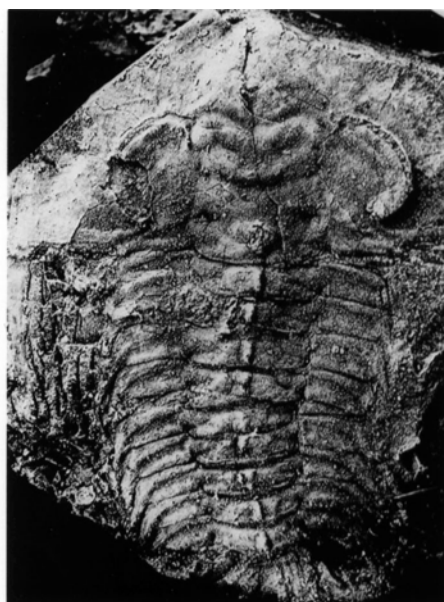
FIG. 261. Holmiidae (p. 414–416)

Posterior margin of cephalon nearly straight or deflected slightly forward distal to intergenal swelling; intergenal swelling closer to genal angle than axial furrow. *Lower Cambrian:* Norway (Oslo region), Denmark (borehole in Sealand), Poland (Holy Cross Mountains), Germany (Gorlitz), *Holmia kjerulfi* group Zone; United Kingdom (Comley, Shropshire), *Callavia* Zone; Morocco (Anti-Atlas), *Sectigena* Zone.——FIG. 263,*2a,b.* **K. lata,* Norway; *a,* cephalon, lectotype, PMO 61376, ×0.8 (Palmer & Repina, 1993, fig. 6.9); *b,* partial cephalon and thorax, paratype, PMO 73170, ×0.8 (Palmer & Repina, 1993, fig. 6.10).

Superfamily FALLOTASPIDOIDEA Hupé, 1953

[*nom. transl.* PALMER & REPINA, 1993, p. 27, *ex* Fallotaspidinae HUPÉ, 1953a, p. 124] [=Daguinaspidae HUPÉ, 1953a, p. 137; Olenellidae POULSEN in MOORE, 1959, p. 191, *partim;* Daguinaspididae POULSEN in MOORE, 1959, p. 197; BERGSTRÖM, 1973b, p. 309, *partim;* Olenelloidea SUVOROVA in TCHERNYSHEVA, 1960, p. 62, *partim;* REPINA, 1979, p. 11, *partim;* Olenellida AHLBERG, BERGSTRÖM, & JOHANSSON, 1986, p. 40, *partim*]

Glabellar outline typically cylindrical or slightly conical in dorsal view. L3 simple, its form similar to L2. *Lower Cambrian.*

Family FALLOTASPIDIDAE Hupé, 1953

[*nom. transl.* REPINA, 1979, p. 19, *ex* subfamily Fallotaspidinae HUPÉ, 1953a, p. 124] [=Daguinaspidae HUPÉ, 1953a, p. 137; Fallotaspidinae POULSEN in MOORE, 1959, p. 194; Holmiinae SUVOROVA in TCHERNYSHEVA, 1960, p. 62, *partim;* Daguinaspididae BERGSTRÖM, 1973b, p. 309, *partim;* AHLBERG, BERGSTRÖM, & JOHANSSON, 1986, p. 40, *partim;* Fallotaspididae PALMER & REPINA, 1993, p. 27]

Projection of anterior margin of ocular lobe more or less tangent to anterior end of LA or continuous as parafrontal band in front of LA. Glabella slightly to moderately tapered forward. Length of LA less than one-third length of glabella, exclusive of occipital ring. Interocular area ranging from significantly wider (tr.) to slightly narrower than extraocular area. *Lower Cambrian.*

Subfamily FALLOTASPIDINAE Hupé, 1953

[=Fallotaspidinae HUPÉ, 1953a, p. 124] [=Fallotaspidinae POULSEN in MOORE, 1959, p. 194; BERGSTRÖM, 1973b, p. 309, *partim;* AHLBERG, BERGSTRÖM, & JOHANSSON, 1986, p. 40, *partim;* PALMER & REPINA, 1993, p. 27; Holmiinae SUVOROVA in TCHERNYSHEVA, 1960, p. 62, *partim;* Fallotaspididae REPINA, 1979, p. 19, *partim*]

Genal spines present. Interocular area slightly wider (tr.) to slightly narrower than extraocular area. *Lower Cambrian.*

Fallotaspis HUPÉ, 1953a, p. 125 [**F. typica* HUPÉ, 1953a, p. 131; OD; holotype (HUPÉ, 1953a, pl. 2, fig. 2), G.26, MNHN, Paris]. Posterior margin of cephalon straight or gently curved forward distally; intergenal spine not developed, but intergenal ridge intersecting posterior border closer to glabella than to genal spine. Glabella slightly tapered forward; ocular lobe directed posterolaterally from junction with LA; width (tr.) of interocular area half or less width of extraocular area. Thorax of 21 segments (17 in prothorax, 4 in opisthothorax); opisthothorax not strongly differentiated; width (tr.) of inner pleural region of each prothoracic segment about same width as axis. Third thoracic segment macropleural. Pygidium small, subquadrate. *Lower Cambrian:* Morocco (Anti-Atlas), *Fallotaspis tazemmourtensis, Choubertella, Daguinaspis,* and *Antat-*

lasia hollardi Zones; USA (White-Inyo Mountains), *"Fallotaspis"* Zone; Russia (Siberian Platform), *Fallotaspis* Zone; ?United Kingdom (Comley, Shropshire), sub-*Callavia* Zone.——FIG. 264,*3.* **F. typica,* Morroco; cephalon and partial thorax, holotype, MNHN G.26, ×2 (Palmer & Repina, 1993, fig. 7.2).

Eofallotaspis SDZUY, 1978, p. 89 [**E. tioutensis;* OD; holotype (SDZUY, 1978, pl. 1, fig. 1–2), 28567, SMF, Frankfurt am Main]. Posterior margin of cephalon nearly straight; small intergenal spine on posterior border approximately midway between axial furrow and genal spine. Glabella slightly tapered forward. Ocular lobe directed posterolaterally from junction with LA. Width (tr.) of interocular area equal to or greater than width of extraocular area opposite midlength of ocular lobe. Occipital ring simple. Thorax narrow; width (tr.) of inner pleural region of each segment less than that of axis; third segment macropleural. External surface strongly pitted. *Lower Cambrian:* Morocco (Anti-Atlas), *Eofallotaspis* Zone.——FIG. 264,*6a,b.* **E. tioutensis; a,* cephalon, holotype, ×5 (Sdzuy, 1978, pl. 1, fig. 1); *b,* cephalon and partial thorax, SMF 41984, ×10 (Sdzuy, 1981, fig. 12).

Lenallina REPINA, 1990a, p. 40 [**L. lata;* OD; holotype (REPINA, 1990a, pl. 3, fig. 1–2), 902/1, CSGM, Novosibirsk]. Posterior margin of cephalon directed anterolaterally distal to intergenal angle; intergenal angle closer to axial furrow than to genal spine. Glabella slightly tapered forward. Interocular area narrow; width (tr.) less than half width of extraocular area. Posterior tip of ocular lobe about opposite occipital furrow. External surface reticulate. *Lower Cambrian:* Russia (southeastern Siberian Platform), *Pagetiellus anabarus* Zone.——FIG. 264,*5.* **L. lata;* cephalon, holotype, TsGM 902/1, ×6 (Repina, 1990a, pl. 3, fig. 2).

Parafallotaspis FRITZ, 1972, p. 27 [**P. grata;* OD; holotype (FRITZ, 1972, pl. 1, fig. 1–2), 27202, GSC, Ottawa]. Posterior margin of cephalon nearly straight or slightly backswept. Glabella moderately tapered forward; plectrum strongly developed; ocular lobe directed posterolaterally from junction with LA; width (tr.) of interocular area slightly more than one-half width of extraocular area opposite midlength of ocular lobe; posterior tip of ocular lobe opposite occipital ring. *Lower Cambrian:* Canada (Mackenzie Mountains); USA (Nevada), *"Fallotaspis"* Zone.——FIG. 264,*1.* **P. grata,* Mackenzie Mountains; cephalon, holotype, GSC 27202, ×3 (Fritz, 1972, pl. 1, fig. 1).

Pelmanaspis REPINA, 1990a, p. 41 [**P. jurii;* OD; holotype (REPINA, 1990a, pl. 4, fig. 1–2), 902/15, CSGM, Novosibirsk]. Posterior margin of cephalon nearly straight. Glabella gently tapered forward; occipital ring with prominent axial spine; length (sag.) of preglabellar field greater than length of border; width (tr.) of interocular area slightly more than half width of extraocular area; ocular lobe directed posterolaterally from junction with LA; posterior tip of ocular lobe about opposite occipital furrow. External surface coarsely pitted, grading to reticulate. *Lower Cambrian:* Russia (southeastern
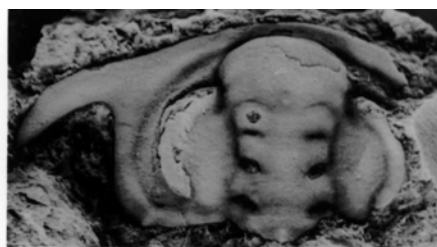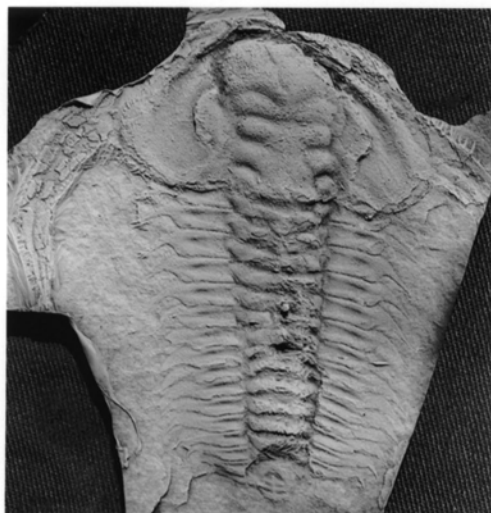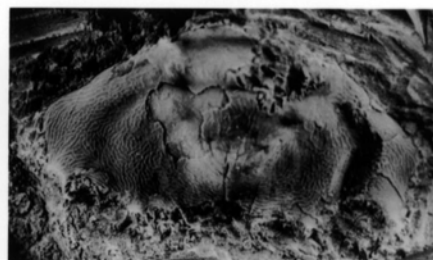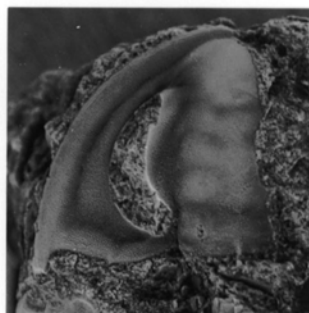
FIG. 262. Holmiidae (p. 414–416)

Siberian Platform), *Pagetiellus anabarus* Zone.——
FIG. 264,*4.* **P. jurii;* cephalon, holotype, CSGM
902/15, ×6 (Repina, 1990a, pl. 4, fig. 2).

Profallotaspis REPINA in KHOMENTOVSKII & REPINA,
1965, p. 110 [**P. jakutensis;* OD; holotype (KHO-
MENTOVSKII & REPINA, 1965, pl. 2, fig. 4), 265/1,
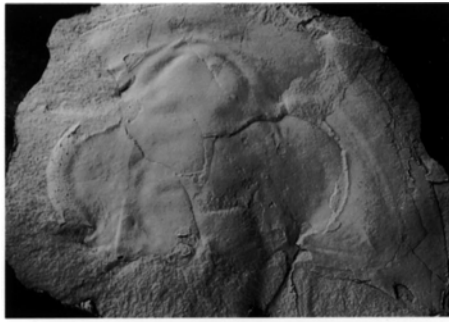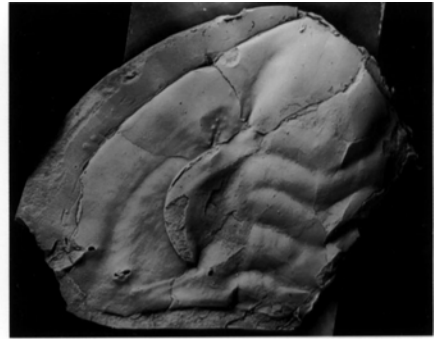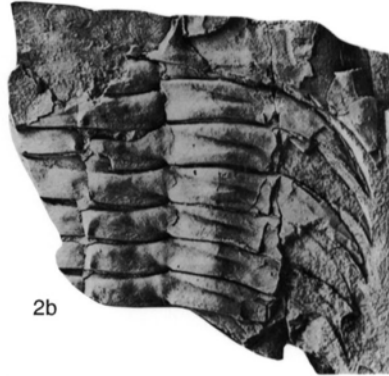
Fig. 263. Holmiidae (p. 416–417)

CSGM, Novosibirsk]. Posterior margin of cephalon straight or slightly backswept. Glabella tapered forward, but area opposite L3 and LA merging laterally with ocular lobe; ocular lobe directed only slightly posterolaterally at junction with LA; interocular area wider (tr.) than extraocular area opposite midlength of ocular lobe; posterior tip of ocular lobe opposite L1. Cephalic border concave in sagittal profile; lateral and posterior border furrows not connected across base of genal spine. External surface coarsely pitted, grading to reticulate. *Lower Cambrian:* Russia (southeastern Siberian Platform), *Profallotaspis jakutensis* Zone.——Fig. 264,*2*. **P. jakutensis;* cephalon, paratype, CSGM 265/13, ×7 (Khomentovskii & Repina, 1965, pl. 2, fig. 5).

Subfamily DAGUINASPIDINAE Hupé, 1953

[*nom. correct.* Poulsen in Moore, 1959, p. 197, *ex* Daguinaspidae Hupé, 1953a, p. 137] [=Daguinaspididae Poulsen in Moore, 1959, p. 197, *partim;* Bergström, 1973b, p. 309, *partim;* Repina, 1979, p. 19; Ahlberg, Bergström, & Johansson, 1986, p. 40, *partim;* Daguinaspidinae Palmer & Repina, 1993, p. 28; Holmiinae Suvorova in Tchernysheva, 1960, p. 62, *partim*]

Interocular area significantly wider (tr.) than extraocular area. Genal spine absent. *Lower Cambrian.*

Daguinaspis Hupé & Abadie, 1950, p. 2112 [**D. ambroggii;* OD; holotype (Hupé, 1953a, pl. 5, fig. 1), G.200, MNHN, Paris]. Anterior margin of

1 Parafallotaspis
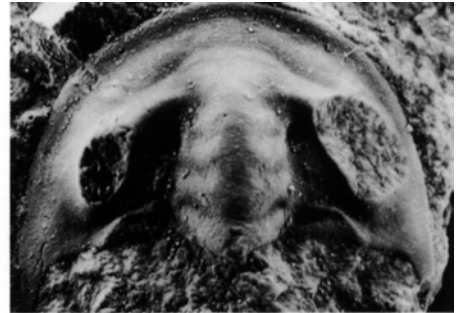
2 Profallotaspis

3 Fallotaspis
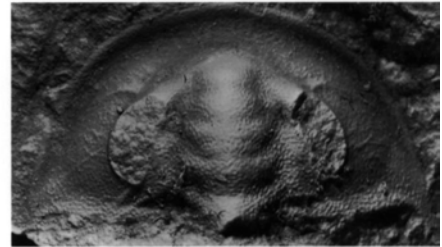
4 Pelmanaspis
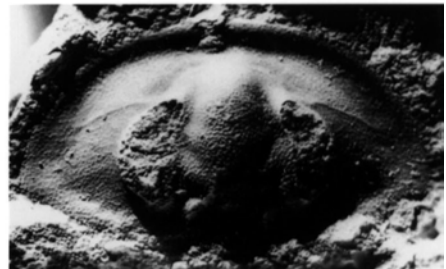
5 Lenallina

6a Eofallotaspis

6b

Fig. 264. Fallotaspididae (p. 418–420)

1 Choubertella

2 Daguinaspis
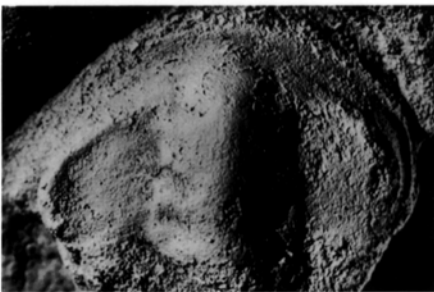
3 Wolynaspis

FIG. 265. Fallotaspididae (p. 420–422)

cephalon bluntly pointed. Width (tr.) of interocular area less than one-half basal glabellar width; width

of extraocular area about equal to width of ocular lobe; length (sag.) of frontal area greater than that of occipital ring. Intergenal ridge well developed. Thorax of 16 (17?) segments; pleura about equal in width to axial lobe, unmodified. Pygidium small, subquadrate. [Hupé (1953a) created three subgenera for minor morphological variations that seem to have limited merit. These are *Eodaguinaspis* (type species, *D. (E.) abadiei*), *Daguinaspis* (type species, *D. (D.) ambroggii*), and *Epidaguinaspis* (type species, *D. (E.) angusta*).] *Lower Cambrian:* Morocco (Anti-Atlas), *Daguinaspis* Zone.——FIG. 265,*2.* **D. ambroggii;* cephala, holotype (at bottom), MNHN G.200, ×3 (Palmer & Repina, 1993, fig. 8.2).

Choubertella Hupé, 1953a, p. 143 [**C. spinosa;* OD; holotype (Hupé, 1953a, pl. 4, fig. 8), G.230, MNHN, Paris]. Anterior margin of cephalon gently curved. Glabella moderately to strongly tapered forward; width (tr.) of interocular area opposite tip of ocular lobe nearly equal to basal glabellar width; width of extraocular area about equal to width of ocular lobe; length (sag.) of frontal area greater than that of occipital ring. Intergenal ridge well developed. *Lower Cambrian:* Morocco (Anti-Atlas), *Choubertella* Zone.——FIG. 265,*1.* **C. spinosa;* cephalon, holotype, MNHN G.230, ×3 (Palmer & Repina, 1993, fig. 8.1).

?Wolynaspis Tchernysheva in Kir'ianov & Tchernysheva, 1967, p. 123 [**W. unica;* OD; holotype (Kir'ianov & Tchernysheva, 1967, fig. 2), 1731/8, GMU, Kiev]. Anterior margin of cephalon gently curved. Glabella gently tapered forward; extraocular area steeply downsloping; width (tr.) of interocular area more than half basal glabellar width; frontal area short (sag.), length about equal to that of occipital ring. *Lower Cambrian:* Ukraine, zone uncertain.——FIG. 265,*3.* **W. unica;* cephalon, holotype, GMU 1731/8, ×2 (Kir'ianov & Tchernysheva, 1967, fig. 2).

Family ARCHAEASPIDIDAE Repina, 1979

[Archaeaspididae Repina, 1979, p. 20] [=Archaeaspidinae Ahlberg, Bergström, & Johansson, 1986, p. 40; Archaeaspididae Palmer & Repina, 1993, p. 29]

Anterior part of LA anterior to line tangent to anterolateral margin of ocular lobe. Parafrontal band usually present, continuing to or nearly to anterior end of LA. Width (tr.) of interocular area approximately same as width of extraocular area. Genal spine usually present. *Lower Cambrian.*

Archaeaspis Repina in Khomentovskii & Repina, 1965, p. 116 [**A. hupei;* OD; holotype (Khomentovskii & Repina, 1965, pl. 4, fig. 1), 265/146, CSGM, Novosibirsk]. Glabella slightly tapered forward; LA slightly conical; width (tr.) of interocular area greater than width of extraocular area opposite midlength of ocular lobe; posterior tip of ocular lobe approximately opposite occipital furrow. Genal

spine short, broadly based; border broad, convex, well defined, its length (sag.) greater than length of preglabellar field. External surface strongly reticulate. *Lower Cambrian:* Russia (southeastern Siberian Platform), lower *Pagetiellus anabarus* Zone.——Fig. 266,*2.* **A. hupei;* cephalon, holotype, CSGM 265/146, ×15 (Khomentovskii & Repina, 1965, pl. 4, fig. 1).

Bradyfallotaspis Fritz, 1972, p. 19 [**B. fusa;* OD; holotype (Fritz, 1972, pl. 3, fig. 1–3), 27226, GSC, Ottawa]. Glabellar outline subcylindrical; anterior end of glabella strongly rounded; length (sag.) of preglabellar field about equal to that of border; width (tr.) of interocular area less than width of extraocular area opposite midlength of ocular lobe; ocular lobe raised above level of glabella. *Lower Cambrian:* Canada (northern Rocky Mountains), *"Nevadella"* Zone.——Fig. 266,*1.* **B. fusa;* cephalon, holotype, GSC 27226, ×6 (Fritz, 1972, pl. 3, fig. 1).

Fallotaspidella Repina, 1961, p. 40 [**F. musatovi;* OD; holotype (Repina, 1961, pl. 1, fig. 1a), 3556/1001, CSGM, Novosibirsk]. Glabella slightly tapered forward, with anterior end bluntly rounded; preglabellar field short (sag.), crossed by plectrum; posterior tip of ocular lobe opposite L1; width (tr.) of interocular area about half or less width of extraocular area opposite midlength of ocular lobe; S1 and S2 usually continuous across glabella. *Lower Cambrian:* Russia (southern Siberian fold belt, Altay-Sayan region), *Sajanaspis* Zone; northern Mongolia, *Fallotaspis-Buliaspis* Zone.——Fig. 266,*4.* **F. musatovi;* cephalon, Altay-Sayan region, topotype, TsGM 3556/1020, ×4 (photograph courtesy of L. N. Repina).

Geraldinella Fritz, 1993, p. 866 [**G. corneiliana;* OD; holotype (Fritz, 1993, fig. 13.10), 102363, GSC, Ottawa]. Cephalon strongly arched (tr.); anterior and lateral borders about equal in breadth to sagittal length of occipital ring; intergenal swelling barely apparent, situated nearer to glabella than to genal spine, and marked by slight anterior deflection of distal part of posterior margin. Intergenal ridge weak. Glabella slightly constricted at L2; L3 slightly expanded distally; preglabellar field absent; width (tr.) of interocular area less than that of extraocular area; posterior tip of ocular lobe opposite L2. External surface has fine, reticulate sculpture. *Lower Cambrian:* Canada (southern Cordillera), *"Nevadella"* Zone.——Fig. 266,*3a,b.* **G. corneiliana; a,* cephalon, holotype, GSC 102363, ×4 (Fritz, 1993, fig. 13.10); *b,* cephalon, paratype, GSC 102355, ×7 (Fritz, 1993, fig. 11.10).

Selindella Repina, 1979, p. 27 [**S. gigantea;* OD; holotype (Repina, 1979, pl. 1, fig. 1), 560/1, CSGM, Novosibirsk]. Glabella slightly tapered forward, sides slightly concave, and anterior end strongly rounded; posterior tip of ocular lobe about opposite midlength of L1; width (tr.) of interocular area about equal to width of extraocular area; length (sag.) of border about equal to that of preglabellar field. *Lower Cambrian:* Russia (southeastern Siberian Platform), lower *Pagetiellus anabarus* Zone;

northern Siberian Platform, *Pseudojudomia* Zone.——Fig. 266,*5.* **S. gigantea;* cephalon, southeastern Siberian Platform, holotype, TsGM 560/1, ×1.2 (Repina, 1979, pl. 1, fig. 1).

Family JUDOMIIDAE Repina, 1979

[*nom. transl.* Palmer & Repina, 1993, p. 29, *ex* Judomiinae Repina, 1979, p. 20] [=Callaviinae Poulsen in Moore, 1959, p. 192, *partim;* Holmiinae Suvorova in Tchernysheva, 1960, p. 62, *partim;* Nevadiinae Bergström, 1973b, p. 309, *partim;* Holmiidae Bergström, 1973b, p. 285, *partim;* Judomiinae Ahlberg, Bergström, & Johansson, 1986, p. 40]

Posterior margin of cephalon straight or curved backward distally. Glabella typically parallel sided; glabellar furrows weakly to moderately developed. LA elongate. Ocular lobe connected only to posterior part of LA. Interocular area very narrow or absent; width (tr.) equal to or less than width of ocular lobe. Inner margin of ocular lobe typically undifferentiated or only weakly differentiated from interocular area. Posterior tip of ocular lobe opposite or posterior to occipital furrow. Intergenal spine not apparent. *Lower Cambrian.*

Judomia Lermontova, 1951a, p. 48 [**J. dzevanovskii;* OD; lectotype (Lermontova, 1951a, pl. 5, fig. 2; SD Palmer & Repina, 1993, p. 30), 53/5156, CNIGR, St. Petersburg]. Glabella barely touching border, or preglabellar field present. Border well defined, with length (sag.) greater than preglabellar field, when present, and about equal to or slightly greater than length (sag.) of occipital ring. Posterior tip of ocular lobe opposite occipital ring. Thorax with 15 to 17 segments; pleural furrows weak or absent; opisthothorax not developed; pleural spines long; width (tr.) of thoracic pleurae more than twice width of axis. Pygidium elongate, with posterior median notch; last 2 thoracic segments may be fused with pygidium in axial region only. *Lower Cambrian:* Russia (southern Siberian Platform), *Judomia* and *Bergeroniellus micmaccaformis-Erbiella* Zones; Russia (Kharaulakh region), *Judomia* Zone.——Fig. 267,*1. J. tera;* complete individual, Kharaulakh region, CSGM 659/50, ×2 (Palmer & Repina, 1993, fig. 10.7).

Judomiella Lazarenko, 1962, p. 48 [**J. heba;* OD; holotype (Lazarenko, 1962, pl. 3, fig. 6), 8270-138, 8270-139, CNIGR, St. Petersburg]. Cephalon strongly arched (tr.). Glabella reaching nearly to anterior margin. Border poorly differentiated. Ocular lobe adjacent to glabella; interocular area poorly differentiated from ocular lobe; posterior tip of ocular lobe reaching to posterior margin of cephalon. *Lower Cambrian:* Russia (northern Siberian Platform), *Protolenus borealis* Zone; Russia (southeastern Siberian Platform), *Bergeroniellus micmaccaformis-Erbiella* Zone.——Fig. 267,*2.* **J. heba;* cephalon, northern Siberian Platform, CSGM 659/55, ×1.5 (Palmer & Repina, 1993, fig. 10.8).

1   Bradyfallotaspis

2   Archaeaspis

3a   Geraldinella
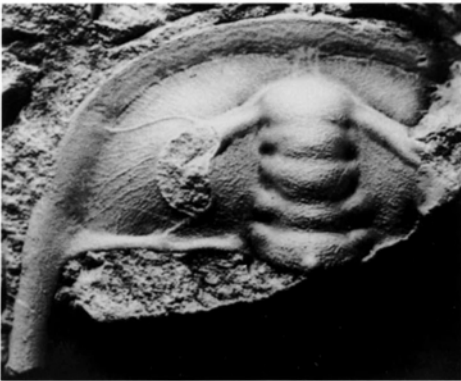
4   Fallotaspidella

3b

5   Selindella

FIG. 266. Archaeaspididae (p. 422–423)
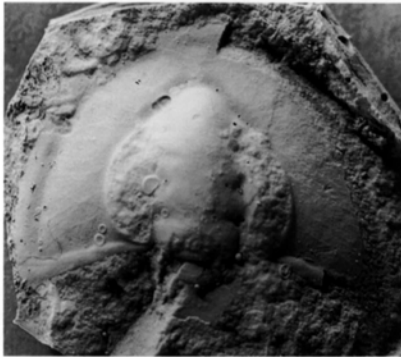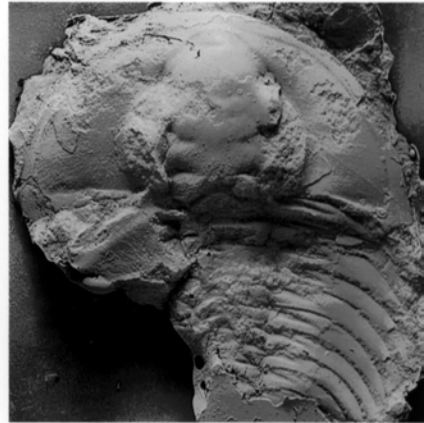
FIG. 267. Judomiidae (p. 423–425)

Paranevadella PALMER & REPINA, 1993, p. 30 [**Paedeumias? subgroenlandicus* REPINA in KHOMENTOVSKII & REPINA, 1965, p. 121; OD; holotype (KHOMENTOVSKII & REPINA, 1965, pl. 3, fig. 8), 265/174, CSGM, Novosibirsk]. Glabella weakly tapered forward to nearly parallel sided; preglabellar field present; posterior tip of ocular lobe opposite occipital ring. Interocular area distinctly developed. *Lower Cambrian:* USA (California), Canada (Mackenzie Mountains), *"Nevadella"* Zone; Russia (Siberian Platform), upper *Pagetiellus anabarus* Zone.——FIG. 267,*3. *P. subgroenlandicus* (REPINA); cephalon, southern Siberian Platform, holotype, CSGM 265/174, ×3 (Palmer & Repina, 1993, fig. 10.4).

Sinskia SUVOROVA, 1960, p. 18 [**S. optabilis;* OD; holotype (SUVOROVA, 1960, pl. 1, fig. 1), 496/121, PIN, Moscow]. LA slightly expanded in front of

ocular lobe. Border narrow, its length (sag.) less than length (sag.) of occipital ring. Length (sag.) of preglabellar field approximately equal to that of border; posterior tip of ocular lobe opposite posterior part of occipital ring. *Lower Cambrian:* Russia (southern Siberian Platform), *Bergeroniellus micmaccaformis-Erbiella* Zone.——FIG. 267,*4. *S. optabilis?;* cephalon and partial thorax, CSGM 452/500, ×1.5 (Palmer & Repina, 1993, fig. 10.5).

Family NELTNERIIDAE Hupé, 1953

[*nom. transl.* PALMER & REPINA, 1993, p. 30, *ex* Neltneriinae HUPÉ, 1953a, p. 125] [=Holmiinae POULSEN in MOORE, 1959, p. 194, *partim;* SUVOROVA in TCHERNYSHEVA, 1960, p. 62, *partim;* REPINA, 1979, p. 20, *partim;* AHLBERG, BERGSTRÖM, & JOHANSSON, 1986, p. 40, *partim;* Neltneriinae POULSEN in MOORE, 1959, p. 196; BERGSTRÖM, 1973b, p. 309, *partim;* REPINA, 1979, p. 20; AHLBERG, BERGSTRÖM, & JOHANSSON, 1986, p. 40]
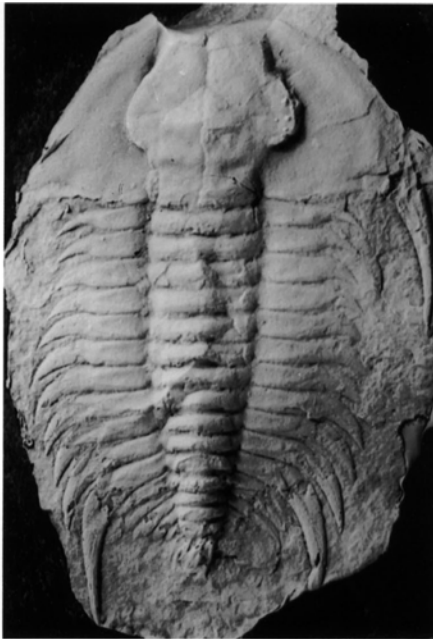
1   Neltneria

2   Bondonella

Fig. 268. Neltneriidae (p. 426)

Posterior margin of cephalon deflected slightly forward distally. Glabella parallel sided, bluntly rounded anteriorly. LA elongate. Ocular lobe connected only to posterior part of LA. Ocular lobe close to glabella; interocular area poorly differentiated. Thorax with 17 segments. *Lower Cambrian.*

Neltneria Hupé, 1953a, p. 133 [**Wanneria Jacqueti* Neltner & Poctey, 1949, p. 74; OD; lectotype (Neltner & Poctey, 1949, pl. 6, fig. 5; SD Palmer & Repina, 1993, p. 30), R50864, MNHN, Paris]. Preglabellar field absent; interocular area poorly defined, its width (tr.) less than half that of extraocular area; posterior tip of ocular lobe opposite L1. Thorax has 17 segments; each segment with short (exsag.) pleural spine; width (tr.) of inner pleural region about same as that of axis; 11th segment macropleural; 12th to 17th segments decreasing in width (tr.) rapidly and progressively backward. Pygidium small, subquadrate, possibly of 2 or 3 segments. *Lower Cambrian:* Morocco (Anti-Atlas), *Antatlasia gutta-pluviae* Zone.——Fig. 268,*1. *N. jacqueti;* complete individual, ICS replica 122, ×2 (Palmer & Repina, 1993, fig. 11.1).

Bondonella Hupé, 1953a, p. 135 [**B. typica* Hupé, 1953a, p. 136; OD; holotype (Neltner & Poctey, 1949, pl. 6, fig. 1), R50865, MNHN, Paris]. Length (sag.) of preglabellar field about equal to that of anterior border; interocular area poorly defined, its width (tr.) more than half width of extraocular area; posterior tip of ocular lobe opposite occipital furrow. Thorax with 17 segments; width (tr.) of inner pleural region of each segment narrower than axis; no macropleural segments. *Lower Cambrian:* Morocco (Anti-Atlas), *Antatlasia gutta-pluviae* Zone.——Fig. 268,*2. *B. typica;* complete individual, holotype, MNHN R50865, ×3 (Palmer & Repina, 1993, fig. 11.2).

Family NEVADIIDAE Hupé, 1953

[*nom. transl.* Repina, 1979, p. 19, *ex* Nevadiinae Hupé, 1953a, p. 124] [=Nevadiinae Poulsen in Moore, 1959, p. 196; Suvorova in Tchernysheva, 1960, p. 62; Bergström, 1973b, p. 309, *partim;* Nevadiidae Repina, 1979, p. 19, *partim;* Ahlberg, Bergström, & Johansson, 1986, p. 40, *partim;* Palmer & Repina, 1993, p. 31]

Glabella weakly to strongly tapered forward in dorsal view. LA elongate. Ocular lobe connected only to posterior part of LA. Interocular area narrow. Posterior tips of ocular lobes opposite or anterior to occipital furrow. Width of interocular area variable. Thorax with 15 to 27 segments, without development of macropleurae. *Lower Cambrian.*

Nevadia Walcott, 1910, p. 256 [**N. weeksi;* OD; lectotype (Walcott, 1910, pl. 23, fig. 2; SD Palmer
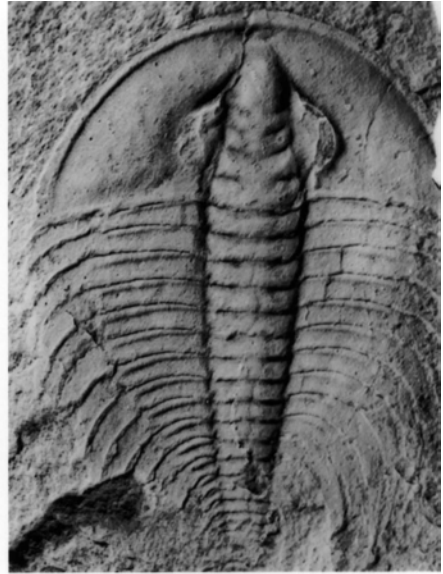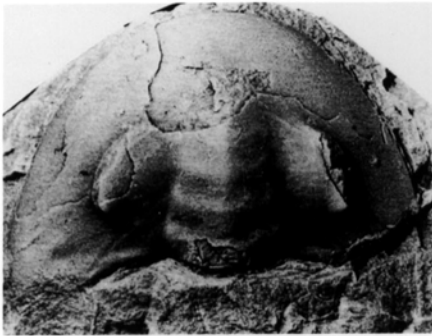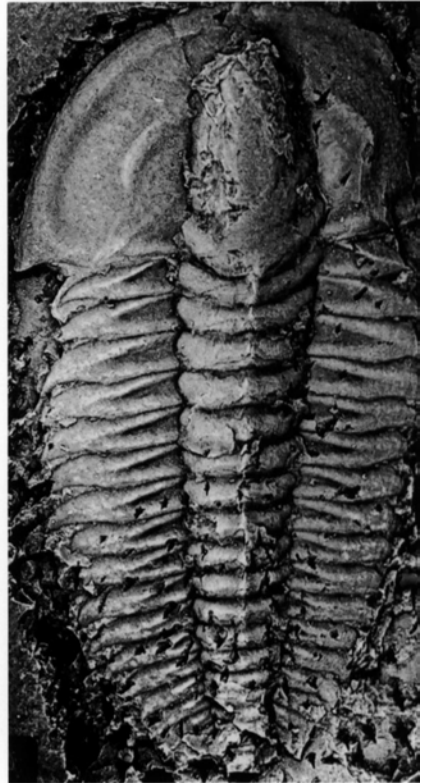
FIG. 269. Nevadiidae (p. 426–428)
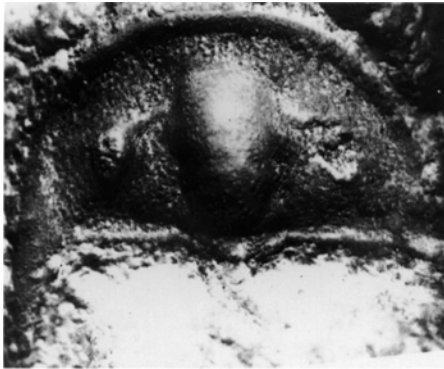
Poletaevella

FIG. 270. Superfamily Uncertain (p. 428)

& REPINA, 1993, p. 31), 56792b, USNM, Washington, D.C.]. Width (tr.) of interocular area less than one-fourth width of extraocular area; preglabellar field present. Thorax with 27 segments; pleural spines long; width (tr.) of pleurae at least twice width of axis; transition to opisthothorax between segments 15 and 18. Pygidium small, subquadrate. *Lower Cambrian:* USA (California, White-Inyo region; Nevada; northeastern Washington), Canada (northern Rocky Mountains), *"Nevadella"* Zone; Russia (northern Siberian Platform), *"Nevadella"* Zone.——FIG. 269,*2. *N. weeksi,* California; complete individual, topotype, LACMIP 7376, ×3 (photograph courtesy of C. A. Nelson).

Buenellus BLAKER, 1988, p. 34 [**B. higginsi* BLAKER, 1988, p. 36; OD; holotype (BLAKER, 1988, fig. 3b), 18.287, MGUH, Copenhagen]. Glabella slightly tapered forward; ocular lobe small, posterior tip about opposite S1 or anterior part of L1; width (tr.) of interocular area equal to or greater than that of extraocular area. Thorax with 17 or 18 segments, maintaining width or widening slightly backward to 8th segment, then tapering posteriorly; posterior segment may be fused with anterior part of simple pygidium; pleural spines short (exsag.); inner pleural regions only slightly wider (tr.) than axis. *Lower Cambrian:* Greenland (Peary Land), *"Nevadella"* Zone; Russia, Novaya Zemlya, *?"Nevadella"* Zone.——FIG. 269,*4. *B. higginsi,* Greenland; complete individual, paratype, MGUH 17.589, ×3 (Blaker, 1988, fig. 5a).

Cirquella FRITZ, 1993, p. 858 [**C. nummularia;* OD; holotype (FRITZ, 1993, fig. 7.2–7.4), 102330, GSC, Ottawa]. Glabella moderately tapered forward; glabellar furrows weakly developed; posterior tip of ocular lobe opposite L1. Genal spine absent or indicated only by slight angularity of margin opposite L1. *Lower Cambrian:* USA (White-Inyo and western Death Valley regions), Canada (southern Rocky Mountains), lower *"Nevadella"* Zone.——FIG. 269,*5. *C. nummularia;* cephalon, Canada, paratype, USNM 458891, ×7 (Fritz, 1993, fig. 7.5).

Nevadella RAW, 1936, p. 250 [**Callavia eucharis* WALCOTT, 1913b, p. 315; SD WHITEHOUSE, 1939, p. 191; holotype (WALCOTT, 1913b, pl. 53, fig. 1), 60079, USNM, Washington, D.C.]. Glabella distinctly tapered forward, sides slightly concave, narrowest opposite L2 or S2; preglabellar field short or absent; basal glabellar width (tr.) about equal to width of extraocular area opposite midlength of ocular lobe; posterior tip of ocular lobe opposite L1; width (tr.) of interocular area more than one-fourth width of extraocular area opposite midlength of ocular lobe. Thorax with 17 to 23 segments. Pleural spines long, falcate; opisthothorax not clearly differentiated. Pygidium small, subquadrate. *Lower Cambrian:* USA (California, Nevada), Canada (Cordilleran region), *"Nevadella"* Zone. ——FIG. 269,*1. *N. eucharis;* complete individual, Canada, holotype, USNM 60079, ×2 (Palmer & Repina, 1993, fig. 13.2).

Pseudojudomia EGOROVA in GORYANSKII, EGOROVA, & SAVITSKII, 1964, p. 22 [**P. egregia;* OD; holotype (GORYANSKII, EGOROVA, & SAVITSKII, 1964, pl. 5, fig. 1a,b), 8363/15, CNIGR, St. Petersburg]. Border furrows weakly developed; cephalon strongly convex (tr.); posterior margin strongly curved backward. Glabella slightly tapered forward; basal glabellar width (tr.) about equal to width of extraocular area. Lateral parts of poorly differentiated border nearly vertical. Ocular lobe poorly differentiated from interocular area; posterior tip about opposite occipital furrow. *Lower Cambrian:* Russia (northern Siberian Platform), *Pseudojudomia* Zone.——FIG. 269,*3. *P. egregia;* cephalon, holotype, CNIGR 8363/15, ×1.5 (Egorova & Savitskii, 1969, pl. 10, fig. 1).

Superfamily Uncertain

Poletaevella DALMATOV & REPINA, 1971, p. 125 [**P. baljutica;* OD; holotype (DALMATOV & REPINA, 1971, fig. 2b–d, 3), 0213/11, BGU, Ulan-Ude]. Olenellinid? with posterior margin of cephalon nearly straight. Glabella parallel sided, bluntly rounded anteriorly; occipital ring unusually short (sag.); palpebral lobe short (exsag.), prominent, located about midway between axial and lateral border furrows, and connected to posterior part of LA by narrow eye ridge, with its posterior tip opposite L2; preglabellar field longer (sag.) than anterior border. Genal spine well developed; intergenal spine not indicated. [The structure of the palpebral lobe is unlike the ocular lobe of all olenellinid trilobites. Assignment of this form even to the Olenellina is questionable.] *Lower Cambrian,* Russia (eastern Sayan region), zone unknown.——FIG. 270. **P. baljutica;* cephalon, holotype, ×13 (Dalmatov & Repina, 1971, fig. 2b).

Postfallotaspis ORLOWSKI, 1985, p. 234 [**P. spinatus;* OD; holotype (ORLOWSKI, 1985, pl. 3, fig. 5a–d), 1.496, IGUW, Warsaw]. The type and only specimen of this genus is too incomplete and poorly illustrated for generic or higher level taxonomic

evaluation. *Lower Cambrian:* Poland (Holy Cross Mountains), *Holmia* Zone.

Suborder REDLICHIINA Richter, 1932

W. T. CHANG, with L. N. REPINA and GERD GEYER

[*nom. corr.* FORTEY & WHITTINGTON, herein, *pro* Redlichiida RICHTER, 1932, p. 852]

Opisthoparian facial suture; rostral plate narrower (tr.) than in Olenellina (except in xystridurinids, Fig. 30.3) and bounded by rostral and connective sutures. Hypostome conterminate in *Redlichia* (Fig. 30), but not in *Dolerolenus* (Fig. 27.3). Thorax fulcrate or nonfulcrate; pygidium small, or large and many-segmented. *Lower Cambrian–Middle Cambrian.*

The diagnosis of this suborder (and of the order) presents problems because it may be paraphyletic and because the systematic section on Redlichiina in this volume is incomplete. Xystriduridae (ÖPIK, 1975b) are not included in the section on Paradoxidoidea. Ellipsocephaloidea will be treated in a subsequent volume; currently authors (GEYER, 1990b; PILLOLA, 1991) include this group in Redlichiina, but FORTEY (1990a, p. 549, 563) considered that at least some ellipsocephaloids should be placed in Ptychopariina.

Superfamily EMUELLOIDEA Pocock, 1970

[*nom. transl.* CHANG, herein, *ex* Emuellidae POCOCK, 1970, p. 527]

Cranidium subquadrate; glabella cylindrical, slightly contracted at S3, with 3 pairs of glabellar furrows; preglabellar field short (sag.) or absent; eye ridge wide (tr.), long, directed slightly posterolaterally; palpebral lobe crescentic; posterior area of fixigena with fulcrum; posterior border with section abaxial to fulcrum directed anterolaterally. Anterior section of facial suture diverging anteriorly to border furrow, curving sharply inwards, and crossing anterior border diagonally before becoming marginal-ventral; connective suture concave abaxially; rostral plate narrow (tr.), notched laterally; posterior section of facial suture divergent; hypostomal suture functional. Hypostome with depressed anterior wings; median body with large, subtriangular lobe, subdivided anteriorly by median depression; posterior lobe small. Librigena with long genal spine. Thorax with prothorax of 6 segments and extremely long opisthothorax of 42 to 55 segments; 6th prothoracic segment macropleural and fused to 5th; macropleural spine long, extending to level of pygidium. Pygidium a minute, segmented disc with border entire. *Lower Cambrian.*

Family EMUELLIDAE Pocock, 1970

[Emuellidae POCOCK, 1970, p. 527]

Characters of the superfamily. *Lower Cambrian.*

Emuella POCOCK, 1970, p. 528 [**E. polymera;* OD; holotype (POCOCK, 1970, pl. 106, fig. 1), F16653, AUGD, Adelaide]. Preglabellar field absent; anterior border furrow becoming shallow abruptly anterior to frontal glabellar lobe; palpebral lobe relatively short, curved; posterior border with section abaxial to fulcrum directed anterolaterally at 45° and slightly depressed; librigena with advanced genal spine. Thorax with 48 to 58 segments; axis more than half thoracic width; pleurae very narrow (tr.); pleural furrow terminating before pleural spine. Strong, closely spaced granules on dorsal surface. *Lower Cambrian:* Australia (Kangaroo Island), *Pararaia janeae* Zone.——FIG. 271,*1. *E. polymera;* holotype, complete dorsal exoskeleton, ×9.5 (new).

Balcoracania POCOCK, 1970, p. 533 [**B. dailyi;* OD; holotype (POCOCK, 1970, pl. 108, fig. 1), F16663, AUGD, Adelaide]. Preglabellar field short (sag.), down-sloping, or may be absent; palpebral lobe long, crescentic; posterior border with section abaxial to fulcrum directed anterolaterally at 60° and strongly depressed; librigena with genal spine only slightly advanced. Thorax with 53 to 61 segments; axis less than half thoracic width; pleural furrows terminating at base of pleural spines. Fine, closely spaced granules on dorsal surfaces. The cephalon of *Balcoracania* differs from that of *Emuella* in having a longer palpebral lobe and consequently shorter posterior section of the facial suture; the abaxial section of the posterior border is much more strongly depressed and not directed forward as strongly. The thoracic axis of *Balcoracania* is narrower than in *Emuella,* and the pleural furrows extend to the base of the spines. *Lower Cambrian:* Australia (Flinders Ranges), *Pararaia janeae* Zone.——FIG. 271,*2. *B. dailyi;* holotype, external mold of nearly complete exoskeleton, ×6.5 (new).

Superfamily REDLICHIOIDEA
Poulsen, 1927

[*nom. transl.* RICHTER, 1932, P. 852 *ex* Redlichiidae C. POULSEN, 1927, p. 318]

Characters of the suborder; preglabellar field short to long (sag., exs.), or lacking. *Lower Cambrian–lower Middle Cambrian.*

Family REDLICHIIDAE
Poulsen, 1927

[*nom. correct.* RICHTER, 1932, p. 852, *pro* Redlichiidae C. POULSEN, 1927, p. 318] [=Latiredlichiidae HUPÉ, 1953a, p. 192, *partim*]

Glabella long, tapering forward, and rounded in front, S1–3 evenly spaced, S3 faint, short, slightly oblique forward or backward, S1 and S2 oblique backward-inward, subparallel to occipital furrow; S4 and S5 present in some genera; preglabellar field short (sag.); anterior border longer, raised; eye lobe arcuate, long, arising from frontal glabellar lobe and extending to level of occipital furrow or farther back; anterior sections of facial sutures slightly to strongly divergent; posterior area of fixigena long or short (exs.); librigena wide, with or without advanced genal spine. Thorax with 14 to 19 segments, pleurae ending in spines, fulcrum distal. Pygidium small, with few segments. Surface of exoskeleton smooth or very finely granulose; facial line may be present on anterior area of fixigena. *Lower Cambrian–lower Middle Cambrian.*

Subfamily REDLICHIINAE
Poulsen, 1927

[*nom. transl.* HARRINGTON in MOORE, 1959, p. 199, *ex* Redlichiidae C. POULSEN, 1927, p. 318]

Proximal portion of anterior section of facial suture close to axial furrow, meeting eye lobe at level of midlength of frontal glabellar lobe; posterior extremity of eye lobe close to axial furrow; thorax with 14 to 17 segments; thoracic axial spine on 10th, 11th, 12th, 13th, or 14th axial ring. Pygidium with semiankylosed segment and slightly bilobed terminal piece. *Lower Cambrian–lower Middle Cambrian.*

Redlichia COSSMANN, 1902, p. 52, *nom. nov. pro Hoeferia* REDLICH, 1899, p. 3, *non* BITTNER, 1895 [**Hoeferia noetlingi* REDLICH, 1899, p. 3; OD; lectotype (REDLICH, 1899, pl. 1, fig. 1; SD WHITE-

HOUSE, 1939, p. 188), 7/232, GSI, Calcutta] [=*Mesodema* WHITEHOUSE, 1939, p. 187 (type, *M. venulosa;* OD); *Dongshania* LIN in QIU & others, 1983, p. 48 (type, *D. triangularis;* OD)]. Glabella conical, S1 may be transglabellar; facial line may be present on anterior areas of fixigenae. *Lower Cambrian (upper Canglangpuan to Longwangmiaoan):* China, Korea, Pakistan, Himalayan region, Iran, Spain, southern Siberia, Antarctica. *Middle Cambrian (Ordian):* Australia.

R. (**Redlichia**). Facial and rostral sutures present; hypostome fused to rostral plate; rostral plate shorter (exs.) than anterior border of the cranidium. Glabella long and tapering forward; glabellar furrows shallow; occipital furrow also shallow, with deeper lateral portions. Eye lobe long, with extremity almost reaching the axial furrow in adults. Librigena wide. Posterolateral limb repeating the structure of the posterior half of the thoracic pleurae and in some also with advanced intergenal spines. Short occipital spine in some species. Hypostome with or without 2 pairs of lateral spines. Thorax gradually decreasing in width (tr.) posteriorly; pleurae with spines advanced on anterior and falcate on posterior segments. Pygidium with 3 segments, dimorphic in each species. One morph with narrow, depressed flanks and arched posterior margin, the other with continuous doublure and more or less rounded posterior margin. *Occurrence and distribution as for genus.*——FIG. 272,*3.* **R. (R.) noetlingi* (REDLICH), Lower Cambrian (upper Canglangpuan), Pakistan (Salt Range); lectotype, cranidium, ×2 (King, 1941).

R. (**Conoredlichia**) W. CHANG, 1966, p. 152 [**Redlichia conica* DU & SHAO, 1963, p. 304; OD; holotype (DU & SHAO, 1963, fig. on p. 304; W. CHANG, 1966, pl. 1, fig. 9), specimen number not traced, YIGS, Kunming]. Similar to *R. (Redlichia),* but having relatively small, conical glabella; broad (sag.), depressed preglabellar field with prominent mesial ridge; large and triangular anterior area of fixigena; and narrower (tr.) eye lobe. Librigena, thorax, and pygidium unknown. *Lower Cambrian (upper Canglangpuan):* China (eastern Yunnan), *Palaeolenus* Zone.——FIG. 272,*2.* **R. (C.) conica,* eastern Yunnan (Wuting); holotype, cranidium, ×1 (Du & Shao, 1963).

R. (**Latiredlichia**) HUPÉ, 1953a, p. 194 [**Redlichia* sp. cf. *R. walcotti* (MANSUY), SAITO, 1934, p. 225, *non* MANSUY, 1912; =*Redlichia saitoi* LU, 1950, p. 166; lectotype herein designated (SAITO, 1934, pl. 26, fig. 19), 344, UMUT, Tokyo]. Differs from *R. (Pteroredlichia)* in having broad and short conical glabella, short (tr.) anterior sections of facial sutures, and shorter (exs.) librigena. *Lower Cambrian (Longwangmiaoan):* China (Liaoning, Shandong, Hubei), northwestern Korea, *Redlichia chinensis* Zone.——FIG. 272,*1a,b.* **R. (L.) saitoi* (LU), northwestern Korea (Antakkol, Hwanghai-do); *a,* lectotype, cranidium, ×2; *b,* paratype, librigena, ×3 (Saito, 1934).
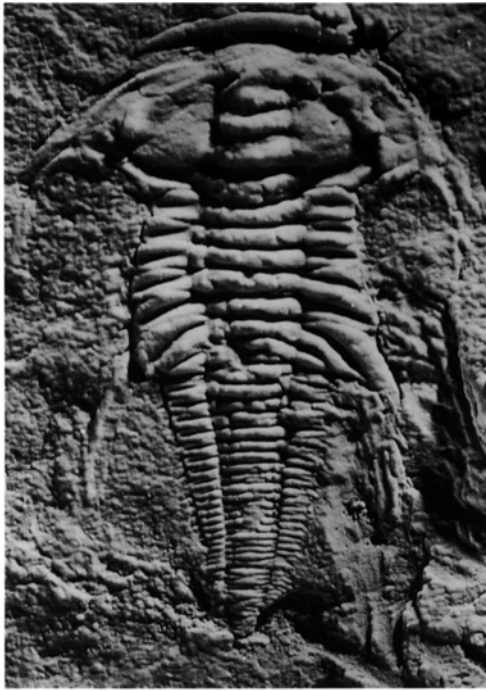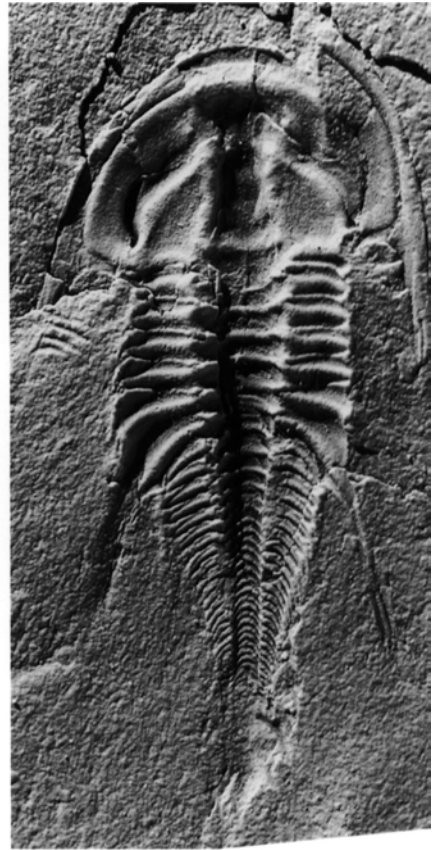
FIG. 271. Emuellidae (p. 429)

R. (Pteroredlichia) W. CHANG, 1966, p. 149 [**R. (P.) lui;* OD; holotype (W. CHANG, 1966, pl. 1, fig. 7), 37606, NIGP, Nanjing] [=*Spinoredlichia* LIU, 1975, p. 14 (type, *S. typicalis;* OD)]. Transverse or almost transverse anterior section of the facial suture extending great distance from glabella (i.e., width of anterior area of fixigenae (tr.) equals at least 1.1 times cranidial length). Thorax with 15 to 16 segments; axial spine on the 11th axial ring. Posterior margin of pygidium either entire with continuous doublure or arched upward and forward without doublure. Hypostome of adults without spines. *Lower Cambrian (Longwangmiaoan):* northern and southwestern China, Korea. *Middle Cambrian (Ordian):* Australia.——FIG. 273*a–c.* **R. (P.) lui,* Longwangmiaoan (*Redlichia chinensis* Zone), northern China (western Henan); *a,* cranidium, ×2.5; *b,* librigena, ×2.5; *c,* thorax, ×2.5 (W. Chang, 1966).

Syndianella LU, 1961, p. 302, 313 [**S. yunnanensis;* OD; holotype (LU, 1961, pl. 3, fig. 9), 12678, NIGP, Nanjing]. Similar to *R. (Redlichia),* but glabellar furrows oblique and horizontal, occipital fur-

row oblique and discontinuous, eye lobe less arcuate, posterior tip of eye lobe distant from the glabella, and preglabellar field longer (sag.). Librigena, thorax, and pygidium unknown. *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan), *Drepanuroides* Zone.——FIG. 274. **S. yunnanensis,* eastern Yunnan (Malong); holotype, cranidium, ×8 (Lu, 1961).

Subfamily METAREDLICHIINAE Zhang & Lin, 1980

[Metaredlichiinae ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 136]

Glabella cylindrical, frontal lobe expanded forward, or broadly conical; up to 5 pairs of glabellar furrows; preglabellar field short (sag.) or absent; intergenal angle present or absent; posterior area of fixigena broad (tr.) and long. Thorax with 15 segments. Pygidium with or without semiankylosed segment; axial lobe convex, transversely broad,
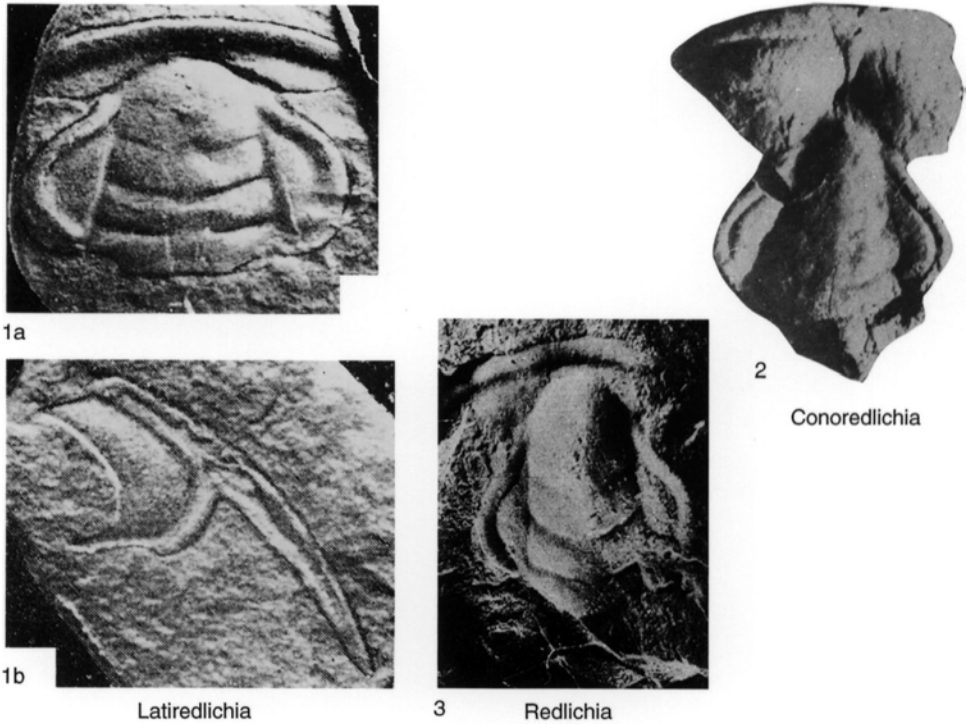
FIG. 272. Redlichiidae (p. 430)

with pair of rounded swellings on terminal portion. *Lower Cambrian.*

Metaredlichia Lu in Lu & others, 1965, p. 66 [**Redlichia cylindrica* W. CHANG, 1953, p. 126; OD; holotype (W. CHANG, 1953, pl. 4, fig. 5), 7059a, NIGP, Nanjing]. Glabella broad, with frontal lobe broadly rounded and 4 pairs of glabellar furrows; occipital ring with small node; eye lobe long and arcuate; preglabellar field very short (sag.), border flat; anterior sections of facial sutures short and divergent. Axial lobe of pygidium with anterior ring; pleural region narrow with pair of pleural furrows situated anterolaterally. Librigena and thorax unknown. *Lower Cambrian (Qiongzhusian):* China (Hubei), *Eoredlichia-Wutingaspis* Zone.——FIG. 275,*1. *M. cylindrica* (CHANG), western Hubei (Yangtze Gorges); holotype, cranidium, ×5 (W. Chang, 1953).

Bornemannaspis RASETTI, 1972, p. 52 [**Olenellus solitarius* BORNEMANN, 1888, p. 470(46); OD; holotype (BORNEMANN, 1888, p. 470(46), pl. 39, fig. 9; SD RASETTI, 1972, pl. 13, fig. 5), MLU, Halle]. Glabella very slightly tapering forward, truncate, slightly expanding in frontal lobe, almost reaching anterior border furrow; lateral glabellar furrows connected medially; anterior border fairly wide (sag.) medially; eye ridge short; palpebral lobe about half as long as glabella; anterior sections of

facial sutures directed outward and forward at an angle of about 45°, relatively short. *Lower Cambrian:* Italy (Sardinia), *Dolerolenus longioculatus* Zone to *Dolerolenus bifidus* Zone.——FIG. 276,*2. *B. solitaria* (BORNEMANN), Sardinia (Canalgrande); upper part of *Dolerolenus longioculatus* Zone, holotype, dorsal view of cranidium, ×2.5 (new).

Breviredlichia CHANG & LIN in YIN & LI, 1978, p. 403 [**B. granulosa;* OD; holotype (YIN & LI, 1978, pl. 149, fig. 12), 31617, NIGP, Nanjing]. Glabella cylindrical, with frontal lobe large and globular and 2 or 3 pairs of glabellar furrows; occipital furrow narrow (sag.), curved backward; occipital ring bending slightly backward, with small median tubercle; librigena broad; advanced genal spine long and strong. Thorax with 15 or 16 segments, pleurae ending in relatively long spines. Surface granulose. *Lower Cambrian (upper Canglangpuan):* China (northern Guizhou, eastern Sichuan), *Megapalaeolenus* Zone.——FIG. 276,*1a. *B. granulosa,* northern Guizhou; holotype, cranidium, ×2 (W. Zhang, Lu, & others, 1980).——FIG. 276,*1b. B. gaoqiaoensis,* eastern Sichuan (Pengshui), dorsal exoskeleton, ×1.5 (W. Zhang, Lu, & others, 1980).

Iglesiella RASETTI, 1972, p. 54 [**I. ichnusae;* OD; holotype (RASETTI, 1972, pl. 8, fig. 1), 108, SG, Rome]. Glabella nearly parallel sided; occipital furrow and preoccipital furrow (S1) consisting of oblique pairs of deep lateral furrows connected medi-
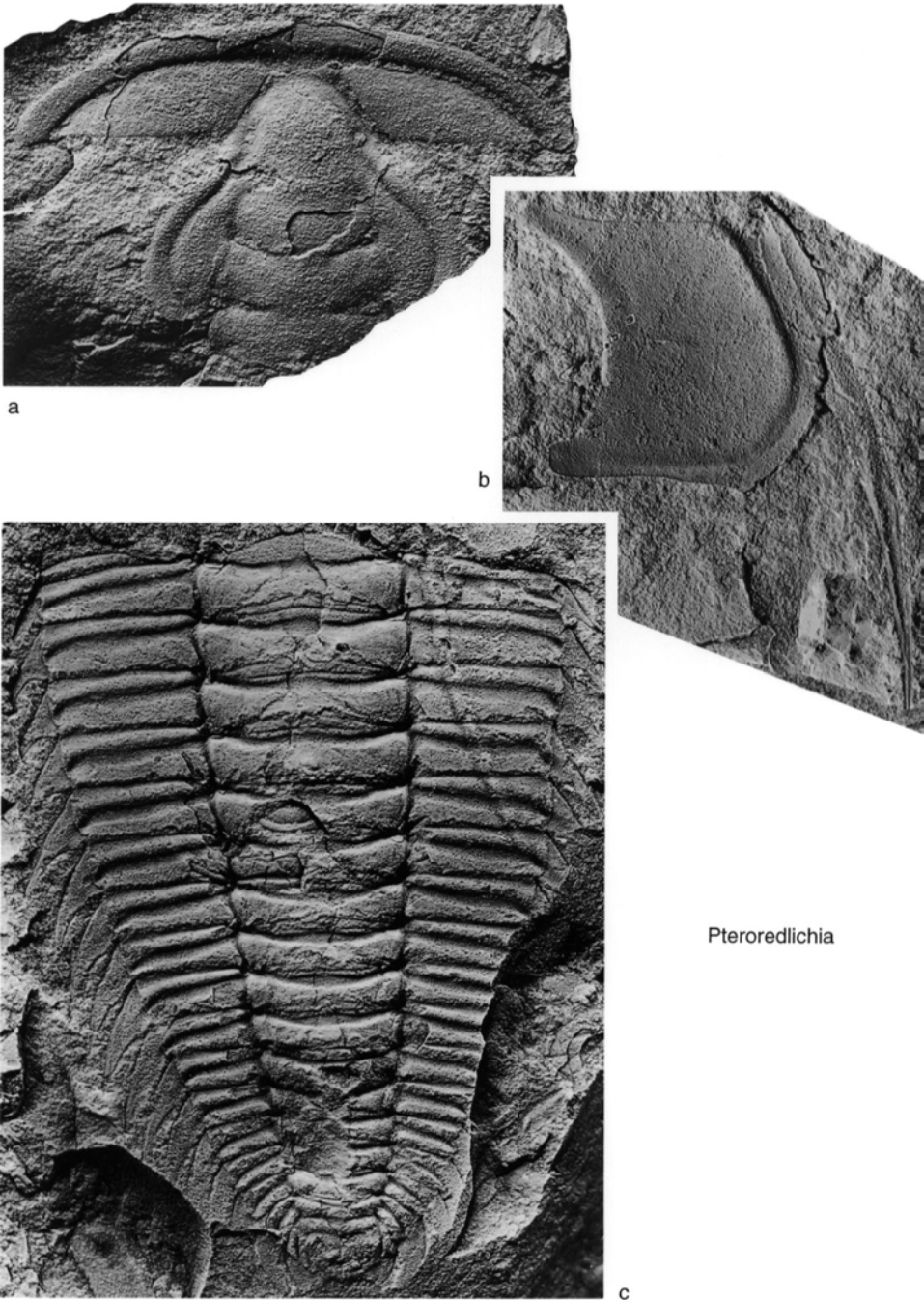
FIG. 273. Redlichiidae (p. 431)

ally by faint depressions; occipital ring with short spine; S2 and S3 faintly visible; preglabellar field long (sag.) and flat; anterior border short; anterior sections of facial sutures presumably strongly divergent at anterior ends of eye lobe close to dorsal furrow; eye ridge short, directed backward; eye lobe

Syndianella

Fig. 274. Redlichiidae (p. 431)

long and narrow; palpebral area of fixigena half as wide as glabella. *Lower Cambrian:* Italy (Sardinia), *Iglesiella ichnusae* Zone.——Fig. 277,*4*. **I. ichnusae;* holotype, cranidium, ×8 (Rasetti, 1972).

Jingyangia Chang & Zhang in Lu, Chang, & others, 1974, p. 88 [**J. zhenbaensis;* OD; holotype (Lu, Chang, & others, 1974, pl. 33, fig. 8), 21476, NIGP, Nanjing]. Cranidium subquadrate; glabella expanded forward with 3 pairs of glabellar furrows; occipital furrow discontinuous; occipital ring broad (sag.) medially; cranidial border furrow narrow and deep; border narrow and convex; preglabellar field as long (sag.) as border; palpebral area of fixigena broad (tr.); posterior area of fixigena short (exs.) and wide (tr.); anterior sections of facial sutures slightly divergent; librigena with short genal spine. Thorax unknown. Pygidium relatively wide (tr.), subtriangular, with large terminal piece divided into 3 rounded lobes. *Lower Cambrian (Qiongzhusian):* China (southern Shaanxi), *Eoredlichia-Wutingaspis* Zone.——Fig. 277,*2*. **J. zhenbaensis,* southern Shaanxi (Zhenba); holotype, cranidium, ×2 (W. Zhang, Lu, & others, 1980).

Maopingaspis Lin & Yin in Yin & Li, 1978, p. 409 [**M. guizhouensis;* OD; holotype (Yin & Li, 1978, pl. 148, fig. 7), Gt-079, SMNH, Shanghai]. Similar to *Metaredlichia* and *Ushbaspis,* but having narrower cranidium, no preglabellar field, relatively narrow (tr.) palpebral areas and anterior areas of fixigenae, broad (tr.) posterior areas of fixigenae, and broad, flat cranidial border. Librigena with broad border and stout, short genal spine. Pygidium elliptical; axial lobe with an anterior axial ring; border flat, broad; posterior margin slightly arched forward. *Lower Cambrian (lower Canglangpuan):* China (northern Guizhou), *Drepanuroides* Zone.——Fig. 275,*4*. **M. guizhouensis,* northern Guizhou (Meitan); holotype, cranidium, ×3 (Yin & Li, 1978).

?Nebidella Rasetti, 1972, p. 51 [**N. limbata;* OD; holotype (Rasetti, 1972, pl. 12, fig. 17), 100, SG, Rome]. Glabella tapering forward, rounded in front; occipital and lateral glabellar furrows shallow, straight, faintly connected medially; preglabellar field long (sag.); border narrow; eye ridge very short; eye lobe long; fixigena with maximum width of palpebral area one-third width of glabella; anterior section of facial sutures directed outward at 45° angle at anterior end of eye lobe close to dorsal furrow. Librigenae wide, flat, with narrow border; facial suture cutting margin at some distance from genal angle, which extends into a short spine. *Lower Cambrian:* Italy (Sardinia), *Dolerolenus longioculatus* Zone.——Fig. 277,*6*. **N. limbata;* holotype, cranidium, ×1.5 (Rasetti, 1972).

Parazhenbaspis Zhu & Lin, 1983, p. 24, 28 [**P. mohershanensis;* OD; holotype (Zhu & Lin, 1983, pl. 1, fig. 8), 69526, NIGP, Nanjing]. Glabella cylindrical, broad and slightly waisted, rounded in front and reaching the border furrow, with 3 or 4 pairs of faint glabellar furrows; eye ridge short; eye lobe long and reaching the posterior border furrow; posterior border narrow and broad (tr.); anterior border convex and arched forward; anterior sections of facial sutures short and divergent, posterior sections long and extending transversely outwards; hypostome ovate, with narrow border and small and triangular anterior wings. Pygidium with wide axial lobe, 1 axial ring; pleural region narrow, with pair of pleural and interpleural furrows. *Lower Cambrian (lower Canglangpuan):* China (eastern Xinjiang, Uygur Autonomous Region), *Tianshanocephalus* Zone.——Fig. 275,*3*. **P. mohershanensis,* eastern Xinjiang (Kuluketage), *Tianshanocephalus* Zone; holotype, cranidium, ×3 (Zhu & Lin, 1983).

Pseudoredlichia Chang & Lin in Yin & Li, 1978, p. 404 [**P. hepingensis;* OD; holotype (W. Zhang, Lu, & others, 1980, pl. 28, fig. 9), 37630, NIGP, Nanjing]. Similar to *R. (Redlichia),* but having 4 or 5 pairs of discontinuous glabellar furrows, occipital furrow, broad librigena, less advanced genal spine, and pair of highly elevated swellings behind pygidial axial ring. Thorax unknown. *Lower Cambrian (lower Canglangpuan):* China (southern Shaanxi). ——Fig. 276,*3*. **P. hepingensis,* southern Shaanxi (Zhenba); holotype, cranidium, ×2 (W. Zhang, Lu, & others, 1980).

Sardoredlichia Rasetti, 1972, p. 48 [**S. praespinosa;* OD; holotype (Rasetti, 1972, pl. 9, fig. 1), 80, SG, Rome]. Glabella moderately tapered; occipital furrow and 3 pairs of lateral glabellar furrows straight and transverse; preglabellar field moderately long, with median preglabellar ridge; border rather narrow; palpebral lobe about half as long as glabella, straight in anterior portion and widening posteriorly; maximum width of palpebral area of fixigena half the glabellar width; anterior sections of facial sutures strongly divergent; librigena with long, advanced genal spine in front of level of glabellar midpoint; hypostome with 2 pairs of lateral and posterior spines and small and triangular anterior wings; rostral plate long (tr.), narrow, and slightly arched
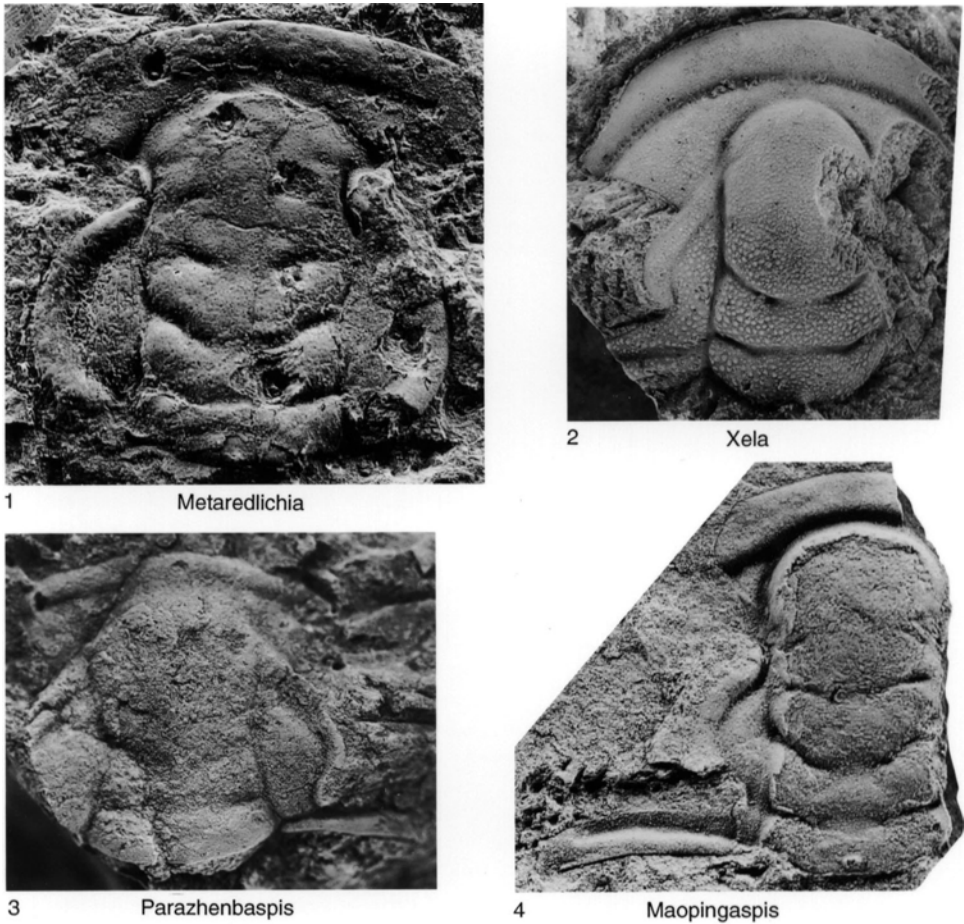
FIG. 275. Redlichiidae (p. 432–437)

forward. Thoracic pleura with long pleural spines. Pygidium with prominent axis and narrow (tr.) pleural region. *Lower Cambrian:* Italy (Sardinia), *Iglesiella ichnusae* Zone to *Dolerolenus bifidus* Zone.——FIG. 277,5. *S. praespinosa;* holotype, cranidium, ×3 (Rasetti, 1972).

Ushbaspis POKROVSKAYA in KELLER & POKROVSKAYA, 1965, p. 81 [*U. granulata;* OD; holotype (KELLER & POKROVSKAYA, 1965, pl. 3, fig. 2), 3579/2, GIN, Moscow] [=*Metaredlichioides* CHIEN & YAO in LU, CHANG, & others, 1974, p. 90 (type, *M. constrictus;* OD)]. Glabella cylindrical, with frontal lobe expanded forward, and 4 pairs of glabellar furrows; occipital ring with a median node; preglabellar field as long (sag.) as cranidial border; posterior border furrow broad (exs.); librigena with stout genal spine. Thorax with 15 segments. Pygidium transversely subelliptical, axis with anterior axial ring and a large terminal piece having a pair of swellings, pleural region narrow (tr.) and with a pair of pleu-

ral furrows. Surface finely granulose or smooth. *Lower Cambrian* (lower Botoman, lower Canglangpuan); Kazakhstan; *Ushbaspis limbata* Zone; China (Hubei, Guizhou, Sichuan, Xinjiang Uygur Autonomous Region), *Drepanuroides* Zone.——FIG. 277,1a. *U. ganulata;* southern Kazakhstan (Ushbas); holotype, cranidium, ×2.5 (Keller & Pokrovskaya, 1965).——FIG. 277,1b,c. *U. constrictus* (CHIEN & YAO); *b,* northern Sichuan (Chengkou), cranidium, ×3; *c,* northern Guizhou (Meitan), exoskeleton, ×2 (W. Zhang, Lu, & others, 1980).

Xela JELL in BENGTSON & others, 1990, p. 285 [*X. drena;* OD; holotype (BENGTSON & others, 1990, fig. 187e), 127161, NMVP, Melbourne]. Large, coarsely tuberculate, with anteriorly rounded glabella terminating anteriorly before border furrow; anterior section of facial suture at 45° to sagittal line and isolating larger anterior area of fixigena; fixigena extremely small; palpebral lobe short; eye
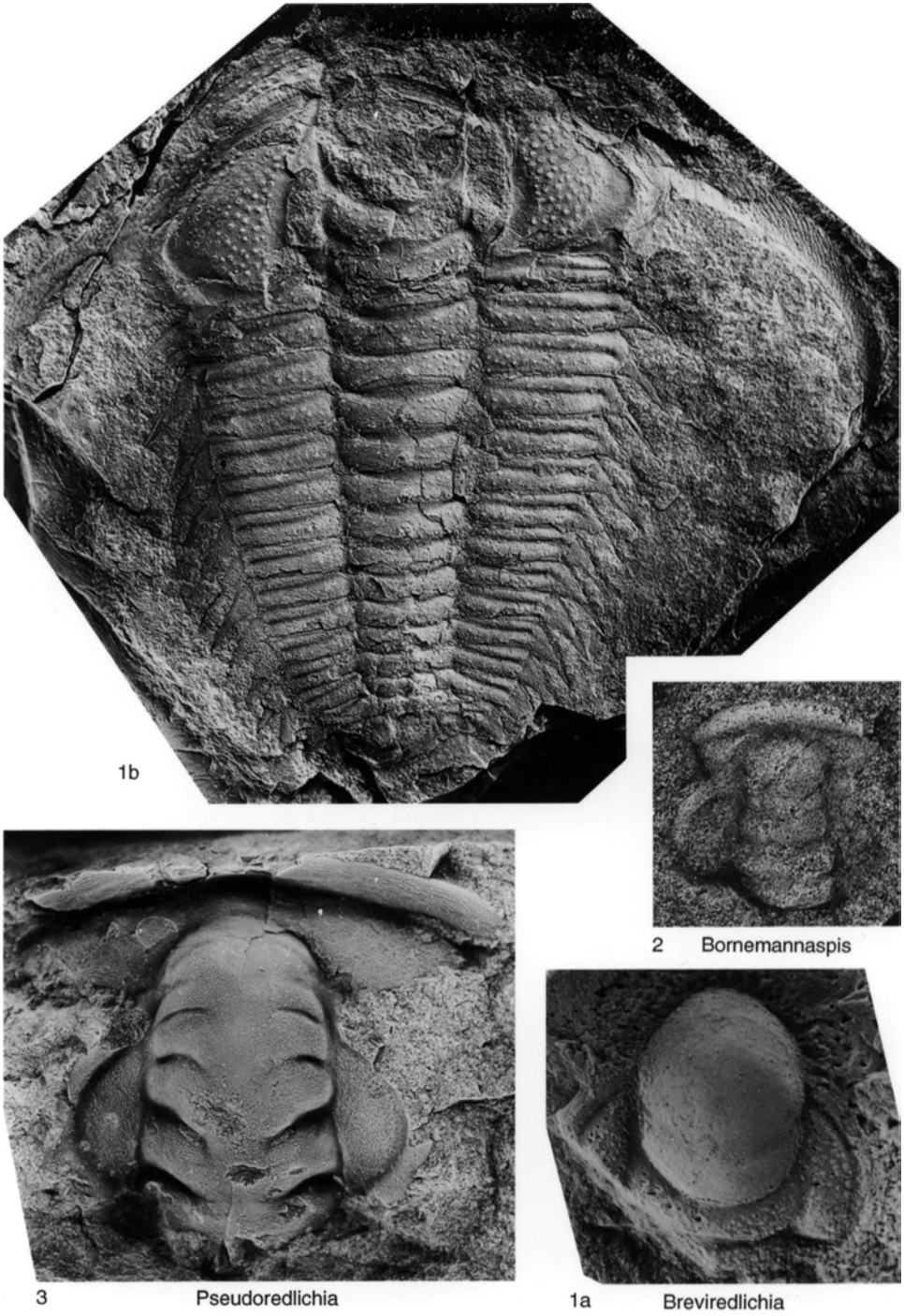
FIG. 276. Redlichiidae (p. 432–434)

ridge meeting axial furrow behind S3; genal spine not advanced, with broad base, relatively short. Pygidium with 3 short rings and distinctly bilobed terminus; posterior margin excavated; pleural area of 3 segments, each with pleural furrow and the 1st with marginal spine. *Lower Cambrian:* Australia (South Australia, Wirrealpa Mine), *Pararaia janeae* Zone.——Fig. 275,*2.* **X. drena;* holotype, cranidium, ×2 (Bengtson & others, 1990).

Zhenbaspis W. Chang & Zhu in Lu, Chang, & others, 1974, p. 89 [**Z. lata;* OD; holotype (Lu, Chang, & others, 1974, pl. 34, fig. 1), 21478, NIGP, Nanjing] [=*Yankongia* Zhou in Lu, Chang, & others, 1974, p. 91 (type, *Y. dashapoensis;* OD); *Zhenbaspis (Zhenxiongaspis)* Lin & Yin in Yin & Li, 1978, p. 411 (type, *Z. (Z.) cylindrica;* OD)]. Cranidium subquadrate; glabella large, broadly cylindrical, with frontal lobe well rounded and 3 pairs of glabellar furrows; preglabellar field gently convex, same length (sag.) as the cranidial border; anterior sections of facial sutures subparallel or slightly divergent; librigena with short and stout genal spine. Thorax and pygidium unknown. *Lower Cambrian (Qiongzhusian):* China (southern Shaanxi, Guizhou, northeastern Yunnan), *Eoredlichia-Wutingaspis* Zone.——Fig. 277,*3.* **Z. lata,* southern Shaanxi (Zhenba); holotype, cranidium, ×4 (Chang in Lu, Chang, & others, 1974).

Subfamily NEOREDLICHIINAE Hupé, 1953

[*nom. transl.* W. Chang, 1966, p. 152, *ex* Neoredlichiidae Hupé, 1953a, p. 149]

Glabella conical; eye lobe long and arcuate; librigena with advanced genal spine; proximal end of anterior section of facial suture and posterior extremity of eye lobe distant from axial furrow. *Lower Cambrian.*

Neoredlichia Saito, 1936, p. 363 [**Redlichia nakamurai* Saito, 1934, p. 224; OD; holotype (Saito, 1934, pl. 26, fig. 15), 312, UMUT, Tokyo]. Frontal glabellar lobe short, with 3 pairs of transglabellar furrows slightly bent backward; occipital furrow deep and connected sagittally; occipital ring of uniform length (sag. and exs.) or slightly longer sagittally; eye lobe reaching level of midlength of occipital ring, posterior tip of eye lobe distant from glabella, preglabellar field absent or slightly depressed; posterior area of fixigena slender; anterior sections of facial sutures divergent; librigena with slightly advanced genal spine. Thorax and pygidium unknown. *Lower Cambrian (Longwangmiaoan):* China (Shandong), northwestern Korea, *Redlichia chinensis* Zone.——Fig. 278,*3a–c.* **N. nakamurai* (Saito), northwestern Korea (Chunghwa); *a,* holotype, cranidium, ×3; *b,* paratype, cranidium, ×3; *c,* paratype, librigena, ×2 (Saito, 1934).

Leptoredlichia W. Chang, 1966, p. 152, 166 [**L. tumidolimbata;* OD; holotype (W. Chang, 1966,

pl. 1, fig. 10), 18146, NIGP, Nanjing] [=*Leptoredlichia (Paraleptoredlichia)* Qiu in Qiu & others, 1983, p. 51 (type, *L. (P.) wushangensis;* OD)]. Three pairs of glabellar furrows; eye lobe reaching posterior border furrow and distant from glabella; anterior sections of facial sutures slightly divergent; cranidial border with slightly developed plectrum. *Lower Cambrian (Longwangmiaoan):* China.

L. (Leptoredlichia). Characters of the genus. *Lower Cambrian (Longwangmiaoan):* northern China (northern Anhui, northern Jiangsu), *Redlichia chinensis* Zone.——Fig. 278,*2.* **L. tumidolimbata,* northern Anhui; holotype, cranidium, ×5 (W. Chang, 1966).

L. (Xenoredlichia) Zhang in Qiu & others, 1983, p. 51 [**L. (X.) suiheensis;* OD; holotype (Qiu & others, 1983, pl. 17, fig. 5), HIT3009, NIGMR, Nanjing]. Similar to *L. (Leptoredlichia),* but having short and conical glabella and prominent plectrum. Librigena like *R. (Redlichia),* with short advanced genal spine. *Lower Cambrian (Longwangmiaoan):* China (northern Anhui), *Redlichia chinensis* Zone.——Fig. 278,*1a,b.* **L. (X.) suiheensis; a,* holotype, cranidium, ×6; *b,* librigena, ×3.5 (Qiu & others, 1983).

?Olgaspis Korobeinikova, 1966, p. 75 [**O. accepta;* OD; holotype (Korobeinikova, 1966, pl. 1), 879/1, CSGM, Novosibirsk]. Glabella tapering forward, with 3 pairs of glabellar furrows; occipital furrow deep; occipital ring convex, long (sag.) in the middle; anterior border convex, thickened sagittally; preglabellar field depressed; palpebral lobe narrow (tr.), arcuate, and long (exs.); palpebral furrow deep; eye ridge oblique; fixigena convex; anterior section of facial suture slightly divergent. Surface of cranidium weakly granulose. Pygidium small, with wide axis gradually tapering backward; pleural region subtriangular, flat or slightly concave. *Lower Cambrian (Botoman or lower Toyonian):* Russia (eastern Sayan Mountains), *Poliellina-Laticephalus* Zone.——Fig. 278,*4.* **O. accepta;* holotype, cranidium, ×6 (Korobeinikova, 1966).

Subfamily PARAREDLICHIINAE Hupé, 1953

[Pararedlichiinae Hupé, 1953a, p. 313]

Proximal end of anterior section of facial suture and posterior extremity of eye lobe distant from axial furrow. Thorax of 14 to 15 segments, axial spine on the 9th segment. Pygidium with semiankylosed segment and large terminal piece, reaching posterior pygidial margin. *Lower Cambrian–Middle Cambrian.*

Eoredlichia Chang in Lu & Dong, 1952, p. 186 [**Redlichia intermedia* Lu, 1940, p. 333; OD; lectotype (Lu, 1940, pl. 1, fig. 10); SD W. Chang, 1962, p. 42), 7061b, NIGP, Nanjing] [=*Archaeops* Hupé, 1953a, p. 194 (type, *A. lui;* OD; =*Redlichia*
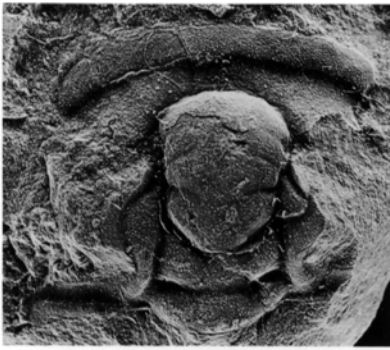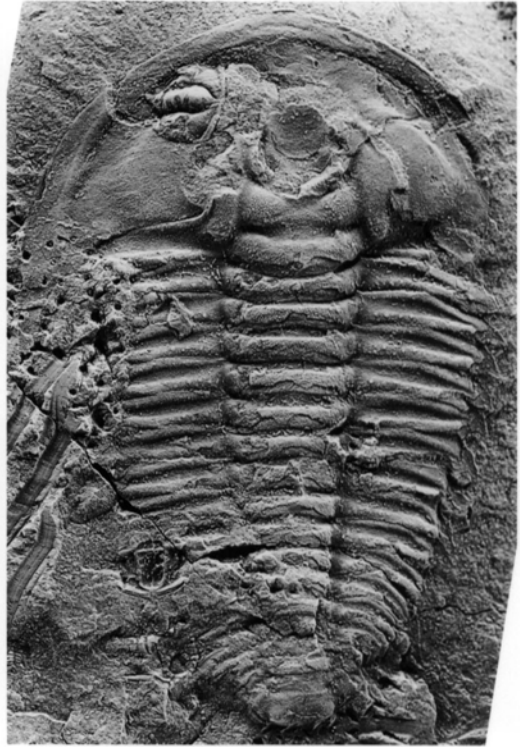
FIG. 277. Redlichiidae (p. 434–437)

walcotti Lu, 1941, p. 79, *non* Mansuy, 1912); *Saukiandops* Hupé, 1953a, p. 151 (type, *Redlichia walcotti* Mansuy, 1912 p. 26; OD); *Pararedlichia* Hupé, 1953a, p. 164 (type, *P. pulchella;* OD);

Galloredlichia Jago in Courtessole & Jago, 1980, p. 15 (type, *G. noiri;* OD)]. Glabella tapering forward, frontal lobe well rounded; S1 and S2 long, deep, and backward-oblique proximally; S3 shallow,

narrow (tr.), and indistinct; occipital ring longer sagittally and slightly trisegmented longitudinally in well-preserved specimens; preglabellar field same length (sag.) as or slightly shorter or longer than cranidial border; anterior sections of facial sutures divergent; facial line near and parallel to the anterior sections of facial suture; slightly advanced genal spine. Hypostome with 2 pairs of small posterolateral marginal spines. Thorax with 15 segments. Pygidium small, transversely ovate, with anteriorly ankylosed segment and large, ovate or subrounded terminal piece having 1 or 2 pairs of pits. *Lower Cambrian:* China (Yunnan, Sichuan, southern Shaanxi), Qiongzhusian (*Eoredlichia-Wutingaspis* Zone); Morocco, northern Spain, southern France, *Fallotaspis tazemmourtensis* Zone.

E. (Eoredlichia). Characters of genus. *Lower Cambrian:* Morocco, northern Spain, southern France, Sous-étage Amouslekien (basal part of *Fallotaspis tazemmourtensis* Zone or *Eofallotaspis* Zone of GEYER, 1990a); China (eastern Yunnan, Sichuan, southern Shaanxi), Qiongzhusian (*Eoredlichia-Wutingaspis* Zone).——FIG. 279,*1a,b.* *E.(E.) intermedia* (LU), eastern Yunnan (Kunming); *a,* lectotype, cranidium, ×3; *b,* paratype, nearly complete dorsal exoskeleton, ×5 (W. Chang, 1962).

E. (Pachyredlichia) W. CHANG, 1966, p. 153 [*E. (P.) shensiensis;* OD; holotype (W. CHANG, 1966, pl. 1, fig. 5), 18143, NIGP, Nanjing]. Cranidium subquadrate. Glabella cylindrical or cylindro-conical, broadly rounded in front; occipital ring convex, with or without a short spine; preglabellar field very short (sag.) or absent; eye lobe medium-sized, slightly shorter (exs.) than that of *E. (Eoredlichia);* border convex; anterior sections of facial sutures slightly divergent; surface with fine granules. *Lower Cambrian (Qiongzhusian):* China (northern Sichuan, southern Shaanxi), *Eoredlichia-Wutingaspis* Zone.——FIG. 279,*2.* *E. (P.) shensiensis,* southern Shaanxi (Nanzheng); holotype, cranidium, ×3 (W. Chang, 1966).

?Irgitkhemia TCHERNYSHEVA, 1977, p. 61 [*I. insolita;* OD; holotype (TCHERNYSHEVA, 1977, pl. 14, fig. 9), 10802/9, CNIGR, St. Petersburg]. Cranidium flattened, subquadrate, with gently curved to almost straight anterior border. Glabella elongate, narrowing towards anterior end, with slight keel; glabellar furrows clear cut, short, numbering 4 pairs; occipital ring wide; fixigena flat; palpebral lobe medium-sized, raised above fixigena, transitional into stout eye ridge; preglabellar field flat, lower than front of glabella, with radial sculpture; anterior border weakly convex. Librigena, thorax, and pygidium unknown. *Lower Cambrian (Toyonian)–Middle Cambrian (Amgaian),* Russia (eastern Sayan Mountains, Tuva, Batenevskii Ridge).——FIG. 280,*2.* *I. insolita,* eastern Sayan; holotype, cranidium, ×4 (Tchernysheva, 1977).

Lemdadella SDZUY, 1978, p. 92 [*L. spectabilis;* OD; holotype (SDZUY, 1978, pl. 1, fig. 10), 28571, SMF, Frankfurt am Main]. Glabella tapering forward, with parafrontal band; eye lobe long and arcuate,
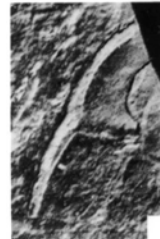
FIG. 278. Redlichiidae (p. 437)

with ocular striga; preglabellar field long (sag.) to moderately long, with plectrum; anterior area of fixigena with facial line. *Lower Cambrian:* Spain; Morocco, *Fallotaspis tazemmourtensis* Zone.——FIG. 279,*3a,b.* *L. spectabilis,* Morocco (Lemdad syncline, Ounein area in the High Atlas); *a,* composite picture of holotype and silicon cast of counterpart, dorsal view of cranidium, ×5; *b,* dorsal view of pygidium, ×4 (photographs courtesy of G. Geyer).

Ningqiangaspis ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 158, 429 [*N. ningqiangensis;* OD;

1a   Eoredlichia

2   Pachyredlichia

3a

3b

Lemdadella

1b

Fig. 279. Redlichiidae (p. 439)

holotype (Zhang & Lin in W. Zhang, Lu, & others, 1980, pl. 39, fig. 6), 37743, NIGP, Nanjing]. Differing from *Eoredlichia* in having longer eye lobe, less divergent anterior section of facial suture, shorter (sag.) cranidial border, and no preglabellar field. Librigena, thorax, and pygidium unknown. *Lower Cambrian (Qiongzhusian):* China (southern Shaanxi), *Eoredlichia-Wutingaspis* Zone.——Fig.

280,*3.* **N. ningqiangensis;* holotype, cranidium, ×6 (W. Zhang, Lu, & others, 1980).

?Redlichops Richter & Richter, 1941b, p. 13 [**Redlichia (Redlichops) blanckenhorni;* OD; holotype (Richter & Richter, 1941b, pl. 2, fig. 1), X1287a, SMF, Frankfurt am Main]. Glabella tapering forward; frontal lobe narrow; S3 furrows slightly directed forward; occipital furrow disconnected

medially; occipital node small; anterior section of facial suture relatively short; eye lobe long and arcuate, widening anteriorly and extending back to level of midlength of occipital ring; palpebral area of fixigenae very wide; surface finely granulose. *Lower Cambrian:* Jordan.——Fig. 280,*1.* **R. (R.) blanckenhorni,* Jordan (Chirbet el-Burj); holotype, dorsal view of cranidial fragment, ×3 (photograph courtesy of G. Geyer).

Subfamily WUTINGASPINAE Chang, 1966

[Wutingaspinae W. Chang, 1966, p. 153]

Glabella broadly conical; preglabellar field short (sag.) or absent; eye ridge slightly oblique, long; eye lobe short or of medium length; palpebral area of fixigena broad (tr.); posterior area of fixigena broad (tr.) and relatively long (exs.). Thorax with 15 to 19 segments, thoracic axial spines absent. Pygidium small. *Lower Cambrian.*

Wutingaspis Kobayashi, 1944c, p. 130 [**W. tingi;* OD; holotype (Kobayashi, 1944c, pl. 10, fig. 7), Y338, UMUT, Tokyo]. Similar to *Eoredlichia,* but having relatively short eye lobe, broad cylindroconical glabella, longer (exs.) and broader posterior area of fixigena, slightly arcuate and more divergent facial lines, and no thoracic axial spine. *Lower Cambrian (Qiongzhusian):* China (eastern Yunnan, Sichuan, Guizhou, southern Shaanxi), *Eoredlichia-Wutingaspis* Zone.——Fig. 281,*2.* **W. tingi,* eastern Yunnan (Wuting); holotype, cranidium, ×2 (Kobayashi, 1944c).

Chaoaspis W. Chang, 1966, p. 154, 167 [**C. ovatus;* OD; holotype (W. Chang, 1966, pl. 1, fig. 13), 18149, NIGP, Nanjing]. Similar to *Wutingaspis,* but having short (sag.) and ovate glabella, relatively small eye lobe, broad (sag.) preglabellar field, broad but relatively short (exs.) posterior area of fixigena, and more divergent anterior sections of facial sutures. Librigena, thorax, and pygidium unknown. *Lower Cambrian (Qiongzhusian):* China (western Sichuan), *Eoredlichia-Wutingaspis* Zone.——Fig. 282,*1.* **C. ovatus,* western Sichuan (Emei); holotype, cranidium, ×4 (W. Chang, 1966).

Chengjiangaspis Zhang & Lin in W. Zhang, Lu, & others, 1980, p. 169 [**C. chengjiangensis;* OD; holotype (Zhang & Lin in W. Zhang, Lu, & others, 1980, pl. 44, fig. 10), 37792, NIGP, Nanjing]. Similar to *Wutingaspis,* but having more conical glabella, long (sag.) and depressed preglabellar field, very shallow anterior border furrow, less divergent anterior sections of facial sutures, deep and broad (sag., exs.) occipital furrow, no occipital node, and narrow librigena. Complete thorax and pygidium unknown. *Lower Cambrian (Qiongzhusian):* China (eastern Yunnan), *Eoredlichia-Wutingaspis* Zone. ——Fig. 281,*3.* **C. chengjiangensis;* eastern Yun-
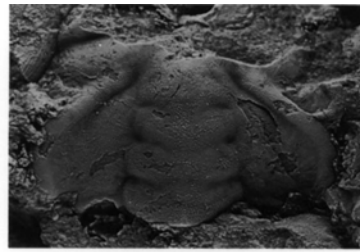
FIG. 280. Redlichiidae (p. 439–441)

nan, (Chengjiang); holotype, cranidium, ×6 (W. Zhang, Lu, & others, 1980).

Kepingaspis T. Chang, 1965, p. 154, 156 [**K. kepingensis;* OD; holotype (T. Chang, 1965, pl. 1, fig. 1), K-01, XIGMR, Urumqi]. Cranidium subtrapezoidal; glabella tapering forward, with well-rounded frontal lobe and oblique glabellar furrows; eye lobe long and arcuate; posterior area of fixigena subtriangular; preglabellar field absent; cranidial border flat; librigena broad (tr.), with advanced genal spine small and short; anterior sections of facial sutures slightly divergent. Thorax with 19 segments; pleural spines short. Pygidium small, with axial ring and terminal piece divided into 2 small swellings. *Lower Cambrian (Canglangpuan):* China (western Xinjiang), *Kepingaspis-Tianshanocephalus* Zone.——Fig. 281,*4.* **K. kepingensis,* western
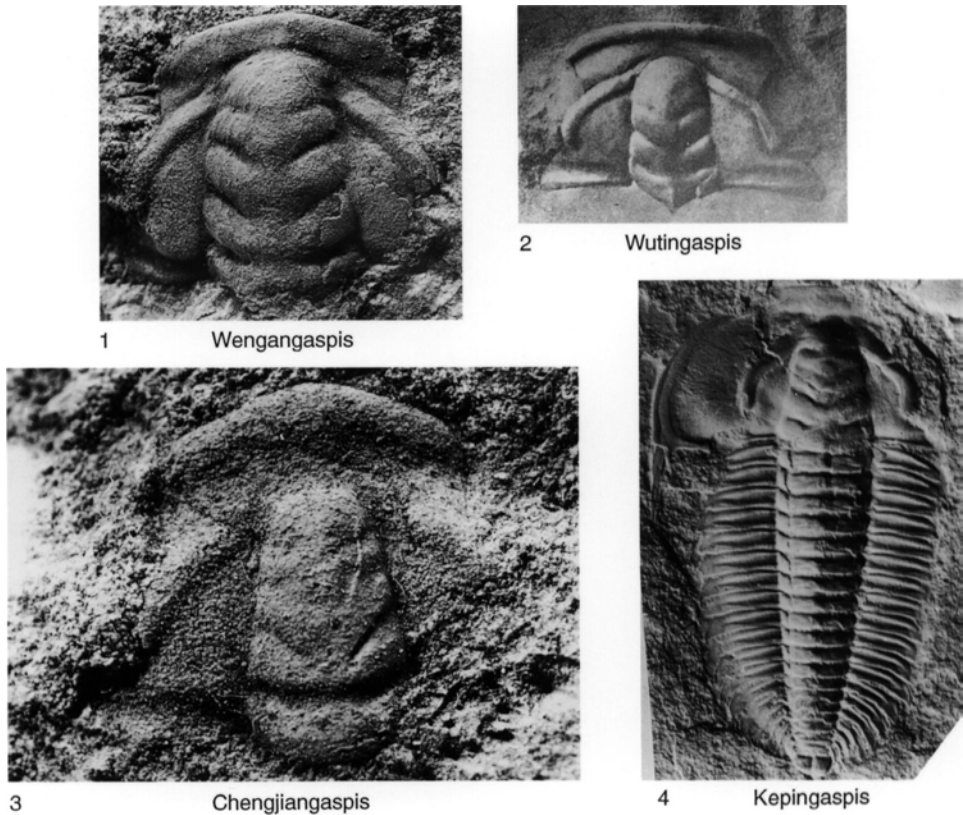
FIG. 281. Redlichiidae (p. 441–444)

Xinjiang (Keping); incomplete dorsal exoskeleton, ×3 (Chang, 1965).

Kuanyangia HUPÉ, 1953a, p. 195 [**Redlichia pustulosa* LU, 1941, p. 78; OD; holotype (LU, 1941, pl. 1, fig. 5), No. 2007, specimen lost during World War II]. Cranidium subquadrate; glabella broad, conical; 3 pairs of oblique glabellar furrows continuous or discontinuous; occipital furrow shallow, with deeper lateral portions; preglabellar field absent or very short (sag.); anterior border convex and slightly arcuate forward; eye ridge stout; eye lobe medium-sized; thorax with 16 segments; surface pustulose. *Lower Cambrian (Qiongzhusian):* China (eastern Yunnan), *Eoredlichia-Wutingaspis* Zone.

K. (Kuanyangia). Characters of the genus. *Lower Cambrian (Qiongzhusian):* China (eastern Yunnan), *Eoredlichia-Wutingaspis* Zone.——FIG. 282,3. **K. (K.) pustulosa* (LU), eastern Yunnan (Kunming); topotype, cranidium, ×3 (W. Zhang, Lu, & others, 1980).

K. (Sapushania) W. CHANG, 1966, p. 155, 167 [**Sapushania granulosa;* OD; holotype (W. CHANG, 1966, pl. 1, fig. 14), 18150, NIGP, Nanjing]. Similar to *K. (Kuanyangia),* but having smaller eye lobe and longer (exs.) triangular posterior area of fixigena. Pygidial axial lobe composed of 2 axial rings and large terminal piece and reaching posterior margin; prominent, longitudinal, depressed area on terminal piece. Surface pustulose. *Lower Cambrian (Qiongzhusian):* China (eastern Yunnan: Wuting, Kunming), *Eoredlichia-Wutingaspis* Zone.——FIG. 282,2. **K. (S.) granulosa* (CHANG), eastern Yunnan (Wuting); holotype, incomplete cranidium, ×1.5 (W. Chang, 1966).

Sardaspis BRASIER, 1976, p. 273 [**S. papillosa;* OD; holotype (BRASIER, 1976, pl. 25, fig. 1), AZ.51a,b, OUM, Oxford; =*Ptychoparia laticeps* BORNEMANN, 1891, p. 23; holotype (BORNEMANN, 1891, p. 47(147), pl. 39, fig. 12; RASETTI, 1972, pl. 13, fig. 11), MLU, Halle]. Glabella conical, S1 continuous; occipital furrow arcuate backward; occipital ring broad (sag.) medially, with or without occipital spine; preglabellar field absent or very short (sag.); border furrow deep; border convex; eye ridge oblique, eye lobe medium-sized; surface pustulose. Librigena, thorax, and pygidium unknown. *Lower Cambrian:* Italy (Sardinia), *Dolerolenus longioculatus* Zone; China (Guizhou, southern Shaanxi), lower Canglangpuan, *?Yiliangella* or *Yunnanaspis* Zone.
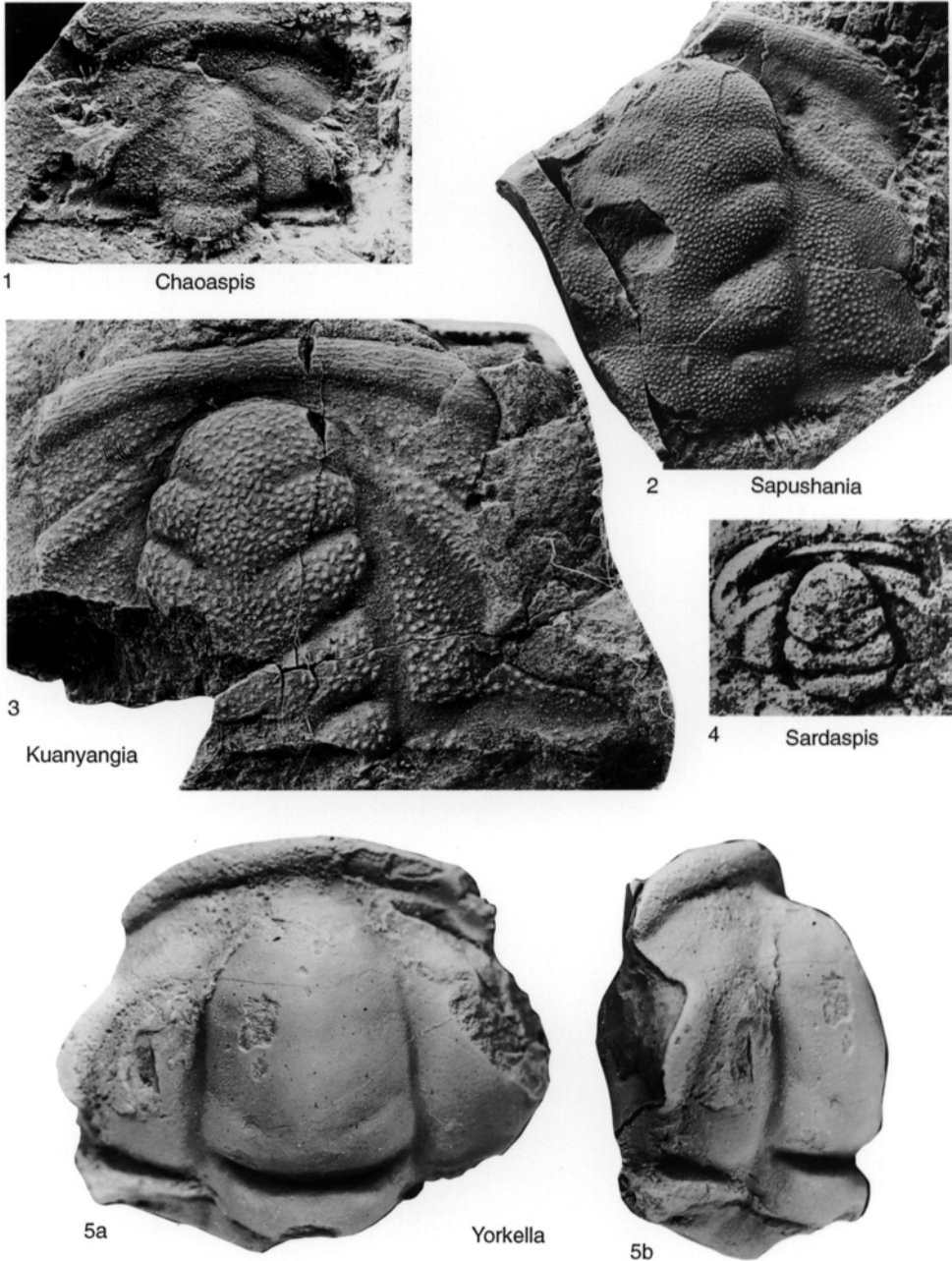
FIG. 282. Redlichiidae (p. 441–444)

——FIG. 282,*4. *S. laticeps* (BORNEMANN), Sardinia, *Dolerolenus longioculatus* Zone; holotype, cranidium, ×2 (Rasetti, 1972).

?**Wengangaspis** YIN in YIN & LI, 1978, p. 415 [**W. baiyanensis;* OD; holotype (YIN in YIN & LI, 1978, pl. 150, fig. 11), Gt-105, SMNH, Shanghai]. Similar to *Kepingaspis,* but having longer (sag.) cranidial border, 4 pairs of glabellar furrows, broader (tr.) palpebral area of fixigena, less divergent anterior sections of facial sutures, and outward- and

forward-bent posterior area of fixigena. Librigena, thorax, and pygidium unknown. *Lower Cambrian (Canglangpuan):* China (Guizhou).——Fig. 281,*1*. **W. baiyanensis,* northern Guizhou (Wengan); holotype, cranidium, ×3 (Yin & Li, 1978).

?*Yorkella* Kobayashi, 1942c, p. 492 [**Conocephalites australis* Woodward, 1884, p. 372; OD; holotype (Woodward, 1884, pl. 11, fig. 2), I.2349, BMNH, London]. Similar to *Wutingaspis* but having large, strongly convex glabella two-thirds to four-fifths as wide as long, with lateral margins either parallel or gently converging in anterior part; broadly rounded glabellar anterior in anterior border furrow; glabellar furrows incomplete across axis; and ornament of coarse, pointed tubercles. Pygidium occupied mainly by axis extending to posterior margin without doublure; small pleurae of 1 segment having expanded anterior pleural band and pair of marginal spines elevated above margin of axis. *Lower Cambrian:* South Australia (Horse Gully), *Pararaia tatei* Zone.——Fig. 282,*5a,b.* **Y. australis* (Woodward); holotype, *a,* dorsal and *b,* lateral views of cranidium, ×3.6 (new).

Family DOLEROLENIDAE
Kobayashi, 1951

[*nom. subst.* Kobayashi in Kobayashi & Kato, 1951, p. 103, *pro* Olenopsidae Kobayashi, 1935, p. 120, invalid name based on junior homonym]

Glabella long, tapering forward, with 3 pairs of faint, evenly spaced, lateral glabellar furrows; occipital furrow straight; anterior border long (sag. and exs.), flat; anterior sections of facial sutures on genal field moderately divergent (less than 45°), on border curved outwards; palpebral lobe arcuate; eye ridge wide, faint; posterior areas of fixigena subtriangular; librigena wide, with stout genal spine. Thorax with 11 to 15 segments. Pygidium small, with 1 to 2 pairs of pygidial spines. *Lower Cambrian.*

Subfamily DOLEROLENINAE
Kobayashi, 1951

[*nom. transl.* Zhang & Lin in W. Zhang, Lu, & others, 1980, p. 80, *ex* Dolerolenidae Kobayashi in Kobayashi & Kato, 1951, p. 103]

Palpebral lobe long, posterior; fixigena wide. Thorax with 14 to 15 segments; axis narrower than pleural regions; pleural spines progressively curved backward; fulcrum proximal. Pygidium small; axis short with 1 or 2 rings; posterior border with pair of small or large spines. *Lower Cambrian.*

Dolerolenus Leanza, 1949, p. 36, *nom. subst. pro Olenopsis* Bornemann, 1891, p. 459, *non*

Ameghino, 1889 [**Olenus zoppii* Meneghini, 1882, p. 163; SD Walcott, 1912d, p. 240; lectotype (Meneghini, 1882, pl. 1, fig. 5, 5a; SD Nicosia & Rasetti, 1970, p. 8, 17), 1, SG, Rome]. Characters of subfamily. *lower Lower Cambrian:* southwestern China, Spain, Italy (Sardinia).

D. (**Dolerolenus**). Glabella rounded in front; preglabellar field as long (sag.) as border; plectrum faintly defined; posterior extremities of facial sutures distant from axial furrows; palpebral lobe extending between level of midlength of L3 and midlength of L1, with curvature increasing rearward. Thorax with 15 segments; pleural spines long, the posterior ones enveloping pygidium. Pygidum subrectangular; axis not tapered, composed of 1 ring and a terminal axial piece; with a median notch; pleural lobes rather long (sag.), with 1 furrow, truncate or extended into a pair of short spines; border indistinct. *Lower Cambrian:* Italy (Sardinia), *Dolerolenus* Zone.——Fig. 283,*1a–c.* **D. zoppii* (Meneghini); *a,* lectotype, distorted dorsal shield, ×2.2 (Rasetti, 1972); *b,* topotype, dorsal shield, ×2 (Pillola, 1991); *c,* topotype, well-preserved cranidium showing facial line, ×1.75 (Pillola, 1991).

D. (**Malungia**) Lu, 1961, p. 307 [**Malungia laevigata;* OD; holotype (Lu, 1961, pl. 3, fig. 1), 12670, NIGP, Nanjing]. Differs from *D. (Dolerolenus)* in having 14 thoracic segments and scissors-shaped pygidium. Hypostome as in *D. (Dolerolenus)* with median body ovate, maculae deeply depressed, posterior lobe short (sag.), border narrow, posterior margin straight or bending backward, anterior margin forward arcuate, and anterior wing triangular. *Lower Cambrian (upper Qiongzhusian to lower Canglangpuan):* China (eastern Yunnan, northern Sichuan), *Eoredlichia-Wutingaspis* Zone to *Malungia* Zone.——Fig. 283,*2a,b.* **D. (M.) laevigata* (Lu), eastern Yunnan (Yiliang); *a,* holotype, incomplete dorsal exoskeleton, ×2.65; *b,* paratype, cranidium, ×1.75 (Lu, 1961).

?Subfamily PARAMALUNGIINAE
Zhang & Lin, 1980

[Paramalungiinae Zhang & Lin in W. Zhang, Lu, & others, 1980, p. 184]

Glabellar furrows effaced; eye lobe small; border furrow faint, only slightly depressed. Thorax of 11 segments. Pygidium with 2 pairs of small marginal spines. *Lower Cambrian.*

Paramalungia W. Chang, 1966, p. 155 [**P. lubrica;* OD; holotype (W. Chang, 1966, pl. 2, fig. 5), 18155, NIGP, Nanjing]. Cranidium similar to *Dolerolenus (Malungia),* but having relatively large, smooth glabella, smooth cranidium, occipital ring with small occipital tubercle, relatively short and
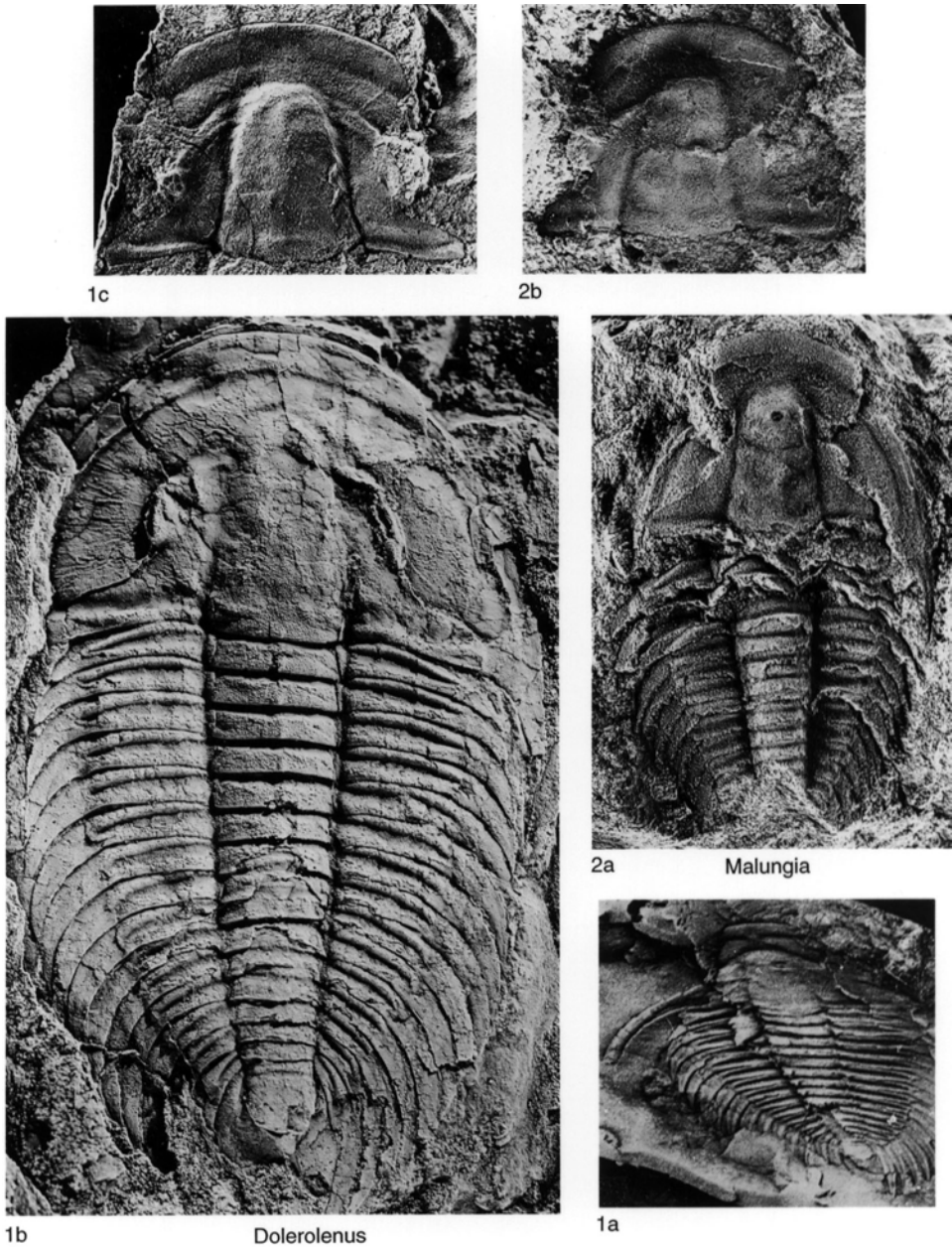
FIG. 283. Dolerolenidae (p. 444)

faint eye ridges, and relatively longer eye lobes. Thorax with 11 segments. Pygidium trapezoidal, with pair of anterior pleural segments extending into a pair of short, anterior, lateral pygidial spines and with a pair of short, slender, and posterior py-gidial spines. *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan), *Drepanuroides* Zone.——FIG. 284. **P. lubrica,* eastern Yunnan (Yiliang); holotype, cranidium, ×2 (W. Chang, 1966).

FIG. 284. Dolerolenidae (p. 445)

Family YINITIDAE Hupé, 1953

[Yinitidae HUPÉ, 1953a, p. 160]

Glabella broadly conical; preglabellar field short (sag.) or absent. Thorax with 9 to 13 segments. Pygidium large and spinose (except in *Parapaokannia*), usually with 3 to 6 pairs of spines. *Lower Cambrian.*

Yinites LU, 1946, p. 188 [*Y. typicalis;* OD; lectotype (LU, 1946, pl. 1, fig. 1a; W. ZHANG, LU, & others, 1980, p. 206, pl. 60, fig. 1), AB126, NIGP, Nanjing]. Glabella long and rounded in front; pre-occipital and occipital furrows gently curved backward; occipital ring of uniform width; proximal end of anterior section of facial suture near axial furrow; posterior area of fixigena triangular; librigena with long and slightly advanced genal spine. Thorax with 13 segments. Pygidium with 3 or 4 axial rings, large terminal axial piece, 3 pleurae, 2 pairs of short, lateral pygidial spines, and a pair of long, backwardly directed posterior spines. Hypostome subtrapezoidal; median body large and ovate; posterior lobe narrow (sag.); posterior border very narrow and distinct; anterior wings triangular. *Lower Cambrian (lower Canglangpuan):* China (northern Guizhou, southeastern Sichuan, southern Shaanxi), *Yiliangella* Zone to *Drepanuroides* Zone. ——FIG. 285,*1a,b.* *Y. typicalis,* northern Guizhou (Gaotai in Meitan); *a,* holotype, cranidium, ×4; *b,* paratype, pygidium, ×10 (W. Zhang, Lu, & others, 1980).

Drepanopyge LU, 1961, p. 303, 314 [*D. mirabilis;* OD; holotype (LU, 1961, pl. 2, fig. 2), 12659, NIGP, Nanjing]. Cranidium subrectangular; glabella broad, slightly tapering forward, and rounded in front; S1–S3 are transglabellar furrows, S3 weak; occipital furrow deeper than glabellar furrows; occipital ring uniform in length (sag. and exs.), with a small median node; preglabellar field very short (sag.); border of cranidium convex; border furrow narrow, marked by a row of small pits; eye lobe

medium-sized; eye ridge distinct; fixigena wide (tr.), nearly half glabellar width; posterior area of fixigena subtriangular; posterolateral furrow broad (exs.) and shallow; librigena with slightly advanced genal spine. Thorax with 10 segments. Pygidial axis convex, with 5 or 6 rings and a large terminal piece; pleural region with 5 pleurae, each ending in a short and stout spine; posterior pair of pygidial pleurae fused behind the terminal piece; posterior margin entire and bent backward. Hypostome broadly ovate; medium body large and elongately ovate, with transverse striations; posterior lobe narrow (sag.); posterior border narrow and distinct; anterior wings triangular. Rostral plate very wide (tr.). *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan: Malong, Yiliang), *Drepanuroides* Zone.——FIG. 285,*4a,b.* *D. mirabilis;* eastern Yunnan (Yiliang); *a,* holotype, cranidium, ×2; *b,* paratype, librigena, ×2 (Lu, 1961).

Drepanuroides W. CHANG, 1966, p. 157 [*D. latilimbata;* OD; holotype (W. CHANG, 1966, pl. 2, fig. 8), 18158, NIGP, Nanjing] [=*Mayiella (Xishuiella)* YIN in YIN & LI, 1978, p. 421 (type, *M. (X. xishuiensis;* OD)]. Differs from *Drepanopyge* in having broad and shallow glabellar furrows, long (sag., exs.) anterior border, and distinct paradoublural line in front of glabella; prominent occipital spine. Librigena with broad (tr.) border and narrower (tr.) genal spine. Thorax with 10 segments and longer pleural spines increasing in size regularly toward posterior. Pygidium with 5 pairs of broad based marginal spines of variable length, anterior pair enlarged or continuing into long spines. Doublure broad. *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan, northern Guizhou), *Drepanuroides* Zone. ——FIG. 286,*2.* *D. latilimbata;* eastern Yunnan (Yiliang); cranidium, ×1 (W. Chang, 1966).

Meitanella LIN & YIN in YIN & LI, 1978, p. 417 [*M. hastata;* OD; holotype (YIN & LI, 1978, pl. 150, fig. 14; W. ZHANG, LU, & others, 1980, pl. 58, fig. 9), 37909, NIGP, Nanjing]. Glabella long (sag.), broad (tr.), and slightly constricted at middle; frontal lobe acutely pointed. All furrows on the cranidium narrow and deep; anterior border long (sag. and exs.) and cranidial border furrow strongly arched forward sagittally; eye ridge short and oblique; eye lobe of medium size, strongly bending outward, and close to the axial furrow; palpebral area of fixigena narrow (tr.); anterior section of facial suture divergent. Librigena, thorax, and pygidium unknown. *Lower Cambrian (lower Canglangpuan):* China (northern Guizhou), *Drepanuroides* Zone.——FIG. 286,*3.* *M. hastata;* northern Guizhou (Meitan); holotype, cranidium, ×2 (W. Zhang, Lu, & others, 1980).

Paokannia HO & LI, 1959, p. 156 [*P. chinensis;* OD; holotype (HO & LI, 1959, pl. 1, fig. 3a), 5803, CUGB, Beijing]. Similar to *Drepanopyge,* but having relatively narrower (tr.) cranidium and palpebral area of fixigena, a very small and short genal spine, and 6 to 7 small pygidial border spines. *Lower Cambrian (Canglangpuan):* Kashmir (Anantnag); China (western Hubei, Sichuan, Guizhou, Jiangsu), ?*Drepanuroides* Zone.——FIG. 285,*3.* *P. chinensis;*
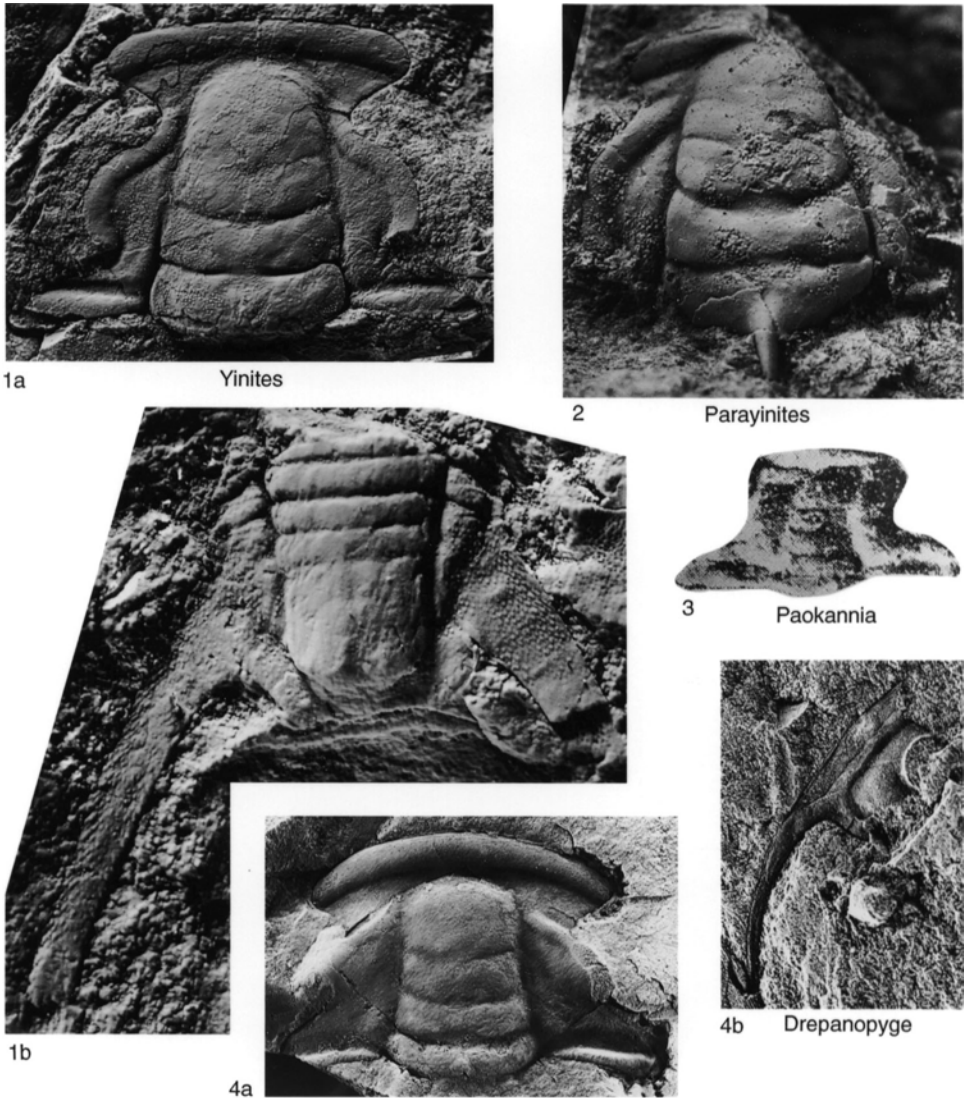
FIG. 285. Yinitidae (p. 446–448)

northwest Hupei (Baokang), holotype, cranidium, ×2 (Ho & Li, 1959).

Parapaokannia ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 198, 431 [**P. sichuanensis;* OD; holotype (W. ZHANG, LU, & others, 1980, pl. 56, fig. 6), 37890, NIGP, Nanjing]. Cranidium subtrapezoidal; glabella broad, long, tapering forward, with frontal lobe broadly rounded and 3 pairs of weak glabellar furrows; preglabellar field absent; occipital ring of uniform length (sag. and exs.); eye ridge stout; eye lobe of moderate length, situated at midlength of cranidium; anterior sections of facial su-

tures short, subparallel or slightly divergent; posterior area of fixigena broad (tr.) and long; librigena narrow, genal spine long. Thorax with 11 segments. Pygidium with prominent axial lobe; pleural field narrow, with 2 or 3 pleural furrows; doublure broadening posteriorly; border spines absent. *Lower Cambrian (lower Canglangpuan):* China (northern Sichuan), ?*Drepanuroides* Zone.——FIG. 286,*1a,b.* **P. sichuanensis,* northern Sichuan (Nanjiang); *a,* holotype, cranidium; *b,* paratype, incomplete dorsal exoskeleton, ×5 (W. Zhang, Lu, & others, 1980).
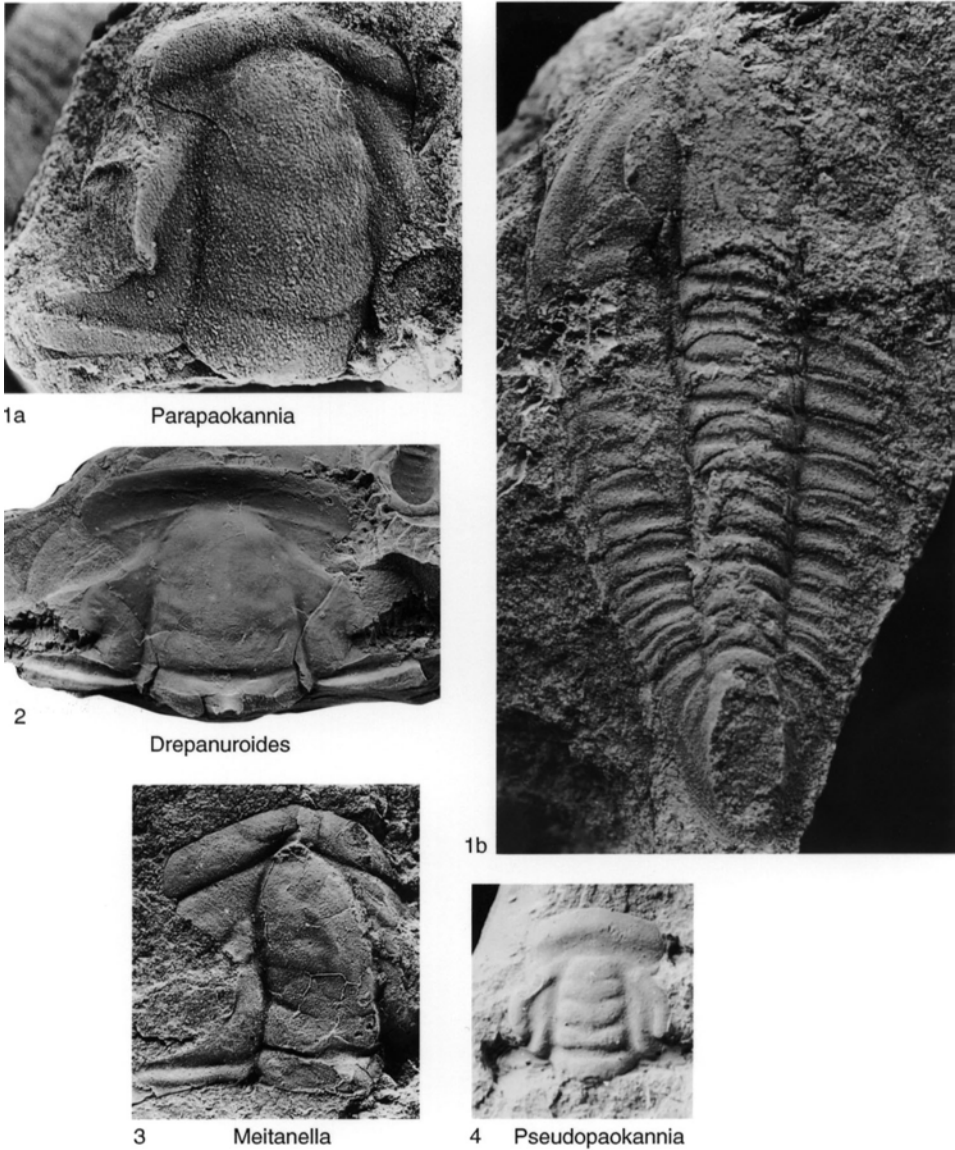
FIG. 286. Yinitidae (p. 446–449)

Parayinites Zhang & Lin in W. Zhang, Lu, & others, 1980, p. 209 [**P. spinosus;* OD; holotype (W. Zhang, Lu, & others, 1980, pl. 62, fig. 10), 37941, NIGP, Nanjing]. Differing from *Yinites* in having broader (tr.), conical glabella, longer eye lobe, large occipital spine, very small anterior area of fixigena, and shorter and less divergent anterior sections of facial sutures. Librigena, thorax, and pygidium unknown. *Lower Cambrian (Canglangpuan):* China (northern Guizhou), ?*Drepanuroides* Zone.——Fig.

285,*2.* **P. spinosus;* northern Guizhou (Yuqing), holotype, cranidium, ×4 (W. Zhang, Lu, & others, 1980).

Pseudopaokannia Yin in Yin & Li, 1978, p. 416 [**P. kaiyangensis;* OD; holotype (Yin & Li, 1978, pl. 149, fig. 2), Gt-087, SMNH, Shanghai]. Cranidium broad (tr.), short (sag.), and subtrapezoidal; anterior border gently convex and long (sag., exs.); glabella short (sag.), tapering forward, with frontal lobe well rounded; preglabellar field long (sag.) and

depressed; anterior area of fixigena broad (tr.); eye lobe long (exs.), its posterior tip reaching the level of occipital furrow; posterior area of fixigena narrow (tr.) and short (exs.). Librigena, thorax, and pygidium unknown. *Lower Cambrian (upper Canglangpuan):* China (northern Guizhou), *Palaeolenus* Zone.——Fig. 286,4. **P. kaiyangensis;* northern Guizhou (Kaiyang); holotype, cranidium, ×2 (Yin & Li, 1978).

Qingkouia Zhang, Lin, & Zhou in W. Zhang, Lu, & others, 1980, p. 190 [**Q. zhangyangouensis;* OD; holotype (W. Zhang, Lu, & others, 1980, pl. 53, fig. 2), 37862, NIGP, Nanjing] [=*Drepanuroides (Paradrepanuroides)* Zhao, Huang, & Mao in Zhao & others, 1984, p. 759 (type, *D. (P.) robusta*)]. Glabella broad, tapering forward, with 3 pairs of very weak glabellar furrows; occipital furrow broad (sag.) medially; occipital ring with small node; anterior sections of facial sutures strongly divergent; border narrow and convex; preglabellar field short (sag.); librigena with long genal spine. Thorax with 9 segments; each axial ring with a small median keel; pleural spines longer posteriorly. Pygidium large; axial lobe with 4 to 5 rings and terminal piece; 5 pairs of broad pleural furrows, interpleural furrows narrow and very shallow; 6 pairs of large marginal spines. *Lower Cambrian (Canglangpuan):* China (northern Guizhou), ?*Drepanuroides* Zone.——Fig. 287,2a,b. **Q. zhangyangouensis; a,* holotype, incomplete exoskeleton, ×0.95; *b,* complete exoskeleton, ×0.95 (W. Zhang, Lu, & others, 1980).

Yunnanaspidella W. Chang, 1966, p. 159, 169 [**Y. spinocaudata;* OD; holotype (W. Chang, 1966, pl. 4, fig. 7), 18177, NIGP, Nanjing]. Similar to *Yunnanaspis,* but preglabellar field shorter (sag.) or absent, eye lobe longer, and posterior area of fixigena shorter (exs.). Thorax with 13 segments. Pygidium with 4 pairs of relatively small border spines and a 5th pair of long, outwardly and backwardly directed spines. *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan), *Drepanuroides* Zone.——Fig. 288a,b. **Y. spinocaudata,* eastern Yunnan (Malong); *a,* incomplete thorax and pygidium, ×8; *b,* topotype, incomplete exoskeleton, ×2 (W. Chang, 1966).

Yunnanaspis W. Chang, 1966, p. 159, 169 [**Y. bilongispinus;* OD; holotype (W. Chang, 1966, pl. 4, fig. 4), 18174, NIGP, Nanjing]. Glabella broad, tapering forward, frontal lobe well rounded, and glabellar furrows obsolete; border furrow shallow; preglabellar field short (sag.); eye ridge distinct; eye lobe small; posterior area of fixigena broad (tr.) and long; librigena with long genal spine. Thorax with 9 segments. Pygidium with 5 rings, large terminal piece, 5 pleurae ending with 5 pairs of short border spines, and a rear pair of long, backward-directed spines. *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan), *Yunnanaspis* Zone.——Fig. 287,1a,b. **Y. bilongispinus,* eastern Yunnan (Malong); *a,* holotype, pygidium, ×4.7; *b,* incomplete dorsal exoskeleton, ×4.7 (W. Chang, 1966).

Family MAYIELLIDAE Chang, 1966

[Mayiellidae W. Chang, 1966, p. 162]

Cranidium quadrate or subquadrate; glabella cylindrical or broadly conical, with or without glabellar furrows; preglabellar field absent or short (sag.); anterior sections of facial sutures short, subparallel to slightly divergent. Thorax with 10 segments. Pygidium medium sized; axial lobe cylindrical and long (sag.), with 1 to 4 axial tubercles and 3 pairs of pleural furrows. *Lower Cambrian.*

Mayiella W. Chang, 1966, p. 162, 170 [**M. tuberculata;* OD; holotype (W. Chang, 1966, pl. 5, fig. 5), 18182, NIGP, Nanjing]. Cranidium trapezoidal, with rounded front; glabella tapering forward, frontal lobe rounded; glabellar furrows absent; occipital furrow shallow; occipital ring of uniform length (sag. and exs.); anterior border furrow shallow and long (sag. and exs.), within which a row of small tubercles may be present; anterior border gently convex, longer sagittally; eye lobe long and arcuate distally; librigena unknown. Thorax with 10 segments, articulating facets well developed on the anterior 3 or 4 thoracic pleurae; pleural spines short. Pygidium semielliptical; border flat; no border spines. *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan), *Drepanuroides* Zone.——Fig. 289,1. **M tuberculata,* eastern Yunnan (Malong); holotype, cranidium, thorax, and pygidium, ×6 (W. Chang, 1966).

Qiaodiella Zhang, Lin, & Zhou in W. Zhang, Lu, & others, 1980, p. 222 [**Q. qiaodiensis;* OD; holotype (W. Zhang, Lu, & others, 1980, pl. 68, fig. 10), 37995, NIGP, Nanjing]. Cranidium subtrapezoidal, with strongly arched front; preglabellar area inflated, preglabellar field and anterior border undivided; anterior border furrow long (sag. and exs.) and shallow, curving adaxially to meet extremity of preglabellar furrow. Glabella convex, slightly tapering toward the front, anterior margin of frontal lobe flat, rounded, with 3 pairs of weak glabellar furrows; posterior border furrow and occipital furrow long (sag. and exs.) and deep; anterior section of facial suture subparallel. Librigena, thorax, and pygidium unknown. *Lower Cambrian (lower Canglangpuan):* China (northern Guizhou), *Drepanuroides* Zone.——Fig. 289,3. **Q. qiaodiensis,* northern Guizhou (Yuqing); holotype, cranidium, ×4 (W. Zhang, Lu, & others, 1980).

Qiaotingaspis W. Chang, 1966, p. 163 [**Q. quadratus;* OD; holotype (W. Chang, 1966, pl. 6, fig. 7), 18190, NIGP, Nanjing]. Cranidium quadrate; glabella oblong, with 3 pairs of weak glabellar furrows, a pair of pits in front of anterolateral margin; anterior border furrow shallow, lacking row of tubercles seen in *Mayiella;* anterior border long (sag. and

FIG. 287. Yinitidae (p. 449)

exs.), of uniform length and gently convex; eye lobe
small. Librigena, thorax, and pygidium unknown.
Lower Cambrian (lower Canglangpuan): China

(northern Sichuan), *Drepanuroides* Zone.——FIG.
289,*2. *Q. quadratus;* northern Sichuan (Nanjiang);
holotype, cranidium, ×3 (W. Chang, 1966).

Family GIGANTOPYGIDAE
Harrington, 1959

[Gigantopygidae HARRINGTON in MOORE, 1959, p. 204]

Glabella tapering slightly forward, with 3 or 4 pairs of glabellar furrows; preglabellar field absent or present; anterior section of facial sutures short, subparallel or moderately divergent; posterior areas of fixigenae wide (tr.) and narrow or long (exs.); librigena with genal spine. Thorax with 14 to 16 segments and long pleural spines. Pygidial axial lobe composed of 1 to 4 rings and large or small terminal piece; pleural regions produced backward into 1 or 2 pairs of spines. *Lower Cambrian.*

Subfamily GIGANTOPYGINAE
Harrington, 1959

[*nom. transl.* ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 81, *ex* Gigantopygidae HARRINGTON in MOORE, 1959, p. 204]

Glabella subtruncate in front, with 4 pairs of glabellar furrows; occipital ring of uniform length (sag. and exs.); preglabellar field absent; anterior border long (sag. and exs.), flat; anterior pit present, transversely elongated; eye ridge long, curving forward beside frontal and anterior glabellar lobes; eye lobe strongly arcuate, extending to level of occipital furrow; anterior sections of facial sutures moderately divergent, subparallel across border; librigenae wide. Thorax with 14 (or ?15) segments. Pygidium long, narrow; axis short, with 3 rings. *Lower Cambrian.*

Gigantopygus HUPÉ, 1953a, p. 181 [**G. papillatus;* OD; holotype (HUPÉ, 1953a, pl. 7, fig. 2), G76 (R50882), MNHN, Paris]. Anterior (S4) lateral glabellar furrows faint; S2 and S1 almost transglabellar; occipital furrow discontinuous at midpoint; palpebral area of fixigena wide (tr.); posterior area of fixigena short (exs.) and broad (tr.). *Lower Cambrian:* Spain, Morocco.——FIG. 290,*3.* **G. papillatus,* Morocco, *Longianda* and *Gigantopygus* Zones; holotype, cranidium, ×0.9 (Hupé, 1953a).

Subfamily YILIANGELLINAE
Zhang & Lin, 1980

[Yiliangellinae ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 211]

Glabella with 3 pairs of glabellar furrows; eye lobe medium-sized or slightly longer; posterior areas of fixigenae broad (tr.) and long (exs.). Thorax with 14 to 16 segments.
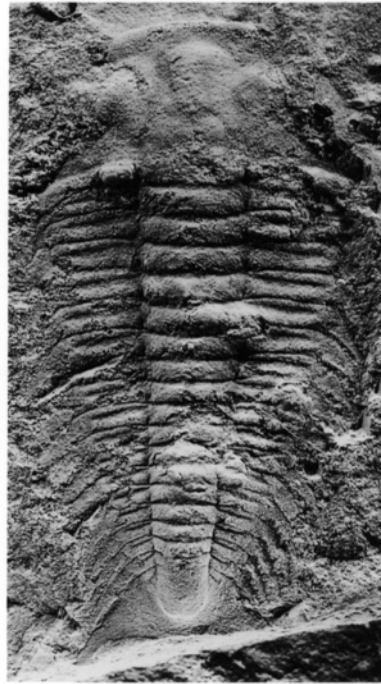
Yunnanaspidella

FIG. 288. Yinitidae (p. 449)

Axial lobe of pygidium with 1 to 4 rings and long (sag.) or small terminal piece; posterior margin deeply notched, or rounded, between inner pair of border spines. *Lower Cambrian.*
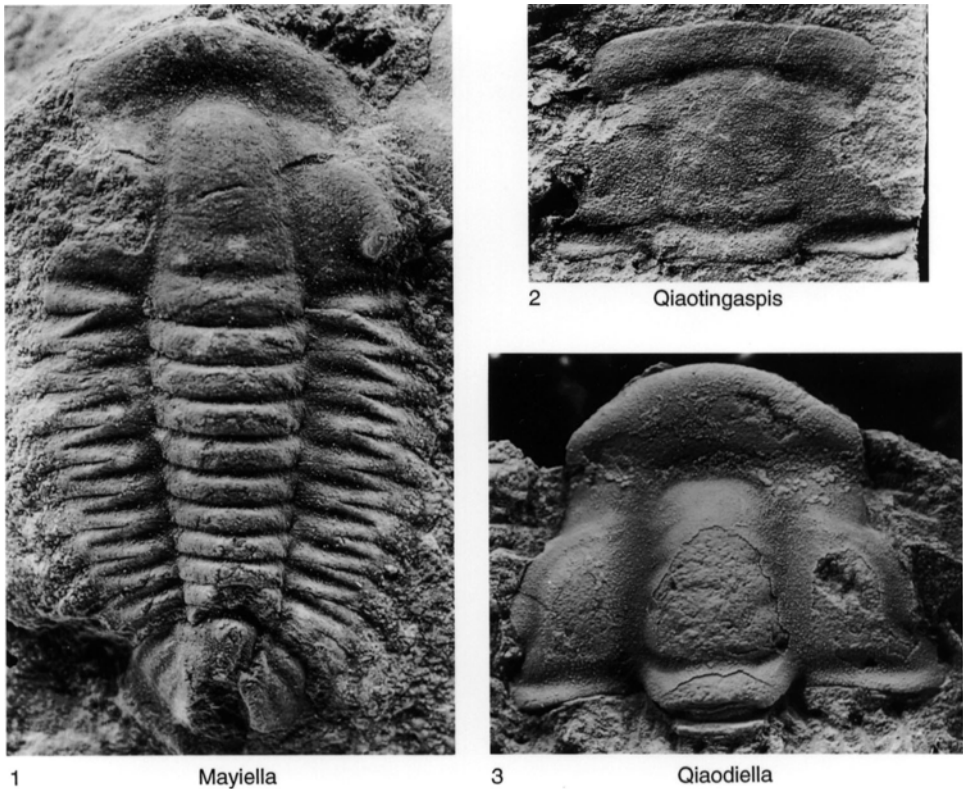
FIG. 289. Mayiellidae (p. 449–450)

Yiliangella W. Chang, 1966, p. 161 [**Y. forficula;* OD; holotype (W. Chang, 1966, pl. 6, fig. 1), 18184, NIGP, Nanjing] [=*Palaeoaspis* Yang, 1981, p. 78 (type, *P. barbutus;* OD)]. Glabella tapering forward, with frontal lobe rounded; preglabellar field absent; eye lobe relatively small; anterior cranidial border short (sag. and exs.) and convex. Thorax with 16 segments. Pygidium small, with 2 pairs of pygidial spines; pygidial axial lobe with an anterior ring and long (sag.), cylindrical terminal piece. Hypostome subtriangular, medial body ovate, border furrow well developed anterolaterally, posterior margin with 11 or 12 small spines. *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan, western Sichuan), *Yiliangella* Zone.——FIG. 290,*2. *Y. forficula,* eastern Yunnan (Yiliang); holotype, cephalon and thorax, ×2.7 (W. Chang, 1966).

Yiliangellina W. Chang, 1966, p. 162, 170 [**Y. formosa;* OD; holotype (W. Chang, 1966, pl. 6, fig. 4), 18187, NIGP, Nanjing]. Differs from *Yiliangella* in having broad, smooth glabella and long (sag.), slightly depressed preglabellar field, a longer eye lobe, and shorter (exs.) posterior area of fixigena. *Lower Cambrian (lower Canglangpuan):* China (eastern Yunnan), *Drepanuroides* Zone.——FIG.

290,*1. *Y. formosa,* eastern Yunnan (Yiliang); holotype, cranidium, thorax, and pygidium, ×6 (W. Chang, 1966).

Zhangshania Li & Zhang in S. Li, Kang, & Zhang, 1990, p. 44 [**Z. typica;* OD; holotype (S. Li, Kang, & Zhang, 1990, pl. 2, fig. 1), Ly-312, CIGMR, Chengdu]. Similar to *Yiliangella,* but having 14 thoracic segments, relatively larger pygidium with 4 axial rings and small terminal piece, pair of lateral pygidial spines, and broad doublure. Posterior margin of hypostome rounded, without marginal spines. *Lower Cambrian (lower Canglangpuan):* China (western Sichuan: Leshan), *Yiliangella* Zone.——FIG. 290,*4. *Z. typica;* complete dorsal exoskeleton, holotype, ×1.8 (S. Li, Kang, & Zhang, 1990).

Family SAUKIANDIDAE Hupé, 1953

[Saukiandidae Hupé, 1953a, p. 152]

Glabella long, cylindrical or constricted posteriorly, with 3 pairs of lateral glabellar furrows; occipital furrow deep; preglabellar field short (sag.) or absent; anterior border
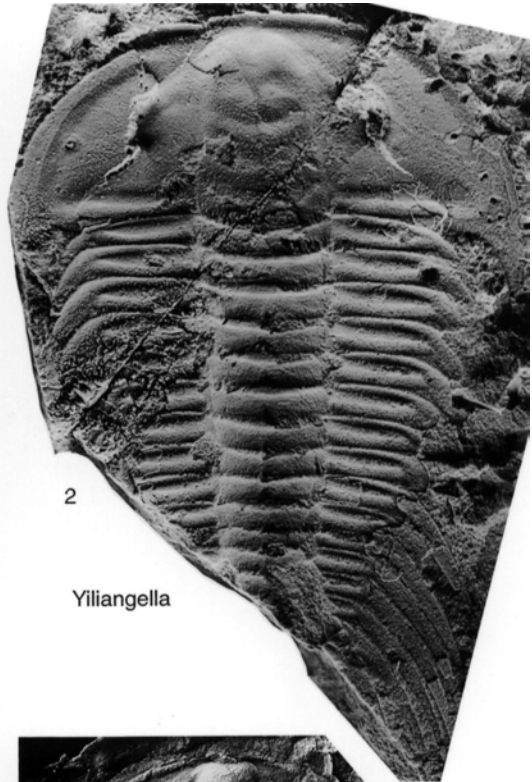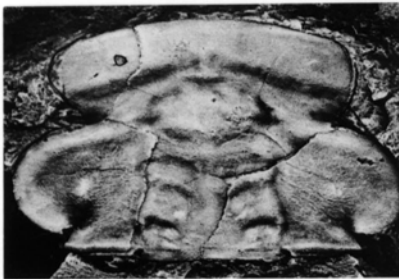
FIG. 290. Gigantopygidae (p. 451–452)

wide; anterior sections of facial sutures moderately divergent to border furrow, gently curved outward across border; eye lobe arcuate, long, reaching level of occipital furrow; palpebral area of fixigena swollen posteriorly; librigena wide. Thorax with 12 to 15 segments; fulcrum proximal. Pygidium with more segments and larger than in Redlichiidae; pygidial border well developed. *Lower Cambrian.*

Subfamily SAUKIANDINAE Hupé, 1953

[*nom. transl.* W. CHANG, herein, *ex* Saukiandidae HUPÉ, 1953a, p. 152]

Glabellar furrow S3 commonly obsolete but short and oblique backward when present; S2 similar to S3; S1 transglabellar, oblique backward abaxially and normal to axis medially; occipital furrow deep. Thorax with 15 segments. Border of pygidium very wide, flat. Surface finely granulose. *Lower Cambrian.*

Saukianda RICHTER & RICHTER, 1940, p. 23 [*S. andalusiae;* OD; holotype (RICHTER & RICHTER, 1940, pl. 1, fig. 1), 1034r, SMF, Frankfurt am Main]. Glabella subtruncate to slightly rounded in front; S3 obsolete; S2 very short; S1 deep, broad; occipital furrow slightly curved backwards; occipital ring of uniform length (sag. and exs.), with short median spine; preglabellar field short (sag. and exs.); genal spines advanced. Pygidium rounded, with wide axis containing 1 to 2 rings and broadly rounded terminal axial piece; pleural fields narrow, connected behind axis; posterior margin slightly inclined. *Lower Cambrian:* Spain, Morocco.
  S. (Saukianda). Glabella subtruncate in front. Genal spines of medium size, clearly differentiated from border. *Lower Cambrian:* Spain, Morocco.——FIG. 291,*2a,b.* *S. (S.) andalusiae* RICHTER & RICHTER, Spain (Alanís, Andalusia); *a,* holotype, cranidium, dorsal view, ×1.7 (new); *b,* nearly complete dorsal shield, PMO A27.035, ×1.36 (Henningsmoen, 1957b, pl. 36, fig. 2).
  S. (Pseudosaukianda) HUPÉ, 1953a, p. 196 [*P. lata;* OD; holotype (HUPÉ, 1953a, pl. 8, fig. 7), G236 (R50867), MNHN, Paris]. Glabella short, broadly conical, and rounded in front; S2 and S3 short; occipital furrow with slight forward bend; genal spine not advanced but a short and very stout continuation of border. *Lower Cambrian:* Morocco, *Longianda* and *Gigantopygus* Zones.——FIG. 291,*1.* *S. (P.) lata* (HUPÉ); holotype, cephalon and incomplete thorax, ×2.1 (Hupé, 1953a).
Longianda HUPÉ, 1953a, p. 201 [*Callavia termieri* NELTNER & POCTEY, 1949, pl. 1, fig 2–4; OD; holotype (HUPÉ, 1953a, pl. 8, fig. 2), G68 (R50913),

MNHN, Paris]. Differs from *Saukianda* in having longer and narrower glabella constricted at level of S1 and rounded in front, occipital furrow bent forward at middle, no occipital spine. Preglabellar field absent; anterior pit present. Thorax with backward curvature of pleural spines progressively increasing posteriorly. Pygidium with 3 axial rings, short terminal axial piece, and 4 ribs. *Lower Cambrian:* Spain; Morocco, *Longianda* and *Gigantopygus* Zones.——FIG. 291,*3.* *L. termieri* (NELTNER & POCTEY), Morocco (Issafène); holotype, incomplete cephalon and thorax, ×1.7 (Hupé, 1953a).

Subfamily DESPUJOLSIINAE Harrington, 1959

[*nom. transl.* W. CHANG, 1966, p. 148, *ex* Despujolsiidae HARRINGTON in MOORE, 1959, p. 204]

Cranidium long; glabella long, constricted at level of L2, with 3 pairs of faint, short, lateral glabellar furrows separated from axial furrow; occipital ring wide (sag.); preglabellar field as long (sag.) as anterior border; palpebro-ocular ridge arcuate, expanded in front, tapering backward, extending from anterolateral corner of glabella to level of occipital furrow; anterior sections of facial sutures moderately divergent. Thorax narrow, with 14 segments; pleurae narrower than axis and spinose, with 11th segment macrospinose and fulcrum distal. Pygidium small, with 4 pairs of tiny marginal spines; axis narrow, unsegmented; pleural regions smooth, wide. *Lower Cambrian.*

Despujolsia NELTNER & POCTEY, 1949, p. 78 [*D. rochi;* OD; holotype (NELTNER & POCTEY, 1949, pl. 2, fig. 3; HUPÉ, 1953a, pl. 8, fig. 3–4), G53 (R50820), MNHN, Paris]. Pseudopalpebral furrow present. Posterior area of fixigena triangular. First 6 thoracic pleurae ending in short, subequal spines; spines increasing rapidly in size between 7th and 11th pleurae; last pleurae having short spines. *Lower Cambrian:* Morocco (Amouslek), ?*Daguinaspis-Resserops* Zone.——FIG. 292. *D. rochi;* holotype, incomplete exoskeleton, ×3 (Hupé, 1953a).

Subfamily RESSEROPINAE Chang, 1966

[Resseropinae W. CHANG, 1966, p. 148]

Glabella tapering slightly forward; preglabellar field moderately long (sag. and exs.), short, or absent; posterior extremity of palpebral lobe distant from axial furrow; advanced genal spine. Thorax with 12 to 14
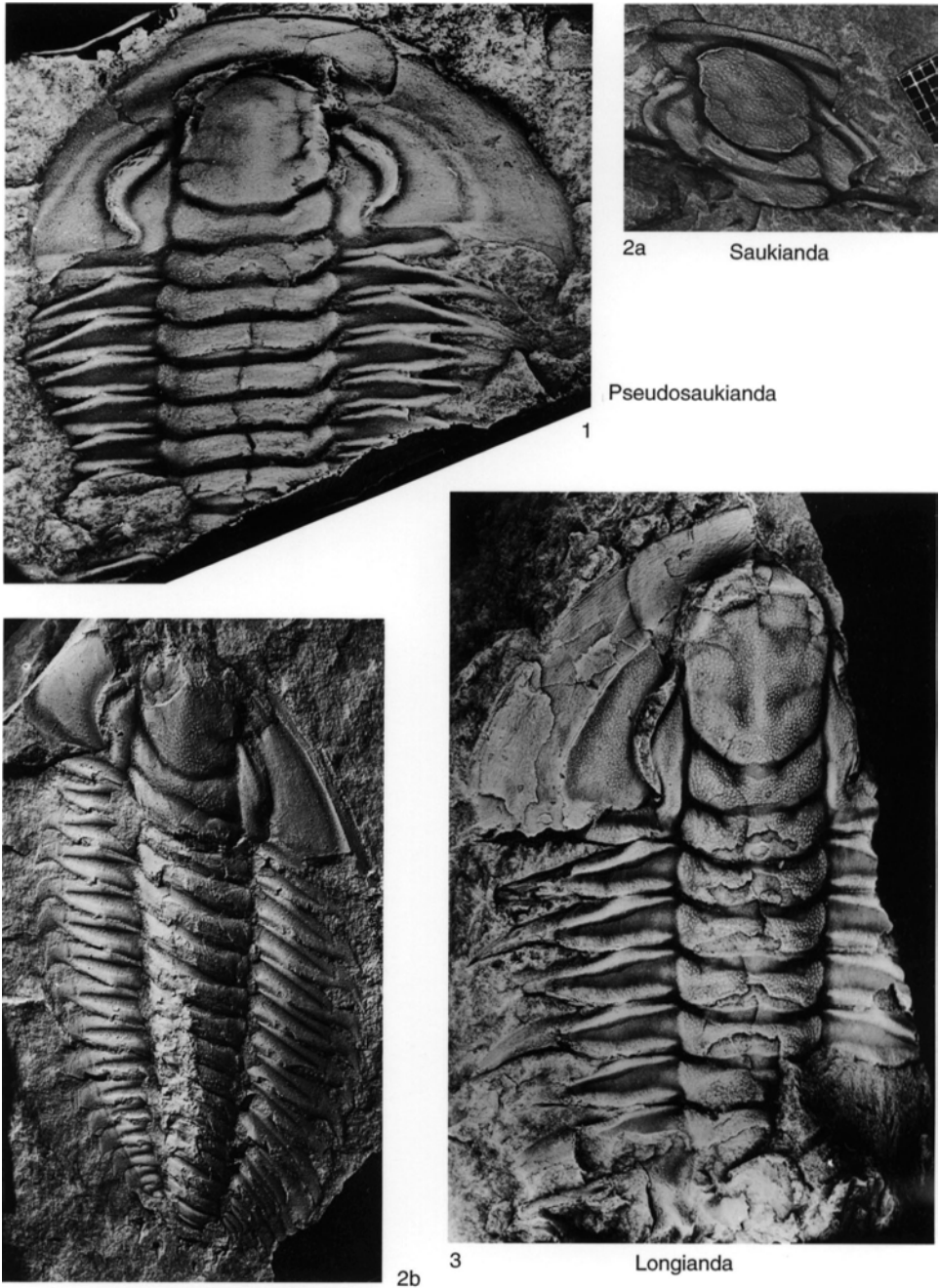
Fig. 291. Saukiandidae (p. 454)

segments; 9th or 11th segment macro-spinose, or macrospinose segment absent. Pygidium parabolical; axis broad, conical, with 3 to 10 rings; pleural regions with 2 to 8 pleurae, not delimited by border furrow. *Lower Cambrian.*
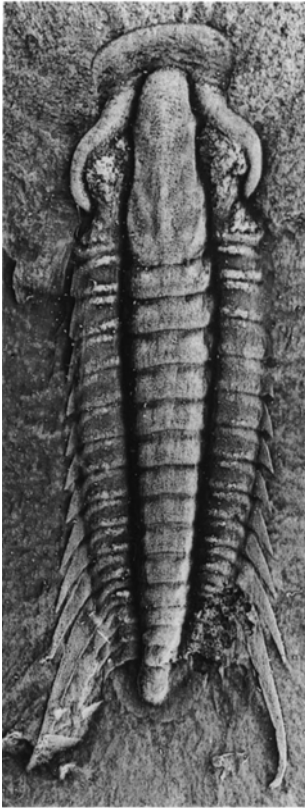
Despujolsia

FIG. 292. Saukiandidae (p. 454)

Perrector RICHTER & RICHTER, 1940, p. 30 [*P. perrectus;* OD; holotype (RICHTER & RICHTER, 1940, pl. 2, fig. 23), X1145a, SMF, Frankfurt am Main] [=*Resserops (Rawops)* HUPÉ, 1953a, p. 173 (type, *Resserops dubius;* OD)]. Lateral glabellar and occipital furrows discontinuous; preglabellar field absent; genal spine well advanced. Pygidium relatively large; both axis and pleural regions multisegmented. *Lower Cambrian:* Spain, Morocco.

P. (**Perrector**). Lateral glabellar and occipital furrows slightly oblique backward; eye lobe reaching level of midlength of occipital ring. Thorax with 12? segments; macrospinose segment absent; pleurae slightly narrower than axis. Pygidium with 6 or 7 axial rings, large terminal axial piece, and 6 to 7 pleurae. *Lower Cambrian:* Spain.——FIG. 293,*5a,b.* *P. (P.) perrectus,* Andalusia (Alanis); *a,* holotype, dorsal view of cranidium, ×3; *b,* paratype, dorsal view of pygidium, ×3 (new).

P. (**Resserops**) RICHTER & RICHTER, 1940, p. 33 [*P. (R.) resserianus;* OD; holotype (RICHTER & RICHTER, 1940, pl. 2, fig. 37), X1140a, SMF, Frankfurt am Main]. Similar to *P. (Perrector)* but having stouter genal spines and macrospinose 9th thoracic pleura. *Lower Cambrian:* Spain.——FIG. 293,*2.* *P. (R.) resserianus* RICHTER & RICHTER; reconstruction of exoskeleton, ×3 (Richter & Richter, 1940).

P. (**Richterops**) HUPÉ, 1953a, p. 173 [*Resserops (Richterops) falloti* HUPÉ, 1953a, p. 176; OD; holotype (HUPÉ, 1953a, p. 346, pl. 6, fig. 1), G74 (R50854), MNHN, Paris (on p. 177 HUPÉ also referred to MNHN G202 as the holotype)] [=*Marsaisia* HUPÉ, 1953a, p. 149 (type, *M. robauxi;* OD)]. Differs from *P. (Perrector)* in having 14 thoracic segments, with 11th segment macrospinose. *Lower Cambrian:* Morocco, *Daguinaspis* and *Resserops* Zones.——FIG. 293,*3.* *P. (R.) falloti* (HUPÉ), Morocco (Tazemmourt); exoskeleton, ×2 (Hupé, 1953a).

Australaspis PALMER & GATEHOUSE, 1972, p. 12 [*A. magnus;* OD; holotype (PALMER & GATEHOUSE, 1972, pl. 1, fig. 2), 169058, USNM, Washington, D.C.]. Glabella bluntly rounded anteriorly, reaching to anterior border; eye lobe stout, elongate, strongly curved; palpebro-ocular ridge bifurcated toward glabella with anterior ridge continuous around and abaxial to anterolateral corner of glabella; posterior area of fixigena moderately long, slender; librigena with broad-based genal spine continuing curvature of lateral margin. Pygidium with broad axis reaching nearly to posterior margin and 4 narrow axial rings; pleural regions less than half width of axis; margin smoothly curved. *Lower Cambrian:* Antarctica.——FIG. 294,*2a–c.* *A. magnus; a,* holotype, boulders from moraine on Mount Spann, cranidium, ×2; *b,* paratype, cranidium, ×2; *c,* paratype, pygidium, ×2 (Palmer & Gatehouse, 1972).

Clariondia HUPÉ, 1953a, p. 188 [*C. chazani;* OD; holotype (HUPÉ, 1953a, p. 187, fig. 44.1,3), G54, MNHN, Paris]. Glabella narrow; lateral glabellar and occipital furrows oblique backward, discontinuous medially; posterior edge of occipital ring semicircular; preglabellar field moderately wide; eye lobe reaching level of occipital furrow. Pygidium with 5 axial rings, short terminal axial piece, and 5 pleurae. *Lower Cambrian:* Morocco, *Antatlasia* Zone. [The type species of this genus is based on HUPÉ's description and a line drawing. G. GEYER reports that no specimens have been traced, and the exact type locality is unknown.]——FIG. 294,*3a,b.* *C. chazani; a,* holotype, cranidium, ×2; *b,* paratype, pygidium, ×3 (Hupé, 1953a).

Dolerolichia SDZUY, 1962a, p. 1089 [*D. pretiosa;* OD; holotype (SDZUY, 1962a, pl. 1, fig. 1), X151a, SMF, Frankfurt am Main]. Anterior glabellar furrows normal to axis; occipital furrow and S1 well-marked laterally, slightly bent backward; all furrows disconnected medially; frontal lobe connected with border by wide (tr.) plectrum; preglabellar field narrow, with facial lines; palpebral lobe long, nearly reaching posterior border furrow; posterior facial suture strongly divergent. Pygidium of roundish shape; axis with 2 rings and large terminal piece; pleural field with 4 or 5 ribs. *Lower Cambrian:*
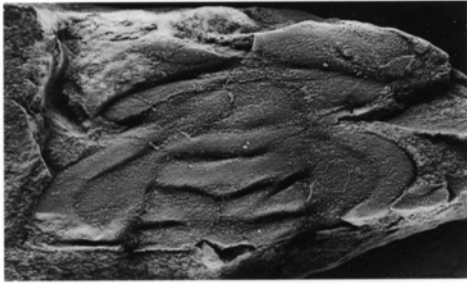
1   Eops
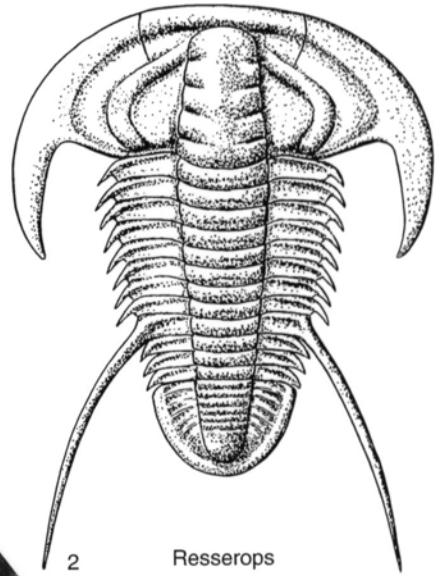
2   Resserops
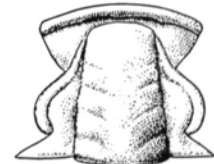
4   Pareops

3   Richterops

5a

5b   Perrector

FIG. 293. Saukiandidae (p. 456–458)
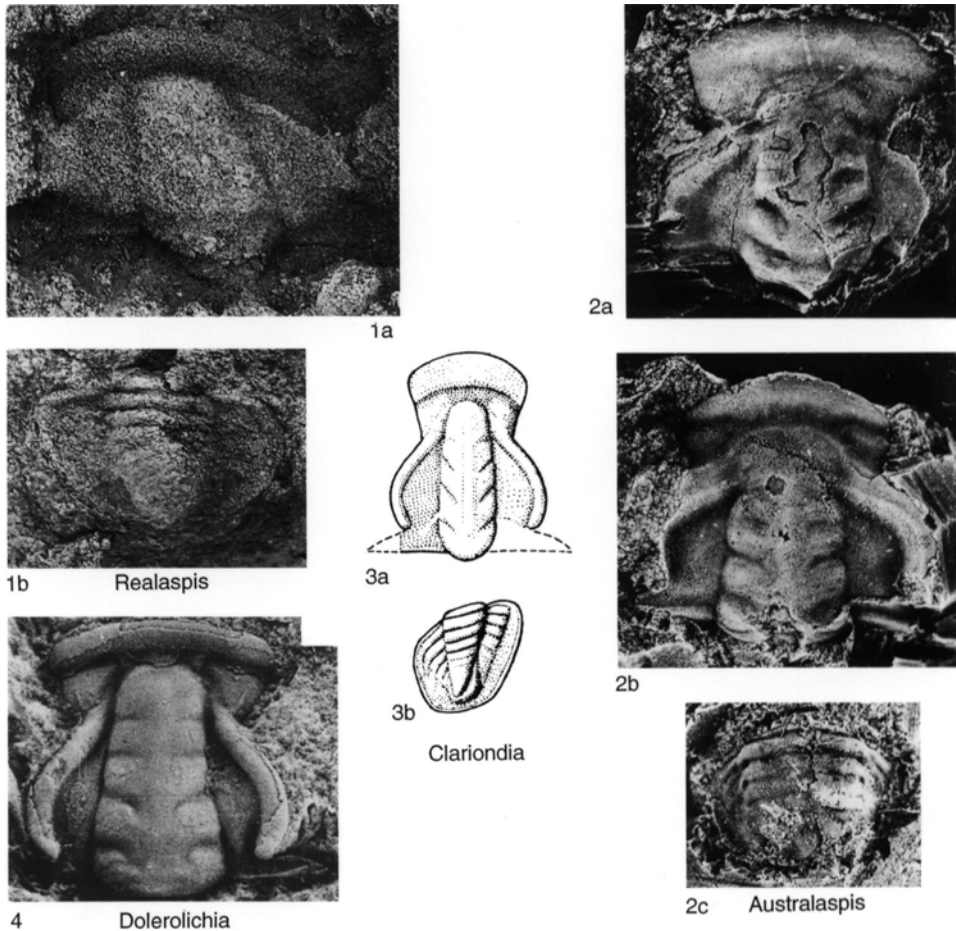
FIG. 294. Saukiandidae (p. 456–458)

Germany.——FIG. 294,*4. *D. pretiosa,* Germany (Doberlug); holotype, cranidium, ×3 (Sdzuy, 1962a).

Eops RICHTER & RICHTER, 1940, p. 36 [*E. eo;* OD; holotype (RICHTER & RICHTER, 1940, pl. 2, fig. 45), X1000b, SMF, Frankfurt am Main]. Glabella with S2 and S3 discontinuous medially; S1 chevron shaped; preglabellar field moderately long (sag.); occipital node or spine absent; anterior border long (sag. and exs.); anterior sections of facial sutures diverging at about 45°. *Lower Cambrian:* Spain, ?Morocco.——FIG. 293,*1. *E. eo,* Andalusia (Alanís); holotype, dorsal view of cranidium, ×2.5 (photographs courtesy of G. Geyer).

Pareops HUPÉ, 1953a, p. 180 [*P. transitans;* OD; holotype (HUPÉ, 1953a, p. 180, fig. 42), G315, repository unknown]. Glabella anteriorly truncate; lateral glabellar furrows slightly directed backwards, disconnected medially; occipital furrow nearly completely effaced medially; occipital ring straight; an-

terior border of moderate width. *Lower Cambrian:* Morocco, *Antatlasia* Zone. [The type species of this genus is based on HUPÉ's description and a line drawing. G. GEYER reports that no specimens have been traced, and the exact type locality is unknown.]——FIG. 293,*4. *P. transitans;* holotype, cranidium, ×1 (Hupé, 1953a).

Realaspis SDZUY, 1961, p. 535 [*R. strenoides;* OD; holotype (SDZUY, 1961, pl. 4, fig. 6), L3082, UMU, Münster]. S1 and S2 directed obliquely backwards; S3 very faint; palpebral lobe less than one-third as long as cranidium, with posterior end widely distant from posterior border furrow; eye ridge faint; preglabellar field very short. Librigena with strong genal spine. Pygidium semielliptical, with 3 axial rings and 2 to 3 ribs. *Lower Cambrian:* Spain.——FIG. 294,*1a,b. *R. strenoides,* Spain (Los Cortijos); *a,* holotype, dorsal view of cranidium, ×3.5; *b,* dorsal view of pygidium, ×3 (photographs courtesy of G. Geyer).

Family METADOXIDIDAE
Whitehouse, 1939

[Metadoxididae WHITEHOUSE, 1939, p. 196] [=Anadoxididae NICOSIA & RASETTI, 1970, p. 9]

Glabella strongly tapering forward; anterior and palpebral areas of fixigenae wide, with well-defined eye ridge and relatively small eye lobe. Thorax with 12 to 22 segments and wide (exs.) pleural furrows; pleural spines present or absent. Pygidium small. *Lower Cambrian.*

Metadoxides BORNEMANN, 1891, p. 462 [**Paradoxides torosus* MENEGHINI, 1888, p. 20; SD VOGDES, 1925, p. 105; =*P. armatus* MENEGHINI, 1881, p. 307; lectotype and paratype (MENEGHINI, 1888, pl. 2, fig. 1–2; pl. 3, fig. 4; SD NICOSIA & RASETTI, 1970, p. 9), SG 19 (lectotype), SG 20–21 (paratype); lectotype for *Paradoxides armatus* MENEGHINI, 1881, p. 307 (NICOSIA & RASETTI, 1970, p. 10, pl. 2, fig. 4; SD RASETTI, 1972, p. 61), 17, SG, Rome] [=*Anadoxides* MATTHEW, 1899b, p. 142 (type, *P. armatus* MENEGHINI, 1881, p. 307; SD VOGDES, 1925, p. 105)]. Cephalon broad (tr.), cephalic width (tr.) about 3 times length (sag.). Cranidium broad (tr.), subtrapezoidal in outline. Glabella rounded in front, reaching anterior border; anterior area of fixigena broad (tr.) and short (exs.); eye ridge long, extending outward and backward; ocular striga distinct proximally; eye lobe small or medium-sized; palpebral area of fixigena as wide as glabella; anterior section of facial sutures subparallel. Librigena wide; border flat, extending into a stout and very short genal spine. Thorax with 22 segments; axial node present on at least some of axial rings; pleurae without spines. Pygidium subtriangular; axis wider than pleural regions, almost reaching posterior margin; with few, faint pleural and interpleural furrows; border indistinct. Surface finely granulose. *Lower Cambrian:* China; Spain; ?Siberia; Italy (Sardinia), *Dolerolenus courtessolei* to *D. zoppii* Zone.——FIG. 295,*1a,b.* **M. armatus* (MENEGHINI), *D. zoppii* Zone, Sardinia; *a,* lectotype, cranidium and incomplete thorax, ×1.45 (Nicosia & Rasetti, 1970); *b,* dorsal exoskeleton, ×1.45 (Pillola, 1991).

?Churkinia PALMER, 1968, p. 39 [**C. yukonensis;* OD; holotype (PALMER, 1968, pl. 1, fig. 7), 146649, USNM, Washington, D.C.]. Cranidium subtrapezoidal; glabella with 3 pairs of transglabellar furrows; L1 divided into a median and 2 lateral lobes; anterior sections of facial sutures subparallel; facial line oblique; anterior ends of eye lobes widely separated from glabella; eye lobe relatively short, terminating opposite S1; posterior area of fixigenae broad (tr.) and long (exs.). Thorax with slender pleural spine developed only from anterior pleural band. Pygidium small; axis broad, with 2 axial rings and bilobed terminal piece. Hypostome elongately ovate. *Lower Cambrian:* USA (Alaska).——FIG. 295,*2a–d.* **C. yukonensis; a,* holotype, cranidium, ×2.9; *b,* librigena, ×2.9; *c,* pygidium, ×3.88; *d,* hypostome, ×4.85 (Palmer, 1968).

Enantiaspis RASETTI, 1972, p. 69 [**Ptychoparia enantiopa* BORNEMANN, 1891, p. 422; OD; lectotype (BORNEMANN, 1891, pl. 39, fig. 14; SD RASETTI, 1972, pl. 11, fig. 1), specimen number not recorded, MLU, Halle]. Glabella with 3 pairs of broad, shallow, transglabellar furrows; eye ridge directed forward from axial furrow, so that anterior end of palpebral lobe is farther forward than front end of glabella; palpebral lobe semicircular, posterior end opposite S2; anterior border of cranidium almost straight. Librigena with sharp genal angle; border almost flat. Thorax with 16? segments; pleural terminations spinelike. Pygidium with long, parallel-sided axis having a posterior median notch; postaxial portion with a slight median notch; posterior margin ending in a pair of short spines. *Lower Cambrian:* Italy (Sardinia), *Dolerolenus longioculatus* Zone.——FIG. 296,*1.* **E. enantiopa* (BORNEMANN), Sardinia (Canalgrande); lectotype, dorsal view of cranidium, ×1.5 (photograph courtesy of G. Geyer).

Fuminaspis ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 172 [**Metadoxides yunnanensis* W. CHANG & LIN in LU, CHANG, & others, 1974, p. 86; OD; holotype (LU, CHANG, & others, 1974, pl. 31, fig. 16), 37797, NIGP, Nanjing]. Similar to *Metadoxides* and *Hongshiyanaspis,* but with narrower (tr.) cranidium, shorter (tr.) and forwardly arcuate glabellar furrows, relatively longer eye lobe, narrow (tr.) palpebral area of fixigena, and lacking intergenal angle and fixigenal spine. Librigena, thorax, and pygidium unknown. *Lower Cambrian (Qiongzhusian):* China (eastern Yunnan), *Eoredlichia-Wutingaspis* Zone.——FIG. 295,*3.* **F. yunnanensis* (ZHANG & LIN), eastern Yunnan (Fumin); holotype, cranidium, ×4.85 (W. Zhang, Lu, & others, 1980).

Hongshiyanaspis ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 171 [**H. yiliangensis;* OD; holotype (W. ZHANG, LU, & others, 1980, pl. 45, fig. 6), 37799, NIGP, Nanjing]. Cranidium trapezoidal, with anterior border short (sag. and exs.) and convex; glabella frontal lobe well rounded, with 3 pairs of glabellar furrows; preglabellar field absent; occipital ring convex, broad in the middle, with a small median tubercle; eye ridge divided by ocular striga; eye lobe small; posterior area of fixigena broad (tr.) and long (exs.); posterior border with intergenal angle and distal fixigenal spine; anterior sections of facial sutures short and subparallel. Thorax having no less than 14 segments. Pygidium and librigena unknown. *Lower Cambrian (Qiongzhusian):* China (eastern Yunnan), *Eoredlichia-Wutingaspis* Zone.——FIG. 296,*4.* **H. yiliangensis,* eastern Yunnan (Yiliang); holotype, cranidium, ×8 (W. Zhang, Lu, & others, 1980).

Minusinella REPINA in KHALFIN, 1960, p. 174 [**M. lochmanae;* OD; holotype (REPINA in KHALFIN, 1960, pl. 19, fig. 11), 3356/267, CSGM, Novosibirsk] [=*Minusella* REPINA, 1966, p. 83, incorrect spelling]. Cranidium subtrapezoidal; glabella with 3
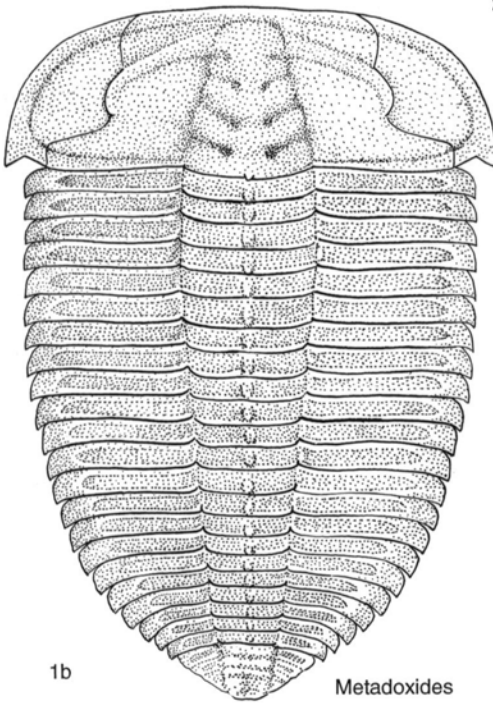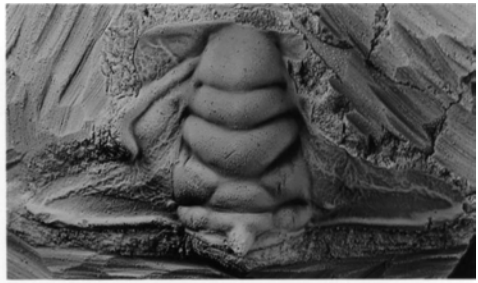
FIG. 295. Metadoxididae (p. 459)

pairs of glabellar furrows; S1 bifurcate proximally; occipital ring longer (sag.) medially; eye ridge long and stout; eye lobe medium-sized; preglabellar field absent; anterior border narrow (sag., exs.); anterior sections of facial sutures short, subparallel to slightly divergent. Librigena, thorax, and pygidium unknown. *Lower Cambrian:* Russia (Kuznetsk Alatau), *Resimopsis* Zone.——FIG. 296,*3.* **M. lochmanae;* holotype, cranidium, ×2.5 (Khalfin, 1960).

?Onaraspis ÖPIK, 1968, p. 151 [**O. somniurna;* OD; holotype (ÖPIK, 1968, pl. 19, fig. 3), CPC 7165, AGSO, Canberra]. Similar to *Metadoxides,* but hav-
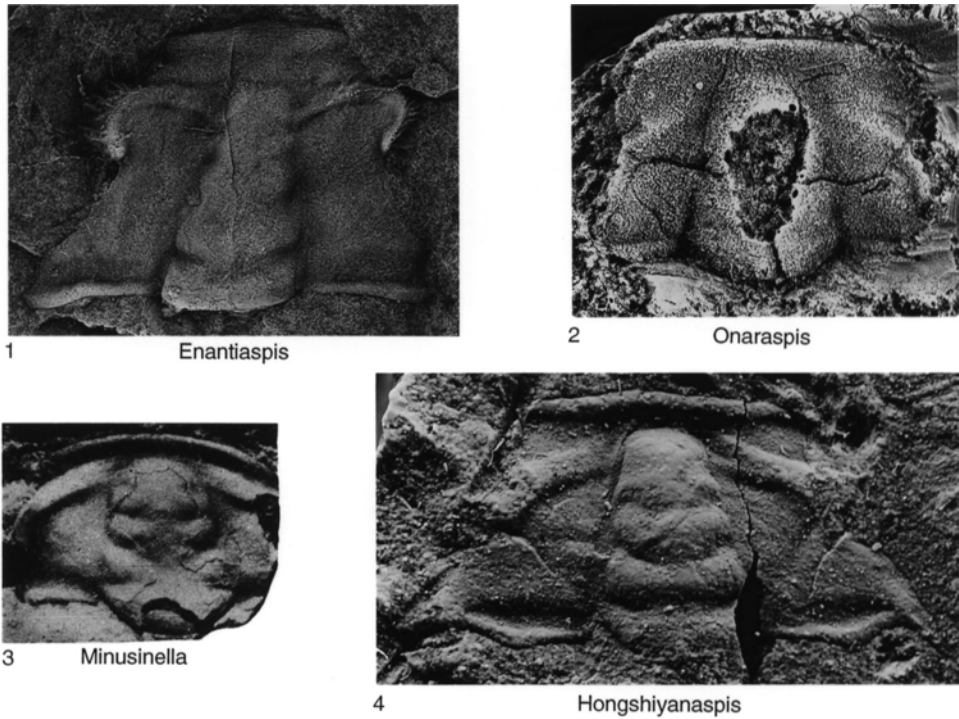
FIG. 296. Metadoxididae (p. 459–461)

ing fewer thoracic segments (12 in the type species), macropleural 11th segment, relatively larger pygidium with a concave flange, and slightly tapering glabella. *lower Middle Cambrian:* Australia (Northern Territory), *?Redlichia chinensis* Zone.——FIG. 296,*2.* *O. somniurna,* Northern Territory (Rodinga area); holotype, cranidium, ×2 (Öpik, 1968).

Family ABADIELLIDAE Hupé, 1953

[Abadiellidae HUPÉ, 1953a, p. 152]

Glabella conical to subovate, with 3 or 4 pairs of glabellar furrows directed obliquely backward, though S3 and S2 may be obsolete; occipital furrow slightly curved backward; occipital ring produced into stout median spine; preglabellar field long (sag.); anterior sections of facial sutures moderately divergent (generally less than 45°), proximal extremities distant from axial furrows; eye lobe arcuate, extending from anterolateral corner of glabella to level of anterior one-third of L1. Thorax with 15 to 17 segments. Pygidium small. *Lower Cambrian.*

Abadiella HUPÉ, 1953a, p. 204 [**A. bourgini;* OD; holotype (HUPÉ, 1953a, p. 204, fig. 45.2), G318, MNHN, Paris]. Cranidium subquadrate; glabella tapering forward, acutely rounded in front; frontal lobe small and subrounded; S3 shallow, short and indistinct; S2, S1 narrow, deep, and steeply oblique backward; occipital ring longer sagittally and produced backward into a strong and longer occipital spine; preglabellar field with low plectrum; anterior area of fixigena and facial line similar to that of *Eoredlichia;* anterior border gently convex, longer sagittally and gradually narrower (exs.) toward distal extremities; eye ridge and eye lobe stout, eye lobe longer (exs.) than in *Parabadiella,* its posterior tip reaching the midlength of L1; posterior area of fixigena long (exs.) and broad (tr.); fulcrum distinct. *Lower Cambrian:* Morocco (Ouijjane), *Daguinaspis* and *Resserops* Zone.——FIG. 297,*1.* **A. bourgini;* holotype, cranidium, ×6 (new).

Guangyuanaspis CHANG & QIAN in LU, CHANG, & others, 1974, p. 88 [**G. modaoyaensis;* OD; holotype (LU, CHANG, & others, 1974, pl. 33, fig. 7), 21475, NIGP, Nanjing]. Similar to *Parabadiella,* but differs in absence of plectrum, parafrontal band, facial line, and occipital spine. Proximal part of eye ridge not visible; glabellar and occipital furrows very shallow. Eye lobe short (exs.), and posterior area of fixigenae long (exs.). *Lower Cambrian (Qiongzhusian):* China (northern Sichuan),

Eoredlichia-Wutingaspis Zone.——Fig. 297,*2*. **G. modaoyaensis,* northern Sichuan (Guangyuan); holotype, cranidium and incomplete thorax, ×4 (Lu, Chang, & others, 1974).

Lunolenus Sdzuy, 1961, p. 549 [**L. lunae;* OD; holotype (Sdzuy, 1961, pl. 7, fig. 9), L3110, UMU, Münster]. Glabella with up to 4 pairs of lateral glabellar furrows; occipital ring with long spine; palpebro-ocular ridge extending around glabella into plectrum; preglabellar field short (sag.); anterior border long (sag. and exs.); anterior sections of facial sutures long, diverging at about 45°. Librigena with long, slender genal spine. Pygidium consisting almost entirely of wide axis with 3 rings and a faintly bilobate terminal axial piece. *Lower Cambrian:* Spain.——Fig. 297,*3a,b*. **L. lunae,* Spain (Los Barrios de Luna); *a,* holotype, dorsal view of cranidium, ×3; *b,* paratype, dorsal view of pygidium, ×5 (photographs courtesy of G. Geyer).

Malongocephalus Zhang & Lin in W. Zhang, Lu, & others, 1980, p. 179 [**M. yunnanensis;* OD; holotype (W. Zhang, Lu, & others, 1980, pl. 48, fig. 5), 37826, NIGP, Nanjing]. Glabella long; preglabellar field very short (sag.); anterior sections of facial sutures subparallel to slightly divergent, posterior sections short; posterior area of fixigena narrow (tr.). Thorax with 15 segments. Pygidium small; axial lobe rounded; pleural regions narrow (tr.), with pair of faint pleural furrows. *Lower Cambrian (Qiongzhusian):* China (eastern Yunnan), *Eoredlichia-Wutingaspis* Zone.——Fig. 298,*3*. **M. yunnanensis,* eastern Yunnan (Malong); holotype, exoskeleton, ×2.85 (W. Zhang, Lu, & others, 1980).

Parabadiella W. Chang, 1966, p. 163, 184 [**P. huoi;* OD; holotype (W. Chang, 1966, pl. 1, fig. 1), 18139, NIGP, Nanjing] [=*Parabadiella (Danagouia)* Chen, 1985, p. 333 (type, *P. (D.) transversa;* OD)]. Cranidium gently convex, rectangular in outline, broad (tr.); eye lobe medium-sized; eye ridge long and oblique; fixigena broad (tr.); anterior area of fixigena with an oblique and slightly arcuate facial line; median plectrum connected to parafrontal band, which extends obliquely backward and joins anterior band of eye ridge; border furrow distinct; anterior border gently convex and slightly arcuate forward; posterior area of fixigena protruding slightly beyond eye lobe; anterior sections of facial sutures slightly divergent from eye lobe; librigena with long genal spine. Thorax with axial spine on the 6th and 9th axial rings. Pygidium similar to that of *Eoredlichia. Lower Cambrian (Qiongzhusian):* China (northern Sichuan, eastern Yunnan, southern Shaanxi), *Parabadiella* Zone.——Fig. 298,*1a,b*. **P. huoi,* southern Shaanxi (Nanzheng); *a,* holotype, cranidium, ×2.85 (W. Chang, 1966); *b,* topotype, exoskeleton, ×2.85 (W. Zhang, Lu, & others, 1980).

Shaanxia Zhang & Lin in W. Zhang, Lu, & others, 1980, p. 176, 430 [**S. curvata;* OD; holotype (W. Zhang, Lu, & others, 1980, pl. 47, fig. 7), 37815, NIGP, Nanjing]. Similar to *Parabadiella,* but anterior border strongly forwardly curved, preglabellar field longer (sag.), glabella narrow and small, plec-

trum absent, border and posterolateral furrows broader, and genal spine longer. Hypostome ovate, with median body ovate, posterior lobe lunate, border narrow, and anterior wing spinulelike. Thorax and pygidium unknown. *Lower Cambrian (Qiongzhusian):* China (southern Shaanxi), *Eoredlichia-Wutingaspis* Zone.——Fig. 298,*2*. **S. curvata;* holotype, cranidium, ×7.6 (W. Zhang, Lu, & others, 1980).

Sibiriaspis Repina in Khalfin, 1960, p. 252 [**S. chomentovskii;* OD; holotype (Repina in Khalfin, 1960, pl. 23, fig. 19; 1966, pl. 16, fig. 4), 3356/10, CSGM, Novosibirsk]. Cranidium subquadrate; occipital spine slender; preglabellar field long (sag.); palpebro-ocular ridge stout; posterior area of fixigena narrow (tr.). *Lower Cambrian:* Russia (Kuznetsk Alatau), Atdabanian (*Resimopsis* Zone); western Mongolia, *Tologoja subquadrata-Sajanaspis modesta* Zone.——Fig. 297,*4a,b*. **S. chomentovskii,* Kuznetsk Alatau, *Resimopsis* Zone; *a,* holotype, cranidium, ×3.5 (Khalfin, 1960); *b,* paratype, cranidium, ×7 (Repina, 1966).

Family KUEICHOWIIDAE Lu, 1965

[Kueichowiidae Lu in Lu & others, 1965, p. 91]

Cranidium subquadrate, glabella cylindrical, with 3 pairs of narrow and oblique glabellar furrows; eye lobe medium to long and arcuate; anterior sections of facial sutures divergent; posterior area of fixigena short (exs.), extending a very short distance (tr.) beyond posterior tip of palpebral lobe; preglabellar field long (sag.); paradoublural line generally distinct. Thorax with no less than 15 segments. Surface granulose. *Lower Cambrian.*

Kueichowia Lu, 1942, p. 182 [**K. liui;* OD; holotype (Lu, 1942, pl. 1, fig. 5a), Lu16, NIGP, Nanjing]. Glabella slightly tapering forward, with frontal lobe well rounded; occipital furrow narrow, deep, and continuous; eye ridge stout and oblique; eye lobe medium-sized; posterior cranidial border furrow narrow and deep; anterior cranidial border furrow shallow; anterior border slightly convex; preglabellar field longer (sag.) than anterior border. Surface pustulose. Librigena, thorax, and pygidium unknown. *Lower Cambrian (lower Canglangpuan):* China (northern Guizhou), *Drepanuroides* Zone.——Fig. 299,*1*. **K. liui,* northern Guizhou (Zunyi); holotype, cranidium, ×5.75 (W. Zhang, Lu, & others, 1980).

Shatania W. Chang & Lin in Lu, Chang, & others, 1974, p. 90 [**S. shatanensis;* OD; holotype (Lu, Chang, & others, 1974, pl. 34, fig. 7), 38003, NIGP, Nanjing]. Cranidial border and border furrow faint; preglabellar area gently convex; eye lobe long and arcuate, its posterior tip reaching posterior border furrow and distant from glabella;
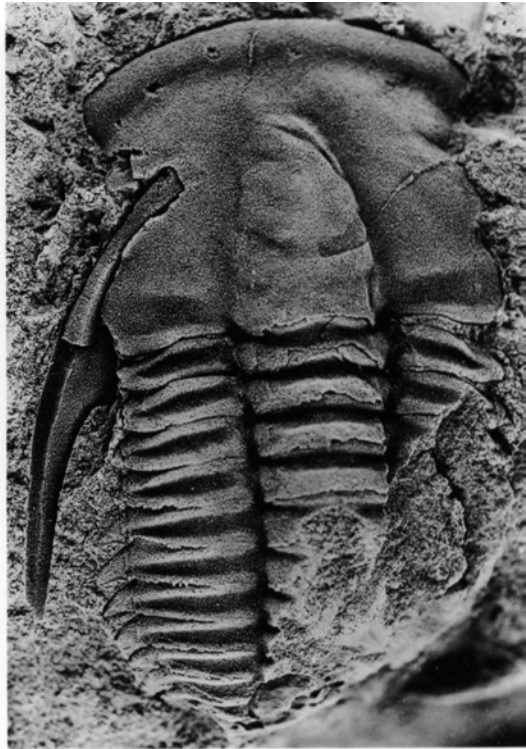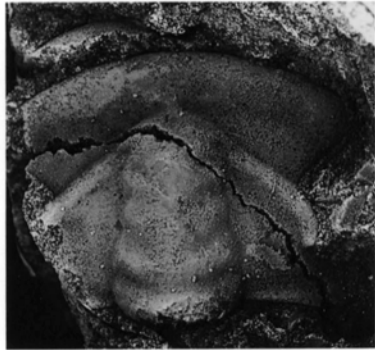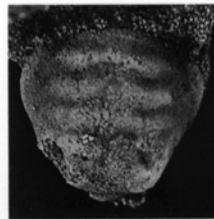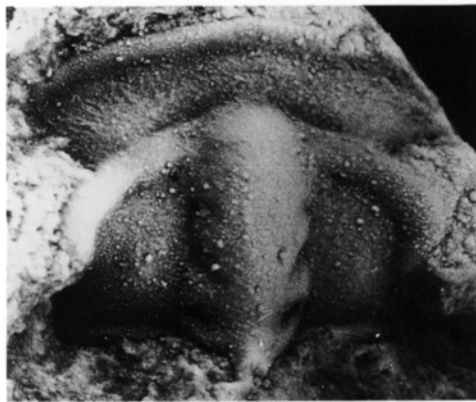
FIG. 297. Abadiellidae (p. 461–462)

paradoublural line faint. Librigena and pygidium unknown. *Lower Cambrian (lower Canglangpuan):* China (northern Sichuan).——FIG. 299,*3. *S.* *shatanensis,* northern Sichuan (Shatan, Nanjiang); holotype, cranidium, ×5.75 (Lu, Chang, & others, 1974).

1a Parabadiella

2 Shaanxia

3 Malongocephalus

1b
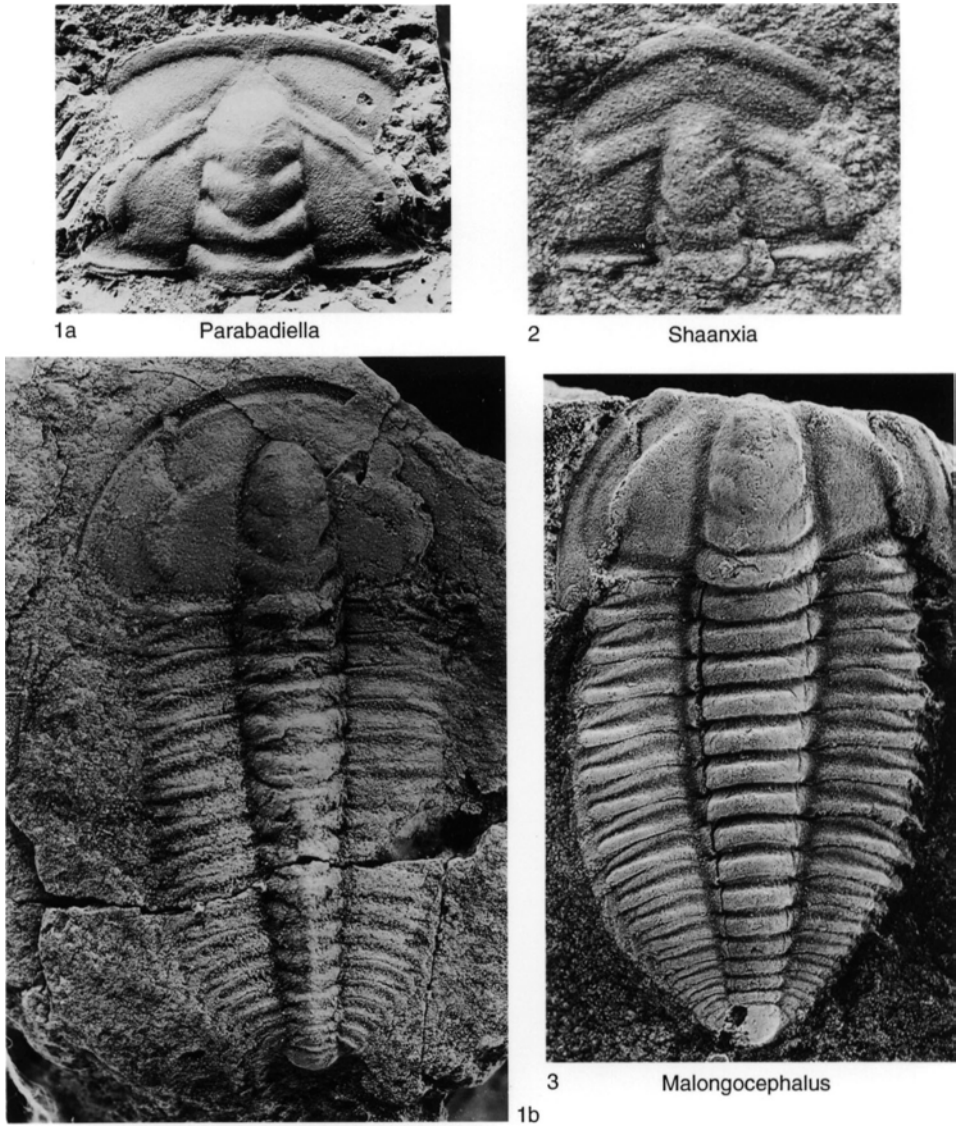
FIG. 298. Abadiellidae (p. 462)

Family MENNERASPIDAE
Pokrovskaya, 1959

[Menneraspidae POKROVSKAYA, 1959, p. 84]

Glabella broadly cylindrical, large, and slightly expanded forward, with 3 or 4 pairs of glabellar furrows; anterior cranidial border short (sag.), convex, and arched forward; no preglabellar field; anterior area of fixigena narrow (tr.); palpebral area of fixigena also narrow (tr.), about one-sixth width (tr.) of basal glabella; anterior sections of facial sutures subparallel; librigena very narrow (tr.), with advanced genal spine. Thorax with 13 segments; axial lobe broader (tr.) than pleural regions. Pygidium small, semielliptical,

1 Kueichowia

2
Menneraspis

3
Shatania
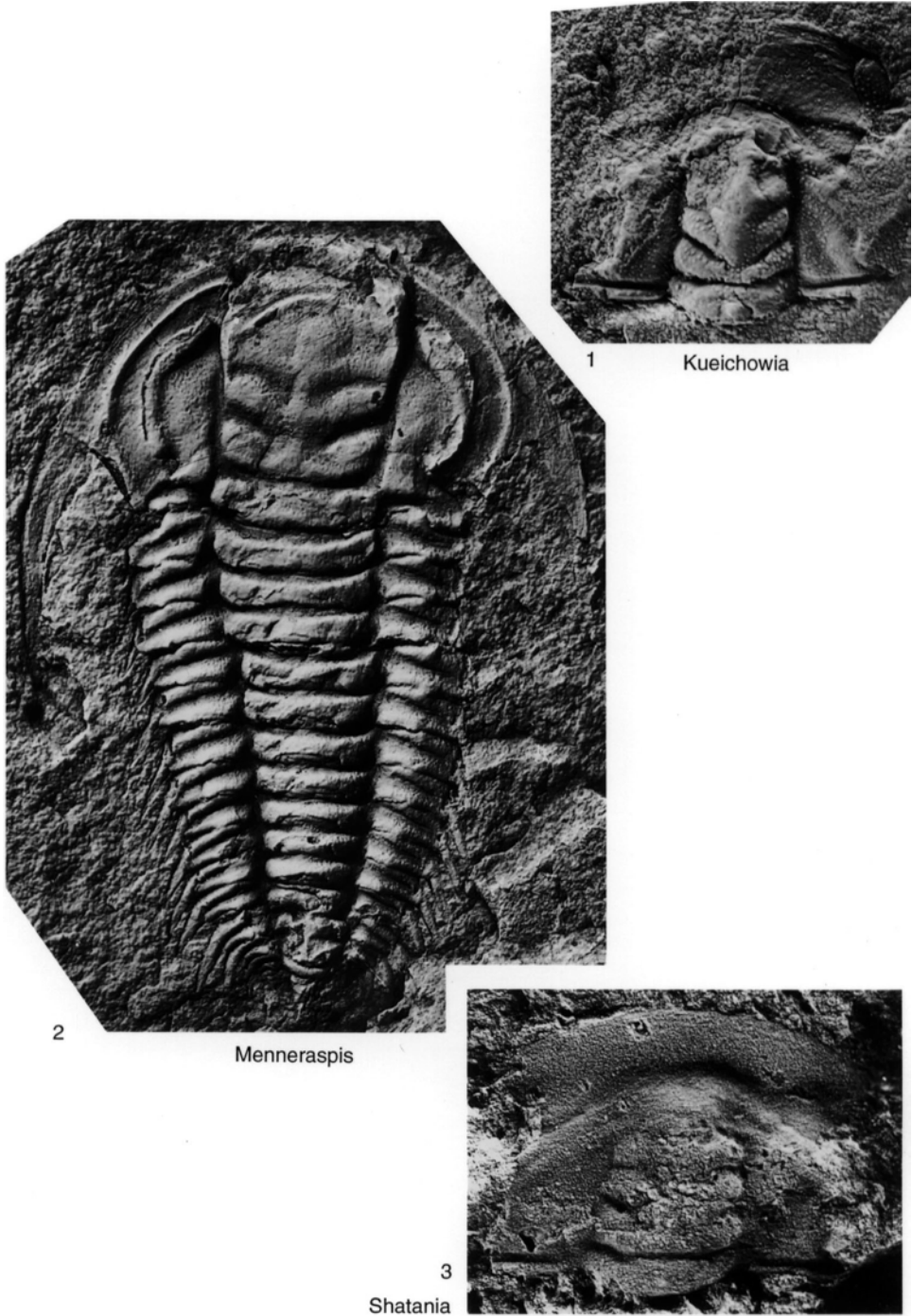
FIG. 299. Kueichowiidae and Menneraspidae (p. 462–466)

with broad axial lobe and broad pleural regions; posterior margin rounded. *Lower Cambrian.*

Menneraspis POKROVSKAYA, 1959, p. 84 [**M. striatus;* OD; holotype (POKROVSKAYA, 1959, pl. 3, fig. 2), 3536/70, repository unknown]. Characters of the family. *Lower Cambrian:* Russia (Tuva), Toyonian (*Kooteniella* to *Edelsteinaspis* Zones); northwestern Siberia (northeastern Krasnoyarsk Basin), *Lermontovia grandis-Paramicamacca petropavlovskii* Zone. ——FIG. 299,*2.* **M. striatus,* Tuva; holotype, incomplete dorsal exoskeleton, ×5.75 (Pokrovskaya, 1959).

Family REDLICHINIDAE
Zhang & Lin, 1980

[Redlichinidae ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 81]

Cephalon without intergenal angle; genal spine not advanced; glabella conical, with frontal lobe well rounded and 3 pairs of glabellar furrows; occipital ring with or without occipital spine; preglabellar field long (sag.); eye lobe long to medium-sized; posterior area of fixigena usually broad (tr.) and long (exs.). Pygidium with large axial lobe having 1 to 5 rings and terminal piece; pleural regions usually flat, broad; pleural furrow absent or with 1 to 2 pairs of furrows; posterior margin arched forward. *Lower Cambrian.*

Redlichina LERMONTOVA, 1940, p. 133 [**R. vologdini;* OD; holotype (LERMONTOVA, 1940, pl. 39, fig. 4; SD REPINA, 1966, p. 50), 9182/127, CNIGR, St. Petersburg]. Similar to *Redlichia,* but having shorter eye lobe, longer (sag.) preglabellar field, longer eye ridge, longer (exs.) posterior area of fixigena and occipital spine. Pygidium with large axis, consisting of 2 to 3 rings and flat, narrow pleurae. *Lower Cambrian (Atdabanian):* Russia (Sayan-Altay).——FIG. 300,*5.* **R. vologdini;* lectotype, cranidium, ×2 (Lermontova, 1940).

Asthenaspis SUVOROVA, 1959, p. 74, *non Astenaspis* SUVOROVA, 1959, p. 70; REPINA, 1960, 1966b, in error] [**A. tenuis;* OD; holotype (SUVOROVA, 1959, p. 74, pl. 6, fig. 10), 711/350, PIN, Moscow]. Palpebral area of fixigena one-third width of basal glabella; eye ridge short; eye lobe long and arcuate, reaching posterior border furrow; anterior border furrow faint; border narrow (sag.); narrow plectrum present; anterior sections of facial sutures divergent; librigena with short genal spine. Pygidial axial lobe broadly rounded, faintly segmented; pleural region bilobed. *Lower Cambrian:* southeastern Siberia, Botomian (*Bergeroniaspis ornata* Zone); southwestern Siberia, *Bathyuriscellus* Zone.——FIG. 300,*2.* **A. tenuis,* southeastern Siberia; holotype, cranidium, ×8 (Suvorova, 1959).

Kolbaspis REPINA in ZHURAVLEVA & others, 1979, p. 29 [**K. sajanica;* OD; holotype (ZHURAVLEVA & others, 1979, pl. 1, fig. 12), 403/40, CSGM, Novosibirsk]. Glabella subcylindrical, with faint glabellar furrows; occipital ring feebly separated; anterior border of medium length (sag.); plectrum narrow (tr.); fixigena narrow (tr.), raised towards long, feebly arcuate palpebral lobe; eye ridge short; anterior branch of facial suture slightly divergent; librigenal spine not advanced. Pygidium small, with semielliptical axial lobe and pleural region not segmented. *Lower Cambrian (Botomian):* Russia (eastern Sayan), *Bathyuriscellus robustus-Jakutus quadriceps* Zone.——FIG. 300,*3.* **K. sajanica;* holotype, cranidium, ×9 (Zhuravleva & others, 1979).

Parasajanaspis TCHERNYSHEVA 1972, p. 212 [**P. lauta;* OD; holotype (TCHERNYSHEVA 1972, pl. 53, fig. 6), 10319/3, CNIGR, St. Petersburg]. Dorsal shield flattened. Cranidium slightly widened transversely. Glabella tapering forward, with 3 pairs of glabellar furrows; occipital ring with medial node; fixigena flat; palpebral lobe long (exs.) merging into oblique eye ridge; preglabellar field of same length (sag.) as slightly convex anterior border. Thorax with at least 12 segments; pleural region narrower (tr.) than axis; pleurae with slightly oblique pleural furrows and slender spines. *Lower Cambrian (?Atdabanian):* Russia (Pamir).——FIG. 300,*1.* **P. lauta;* holotype, incomplete dorsal shield, ×1 (Tchernysheva, 1972).

Sajanaspis REPINA, 1960a, p. 196 [**S. pokrovskayae;* OD; holotype (REPINA, 1960, pl. 11, fig. 1), 3548/46, CSGM, Novosibirsk]. Anterior area of fixigena narrow (tr.); anterior border short (sag. and exs.); eye lobe long (exs.) and arcuate; posterior areas of fixigena very broad (tr.) and long (exs.); librigena with narrow border and short genal spine. Thorax with 15 segments. Pygidium small, with broad (tr.) axial lobe and broad pleural regions. *Lower Cambrian:* Russia (eastern and western Sayan, Altay, Gornaja Shoria, Tuva, Kuznetsk Alatau), Atdabanian (*Sajanaspis* Zone); western Mongolia, *Tologoja subquadrata-Sajanaspis modesta* Zone; northern Mongolia, *Tologoja subquadrata-Margodiscus rackovskii-Sajanaspis* Zone.——FIG. 300,*6.* **S. pokrovskayae,* eastern and western Sayan mountains; holotype, cranidium, ×5 (Repina, 1960).

Tungusella REPINA, 1960, p. 178 [**T. manica;* OD; holotype (REPINA, 1960, pl. 4, fig. 6), 3544/290, CSGM, Novosibirsk]. Occipital furrow very shallow medially; occipital ring with a small median node; anterior border short (sag. and exs.); preglabellar field longer (sag.) than anterior border, with radiating striations; eye ridge oblique; eye lobe medium-sized; anterior sections of facial sutures divergent. Thorax with no less than 14 segments. Pygidium with 1 to 2 pairs of pygidial spines; posterior margin rounded or slightly arched forward. Librigena unknown. *Lower Cambrian:* western Krasnoyarsk Territory (Irkutsk region, eastern Sayan), Atdabanian–lower Botoman (*Tungusella* Zone); southwestern Yakutia, Botoman (*Bergeroniellus micmacciformis-Erbiella* Zone).——FIG. 300,*4a,b.* **T. manica,* western Krasnoyarsk Terri-

tory; *a,* holotype, cranidium, ×3; *b,* paratype, pygidium, ×5 (Repina, 1960).

Family CHENGKOUASPIDAE
Zhang & Lin, 1980

[Chengkouaspidae ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 227]

Glabella long, convex, parallel sided, or tapering forward, with 2 to 3 pairs of glabellar furrows; anterior field of fixigena absent or short (exs.); preglabellar field absent or short (sag.); eye lobe stout and very long, not differentiated from eye ridge. Pygidium relatively large; axial lobe long and broad (tr.); pleural region broad, with or without pleural furrows; border narrow. *Lower Cambrian.*

Chengkouaspis ZHANG & LIN in W. ZHANG, LU, & others, 1980, p. 227, 432 [*C. longioculus;* OD; holotype (W. ZHANG, LU, & others, 1980, pl. 70, fig. 4), 38008, NIGP, Nanjing]. Differs from *Terechtaspis, Belliceps, Pseudoresserops,* and *Inella* in having longer (sag.) glabella, backward-bent transglabellar and occipital furrows, and very small anterior field of fixigena. *Lower Cambrian (Canglangpuan):* China (northern Sichuan), *Drepanuroides* Zone or *Palaeolenus* Zone.——FIG. 301,*3.* *C. longioculus, Drepanuroides* Zone, holotype, cranidium, ×5 (W. Zhang, Lu, & others, 1980).

Belliceps REPINA, 1966, p. 77 [*B. simplex;* OD; holotype (REPINA, 1966, pl. 13, fig. 5), 3354/500, CSGM, Novosibirsk]. Cranidium subcircular; axial furrow shallow; glabella convex, tapering forward; frontal lobe bluntly rounded; 3 pairs of pitlike glabellar furrows; occipital furrow deeper distally, not connected in middle; occipital ring longer sagittally and produced backward into occipital spine; anterior border convex and slightly longer sagittally and shorter exsagittally; eye ridge and lobe convex and arcuate; palpebral area of fixigena flat or slightly depressed, about one-half the basal width (tr.) of glabella. Librigena, thorax, and pygidium unknown. Surface finely granulose. *Lower Cambrian (Atdabanian):* Russia (Gornaya Shoria), *Resimopsis* Zone.——FIG. 301,*4.* *B. simplex;* holotype, cranidium, ×3 (Repina, 1966).

Bulaiaspis LERMONTOVA in REPINA, 1956, p. 145 [*B. vologdini;* OD; holotype (REPINA, 1956, pl. 28, fig. 1), 3544/45, CNIGR, St. Petersburg]. Cranidium subtrapezoidal; glabella tapering forward; proximal end of eye ridge trifid; librigena narrow (tr.), with advanced genal spine; eye lobe medium-sized or very long. Thorax with 17 segments; axial spine on 11th segment. Pygidium semicircular, with axial rings and terminal piece; pleural regions with pleural furrows; border narrow. *Lower Cambrian:* Russia (southwestern Yakutia, Irkutsk, southern Krasnoyarsk Territory, Transbaikal region, eastern Sayan mountains, Kuznetsk Alatau), *Bulaiaspis* and *Tungusella* Zones; northern Mongolia, *Tologoja*

subquadrata-Margodiscus rackovskii-Sajanaspis Zone and *Fallotaspidella-Bulaiaspis* Zone.——FIG. 301,*1a,b.* *B. vologdini,* Irkutsk, late Atdabanian stage, *Bulaiaspis* Zone; *a,* holotype, cranidium, ×5; *b,* paratype, pygidium, ×11 (Repina, 1956).

Inella REPINA in REPINA & others, 1964, p. 269 [*I. monstrabilica;* holotype (REPINA & others, 1964, pl. 35, fig. 4), 252/4, CSGM, Novosibirsk]. Cranidium semielliptical; axial furrow deep and broad (tr.); glabella subparallel behind S2, then rapidly tapering in front of S2; frontal lobe of glabella acutely rounded; 3 pairs of narrow and shallow glabellar furrows; occipital furrow deeper distally, but not connected in middle; anterior border short (sag., exs.) and convex; eye ridge bifid proximally; palpebral furrow broad (tr.) and deep; palpebral areas of fixigenae convex, about one-third glabellar width (tr.); posterior areas of fixigenae well developed and wide (tr.); posterior border furrow long (exs.) and wide (tr.). Librigena, thorax, and pygidium unknown. *Lower Cambrian (Atdabanian):* Russia (Sayan-Altay), *Pagetiellus* Zone.——FIG. 302. *I. monstrabilica;* holotype, cranidium, ×5 (Repina & others, 1964).

Pseudoresserops REPINA in KHOMENTOVSKII & REPINA, 1965, p. 126 [*P. oculatus;* OD; holotype (KHOMENTOVSKII & REPINA, 1965, pl. 5, fig. 2), 265/537, CSGM, Novosibirsk (although the catalog number of holotype is given as "265/537, pl. 5, fig. 1" in the text, in the plate explanation, the specimen illustrated on pl. 5, fig. 2 is 265/537]. Cranidium subtrapezoidal; glabella convex, slightly contracted at the middle, tapering rapidly in front of S3; frontal lobe acutely rounded; S1 bifurcate proximally; occipital furrow shallow and narrow (sag., exs.), bending slightly backward; posterior margin of occipital ring rounded; anterior border flat, becoming shorter (exs.) distally; eye ridge and lobe convex, stout, feebly arcuate, its posterior tip reaching level of occipital furrow; palpebral area of fixigena about one-third basal glabellar width (tr.); posterior areas of fixigenae long (exs.) and wide (tr.). Librigena, thorax, and pygidium unknown. *Lower Cambrian (Atdabanian):* Russia (southern and western Yakutia), *Pagetiellus anabarus* Zone; northern Mongolia, *Tologoja subquadrata-Margodiscus rachovskii-Sajanaspis* Zone and *Elganellus-Malykania* Zone. ——FIG. 301,*2.* *P. oculatus,* south bank of Lena River, about 300 km west of Yakutsk; holotype, cranidium, ×5 (Khomentovskii & Repina, 1965).

Terechtaspis REPINA, 1960, p. 208 [*T. coronaria;* OD; holotype (REPINA, 1960, pl. 13, fig. 6), 3548/382, CSGM, Novosibirsk] [=*Nellina* POKROVSKAYA, 1967, p. 115 (type, *N. miranda;* OD)]. Cranidium semicircular; axial furrow shallow; glabella (except occipital ring) as wide as long, tapering forward; S3 and S2 deep and near transverse; S1 longer and oblique proximally backward; occipital furrow slightly bending backward; occipital ring of uniform length (sag. and exs.); anterior border rimlike; preglabellar field and anterior areas of fixigenae absent; eye ridge and lobe arcuate; posterior area of fixigena very short (exs.) and narrow (tr.).
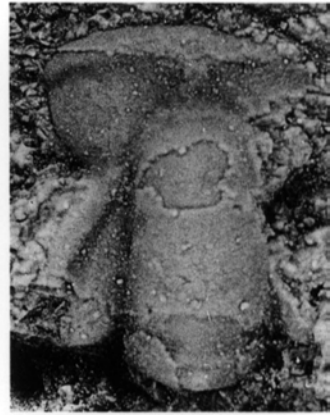
FIG. 300. Redlichinidae (p. 466–467)

Librigena, thorax, and pygidium unknown. *Lower Cambrian (Atdabanian–lower Botoman):* Russia (eastern and western Sayan, Tuva), *Sajanaspis* and *Poliellina-Serrodiscus* Zones.——FIG. 301,5. **T. coronaria;* eastern Sayan, holotype, cranidium, ×4.5 (Repina, 1960).

Family UNCERTAIN

Akbashichia KOROBOV, 1989, p. 75 [**A. plana;* OD; holotype (KOROBOV, 1989, pl. 3, fig. 5), 4726/39, GIN, Moscow]. Similar to *Redlichia* in conical glabella, in long (exs.) and arcuate palpebral lobe, and
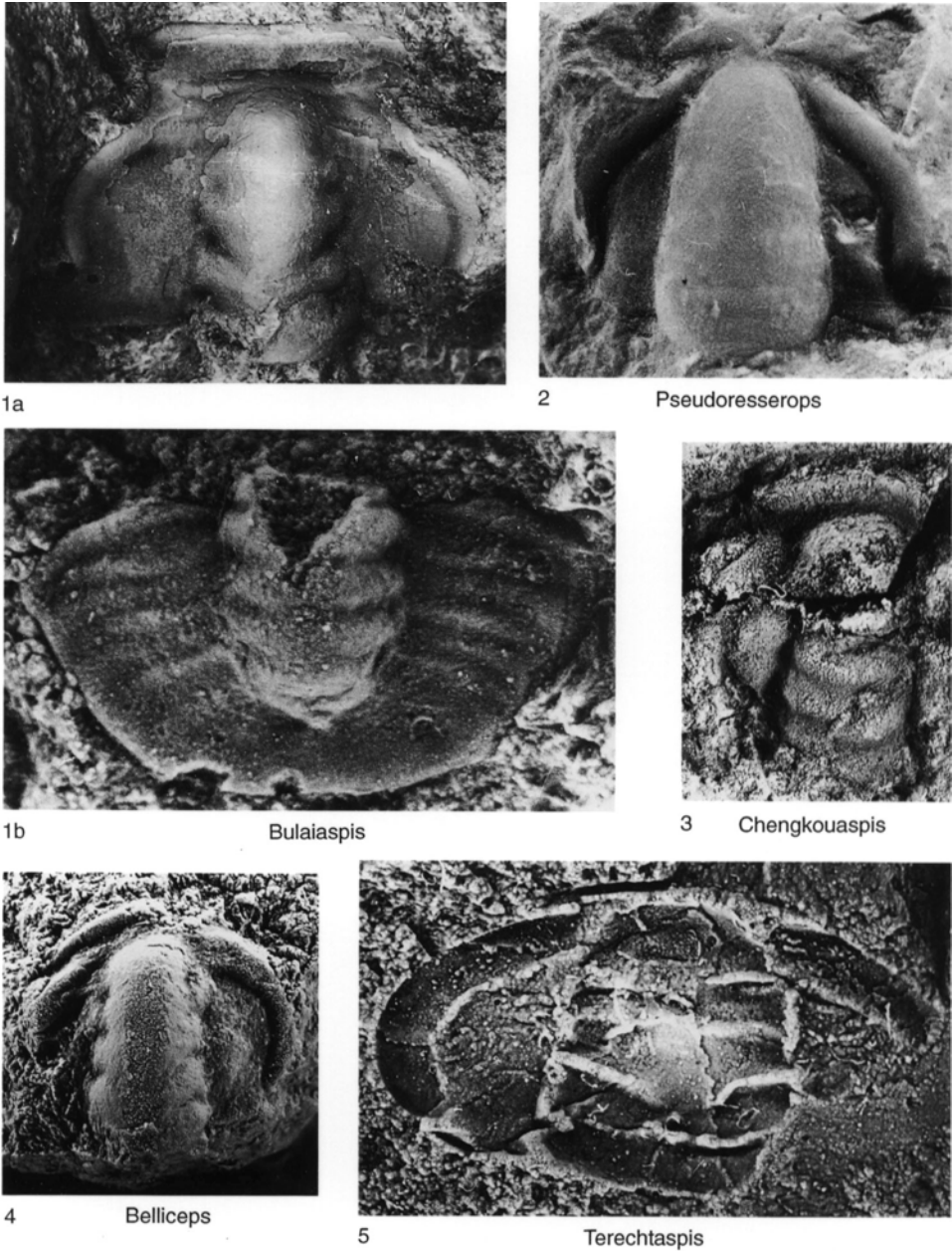
FIG. 301. Chengkouaspidae (p. 467–468)

in course of anterior section of facial suture, but frontal area longer (sag.) and cranidial border furrow and glabellar furrows less distinct. Librigena, thorax, and pygidium unknown. *Lower Cambrian (upper Atdabanian):* western Mongolia (Akbashi, 40 km northeast of Kobodo).——FIG. 303,*1.* **A. plana;* holotype, cranidium, ×2 (Korobov, 1989).

Elegestina POKROVSKAYA, 1959, p. 63 [**E. antiqua;* OD; holotype (POKROVSKAYA, 1959, pl. 1, fig. 11), 3536/18, GIN, Moscow]. Glabella convex, short

Inella

FIG. 302. Chengkouaspidae (p. 467)

(sag.), and broad (tr.); anterior margin of frontal lobe more or less acutely rounded; glabellar furrows indistinct; preglabellar field very short (sag.); border furrow narrow; border convex and long (sag.); occipital furrow narrow and nearly straight; occipital ring longer (sag.) medially; oblique eye ridge narrow; palpebral lobe close to glabella. *Lower Cambrian (Botomian):* Russia (Tuva), *Poliella-Laticephalus* Zone.——FIG. 303,*5.* *E. antiqua;* holotype, cranidium, ×1.5 (Pokrovskaya, 1959).

Elganellus SUVOROVA, 1958, p. 918 [*E. probus;* OD; holotype (SUVOROVA, 1958, fig. 4d), 711/3, PIN, Moscow]. Cranidium subquadrate, strongly convex; glabella broad, tapering forward, with well-rounded frontal lobe; eye lobe medium-sized; parafrontal band prominent; anterior border short (sag. and exs.); preglabellar field same length (sag.) as border; anterior sections of facial sutures slightly divergent; occipital node distinct; librigena with short genal spine. *Lower Cambrian:* Russia (southwestern Siberia), Atdabanian, *Elganellus* Zone, (Kuznetsk Alatau, Batenevskiy Ridge, Gorniy Altai), *Resimopsis* Zone; northwestern Mongolia, *Elganellus-Malykania* Zone.——FIG. 303,*4.* *E. probus,* southwestern Siberia; holotype, cranidium, ×4 (Suvorova, 1958).

Iolgia KRAEVSKY, 1965, p. 50 [*I. prima;* OD; holotype (KRAEVSKY, 1965, pl. 1, fig. 13a), 871/13, CSGM, Novosibirsk]. Cranidium small; palpebral lobe upturned over fixigena; preglabellar field concave, with narrow median ridges connecting glabella with narrow anterior border; anterior branch of facial suture divergent (about 45°); librigena with long genal spine. *Lower Cambrian (Botomian):* Russia (Gornyi Altai), *Poliella-Laticephalus* Zone.——FIG. 303,*6.* *I. prima;* holotype, cranidium, ×6 (Kraevsky, 1965).

Paratungusella REPINA & others, 1964, p. 71 [*P. triangulata;* OD; holotype (REPINA & others, 1964, pl. 1, fig. 9), 246/11, CSGM, Novosibirsk]. Cranidium subtrapezoidal; glabella conical, with well-rounded frontal lobe; occipital ring with small median node; eye ridge long (tr.); eye lobe medium-sized; palpebral area of fixigena broad (tr.); border convex; plectrum prominent; anterior sections of facial sutures slightly divergent. *Lower Cambrian*

(Botomian): Russia (Kuznetsk Alatau), *Poliellina-Serrodiscus* Zone.——FIG. 303,*3.* *P. triangulata;* holotype, cranidium, ×2 (Repina & others, 1964).

Sarassina ROMANENKO in POSPELOV & ROMANENKO, 1980, p. 69 [*S. alutacea;* OD; holotype (POSPELOV & ROMANENKO, 1980, pl. 13, fig. 8), 1931/16, MWSGPC, Novokuznetsk]. Cranidium subquadrate, flattened, with broadly rounded anterior margin; glabella faintly tapered to anterior end, with 3 pairs of glabellar furrows; occipital ring with node or spine; palpebral lobe moderately curved, widened in posterior half; eye ridge bifid, the anterior branches embracing glabella anteriorly, and connected with anterior border by median plectrum; border distinct; preglabellar field relatively long (sag.). Surface densely anastomosing. *Lower Cambrian (Atdabanian):* Russia (Siberia, Altay).——FIG. 303,*2.* *S. alutacea;* holotype, cranidium, ×7 (Pospelov & Romanenko, 1980).

UNRECOGNIZABLE REDLICHIOID GENERA

Eomalungia S. LI, 1978, p. 197 [*E. latilimbata;* OD]. *Lower Cambrian:* southwestern China (Sichuan).

Fandianaspis S. LI, 1978, p. 213 [*F. fandianensis;* OD]. *Lower Cambrian:* southwestern China (Sichuan).

Guangyuania S. LI, 1978, p. 209 [*G. conica;* OD]. *Lower Cambrian:* southwestern China (northern Sichuan).

Longmenshania S. LI, 1978, p. 198 [*L. longmenshanensis;* OD]. *Lower Cambrian:* southwestern China (northern Sichuan).

Micangshania ZHOU in Y. LI & others, 1975, p. 140 [*M. gracilis;* OD]. *Lower Cambrian:* China (southern Shaanxi).

Parawutingaspis S. LI, 1978, p. 191 [*P. convexa;* OD]. *Lower Cambrian:* China (northern Sichuan).

Pseudowutingaspis S. LI, 1978, p. 190 [*P. longmenshanensis;* OD]. *Lower Cambrian:* China (northern Sichuan).

Runnania LI in YIN & LI, 1978, p. 413 [*R. runnanensis;* OD]. *Lower Cambrian:* southwestern China (northern Guizhou).

Shangsiaspis S. LI, 1978, p. 214 [*S. shangsiensis;* OD]. *Lower Cambrian:* China (northern Sichuan).

Xingzishania ZHOU in Y. LI & others, 1975, p. 139 [*X. lata;* OD]. *Lower Cambrian:* China (southern Shaanxi).

Yiliangella (Pseudoyiliangella) YIN in YIN & LI, 1978, p. 420 [*Y. (P.) xishuiensis;* OD]. *Lower Cambrian:* southwestern China (northern Guizhou).

Superfamily PARADOXIDOIDEA Hawle & Corda, 1847

W. T. DEAN and A. W. A. RUSHTON

[*nom. correct.* DEAN & RUSHTON, herein, pro Paradoxidacea POULSEN in MOORE, 1959, p. 212, *pro* Paradoxides HAWLE & CORDA, 1847, p. 15]

Opisthoparian, often large; cephalon subsemicircular with long librigenal spine;
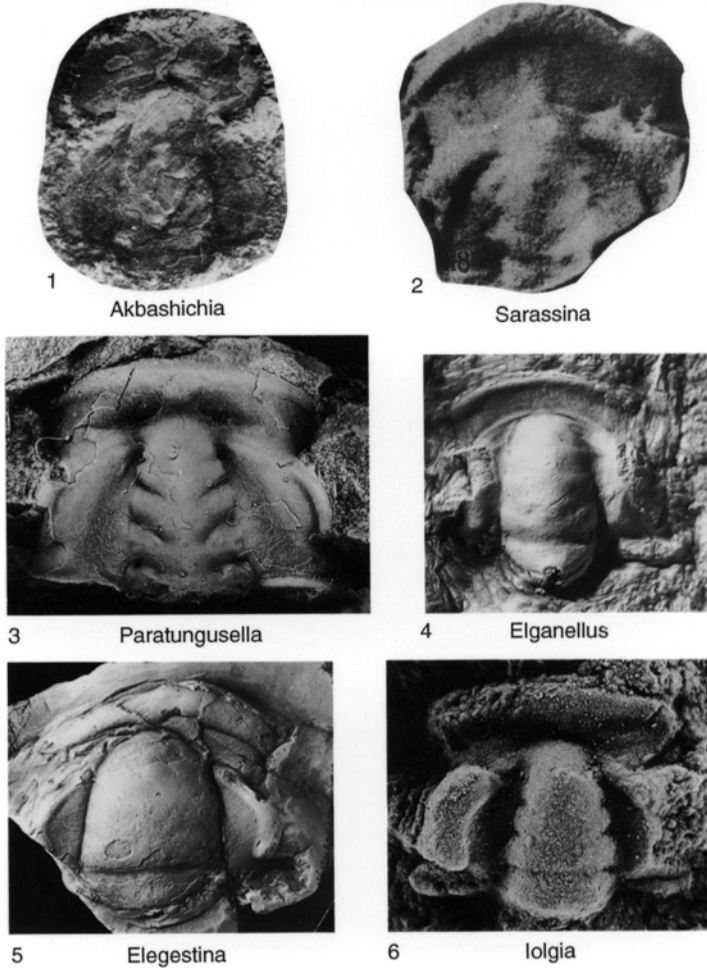
FIG. 303. Family Uncertain (p. 468–470)

glabella widening anteriorly to rounded or bluntly pointed frontal lobe or may be parallel sided in early forms; L1 to L4 of equal or subequal length; S1 generally transglabellar, shallower medially; S2 long (tr.), subparallel to S1, may be transglabellar; S3 and S4 short (tr.), less deep; preglabellar field typically absent in adult stage; eye short to long (exs.), gently to strongly curved; anterior section of facial suture moderately divergent to retrodivergent (Centropleuridae); rostral suture long (tr.) and curved, delimiting rostral plate that may be fused with large hypostome to form rostral-hypostomal plate. Thorax with 14 to 21 segments ending in short to long pleural spines directed progressively more strongly backwards from front to rear (Paradoxididae) or in bluntly truncated tips (Centropleuridae); first and second segments may be macropleural. Pygidium typically small in Paradoxididae, may be medium sized in Centropleuridae. *Lower Cambrian–Middle Cambrian.*

Family PARADOXIDIDAE Hawle & Corda, 1847

[Paradoxides Hawle & Corda, 1847, p. 15; ICZN Opinion 496, 1957, Family-Group Name No. 204]

Glabella widest across L3 or L4; S3 and S4 may be defined abaxially; palpebral lobe

oblique and short (exs., extending from opposite S1 to S3) to semicircular and long (from LO to L4); visual surface apparently low, with circumocular suture; preglabellar field absent in holaspis, with front of glabella typically indenting anterior border; preglabellar field and preglabellar ridge generally present in meraspis; small occipital node behind midlength of occipital ring; anterior section of facial suture arcuate, moderately to strongly divergent; rostral suture traversing outer surface of anterior border; connective sutures converging to delimit wide (tr.) rostral plate; cephalic border continuous with long librigenal spine; intergenal angle may be present. Hypostome typically narrow (tr.) posteriorly, expanding forward to arched anterior margin; large anterior wing confluent with anterior lobe of middle body; small posterior lobe may be swollen distally, separated from lozenge-shaped anterior lobe by middle furrow that is obsolete medially; narrow (sag.) posterior border may carry pair of short spines. Thorax with up to 21 segments that may be fulcrate, nonfulcrate, or questionably both; axis well defined, occupying less than one-fourth to one-third of overall breadth; pleura may be directed slightly forwards abaxially, divided by nearly straight pleural furrow into subequal anterior and posterior bands, and ending in spine, often falcate; hindmost spines longer, directed more strongly backward, and last pair may be subparallel beside pygidial facets. Pygidium with posterior margin truncate, rounded, bluntly pointed or concave; postaxial region in some species prolonged to form long, spatulate extension that may end in pair of spines; axis may be large in relation to pleural field, with 2 or 3 rectangular axial rings and terminal piece rounded or bluntly pointed; anterior half rib directed backward, often long, with confluent lateral and posterior margins correspondingly short. Surface (excluding furrows) granulose, smooth, or covered with anastomosing terrace ridges. Includes some of the largest known trilobites, with length (sag.) of 40 to 50 cm. *upper Lower Cambrian–upper Middle Cambrian.*

Paradoxides BRONGNIART, 1822, p. 30 [**Entomostracites paradoxissimus* WAHLENBERG, 1818, p. 34; SD BARRANDE, 1852, p. 361; lectotype (WESTERGÅRD, 1953, p. 34, pl. 8, fig. 2), Ar 46147, RM, Stockholm] [*=Vinicella* ŠNAJDR, 1957, p. 237 (type, *Trilobites desideratus* BARRANDE, 1846, p. 20, based on teratological pygidium of *Paradoxides gracilis* BOECK, 1827, *fide* ŠNAJDR, 1978, p. 24–25)]. Glabella with S2 transglabellar and shallow medially; S3 and S4 short (tr.), often faint; anterior border narrow (sag.) medially; eye lobe short (S1 to S3), with moderately deep palpebral furrow; eye ridge may be present; strongly arcuate anterior section of facial suture cutting anterior margin almost in exsaggittal line with outer margin of eye lobe; posterior section of facial suture straight or sigmoidal, cutting posterior margin almost in exsagittal line with outer margin of eye lobe; large rostral-hypostomal plate with strongly convex anterior margin. Thorax with 19 to 21 segments where known; segments directed slightly forwards abaxially; hindmost pair of pleural spines subparallel, ending far behind tip of pygidium. Pygidium small, subhexagonal, widest behind midlength, at posterior end of long facet directed strongly backward; lateral margin short, slightly convex; posterior margin convex, straight, or concave; axis subtriangular; pleural and postaxial regions confluent and uniformly convex. [Many specimens supposedly of *Paradoxides* are based on material too incomplete for confident generic determination; for example, specimens from Colombia, South America (RUSHTON, 1963), and a record from Australia (WHITEHOUSE, 1939, p. 276) are here excluded.] *middle Middle Cambrian–upper Middle Cambrian:* England, Wales, *H. parvifrons?–Pt. punctuosus* Zones; Sweden, Norway, Denmark, *P. paradoxissimus* and *P. forchhammeri* Stages; Czech Republic, *P. gracilis* Zone; Canada (eastern Newfoundland), *Pt. punctuosus* Zone; ?USA (South Carolina), ?Russia (Novaya Zemlya).——FIG. 304,*1a*. **P. paradoxissimus* (WAHLENBERG), middle Middle Cambrian (*P. paradoxissimus* Stage), Sweden (Öltorp, Västergötland); lectotype, exoskeleton, RM Ar46147, ×1 (new).——FIG. 304,*1b*. *P. gracilis,* middle Middle Cambrian, Czech Republic (Jince); rostral-hypostomal plate, SM A.1561, ×1 (new).

Acadoparadoxides ŠNAJDR, 1957, p. 238 [**Paradoxides Sacheri* BARRANDE, 1852, p. 369; OD; holotype (ŠNAJDR, 1958, p. 147), CC 185, No. 76, NMP, Prague] [*=Eoparadoxides* SOLOVIEV, 1969, p. 16 (type, *Paradoxides harlani* GREEN, 1834, p. 335; OD)]. Glabella widening anteriorly, either with axial furrow nearly straight, or with stronger widening in front of L2; S2 transglabellar, S3 and S4 faint; palpebral lobe arcuate, long (SO to L4); palpebral area narrower (tr.) and palpebral lobe wider than in *Eccaparadoxides;* intergenal angle obtuse. Librigena with broad-based genal spine; inner spine angle obtuse. Thorax (where known) with 17 to 19 segments, inner pleural region narrower (tr.) than axis; pleural spines short, hindmost extending back only to tip of pygidium. Pygidium rounded to
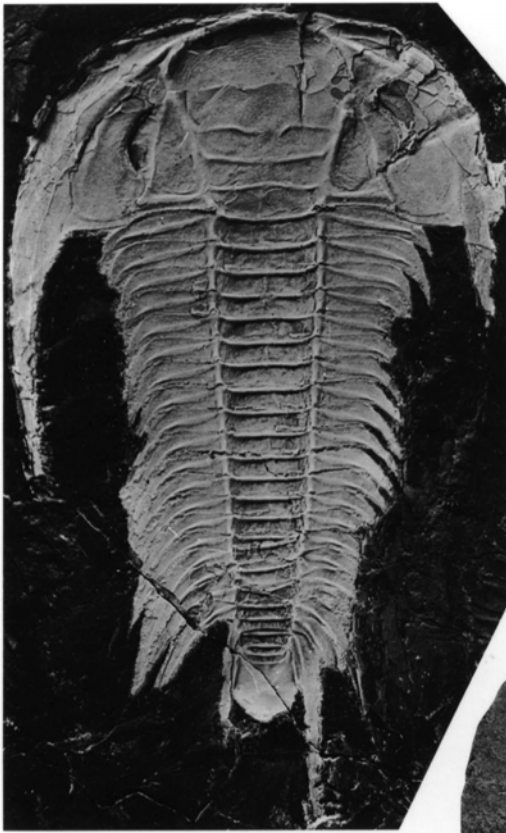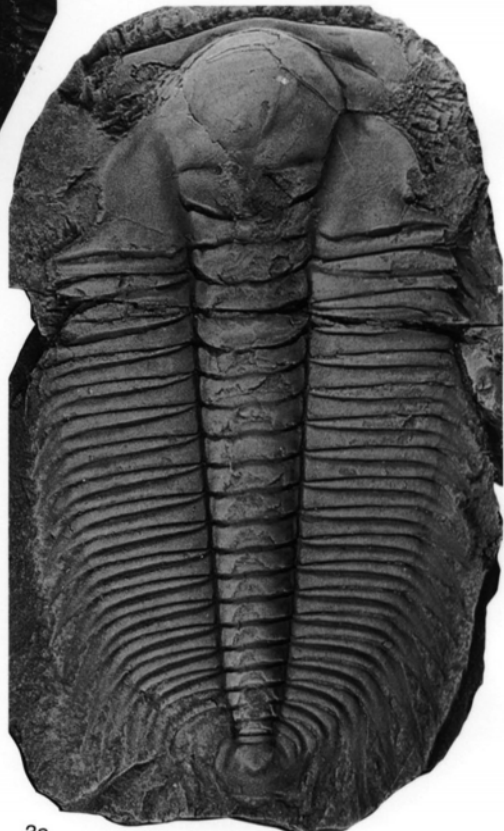
FIG. 304. Paradoxididae (p. 472–478)
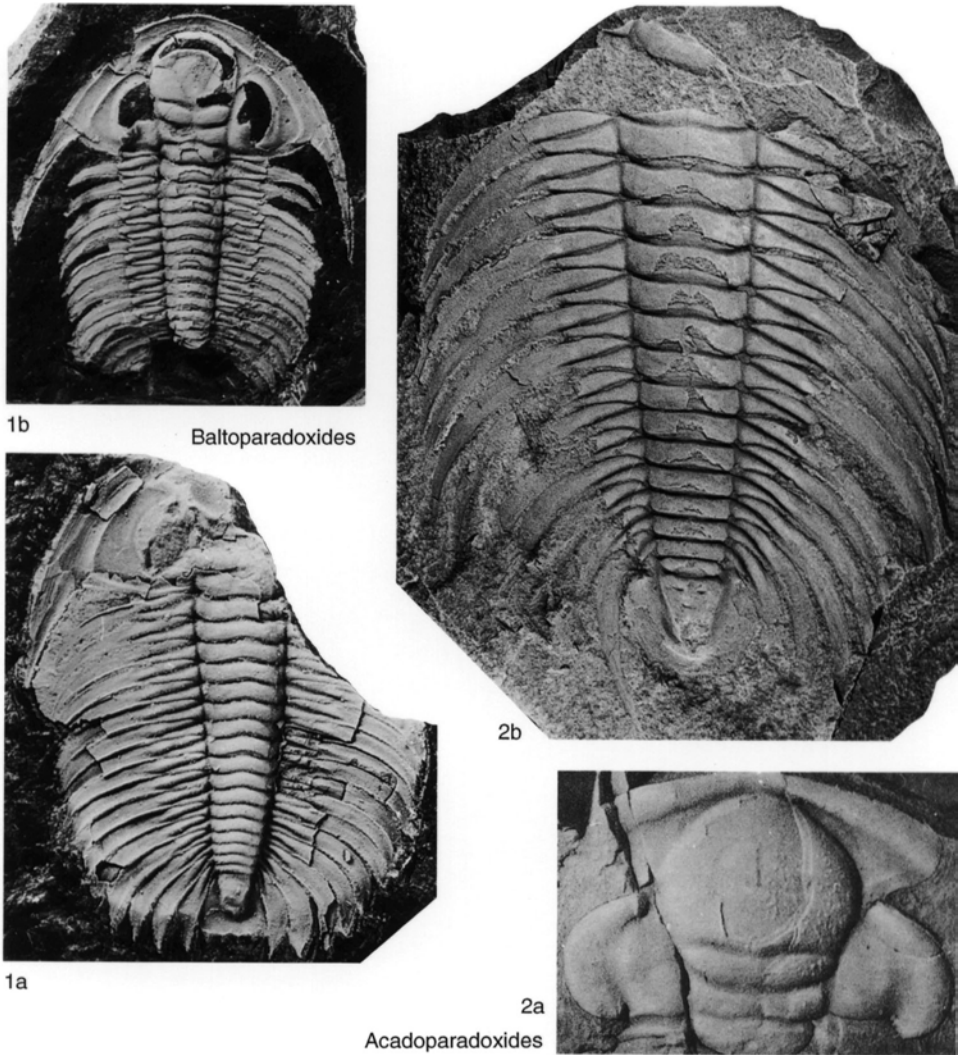
FIG. 305. Paradoxididae (p. 474–475)

hexagonal. *lower Middle Cambrian–upper Middle Cambrian:* England, Wales, Scandinavia (Sweden, Norway), Czech Republic, Poland, Spain, Morocco, Turkey, eastern Canada, USA (Massachusetts), Russia (northern Siberia), ?western Mongolia.

A. (**Acadoparadoxides**). S2 shallow medially. Thorax (where known) with 19 segments. Pygidium widest at or in front of midlength, as wide as or slightly wider than long; margin rounded or subangular posteriorly; axis subtriangular, about half of pygidial length, with up to 2 axial rings; pleural fields behind axis form ridge that may be as high as, and coalesce with, terminal piece of axis. *lower Middle Cambrian–upper Middle Cambrian:* England, Wales, Czech Republic, Scandi-

navia (Sweden), Poland, eastern Canada (eastern Newfoundland, New Brunswick), Spain, Morocco, Turkey, USA (Massachusetts), Russia (northern Siberia), ?western Mongolia.——FIG. 305,*2a,b.* **A. (A.) sacheri* (BARRANDE), *E. pusillus* Zone, middle Middle Cambrian, Czech Republic (Jince); *a,* cranidium, MŠ 360, ×2 (Šnajdr, 1958, pl. 16, fig. 5); *b,* thorax and pygidium, Schary Collection, MCZ 2752, ×1 (new).

A. (**Baltoparadoxides**) SNAJDR, 1986, p. 174 [**Paradoxides oelandicus* SJÖGREN, 1872, p. 72; OD; holotype (SJÖGREN, 1872, pl. 5, fig. 1, *fide* WESTERGÅRD, 1936, p. 35), Ar 1449, RM, Stockholm]. Glabella nearly straight sided, in holaspis expanding forward slightly, in meraspis
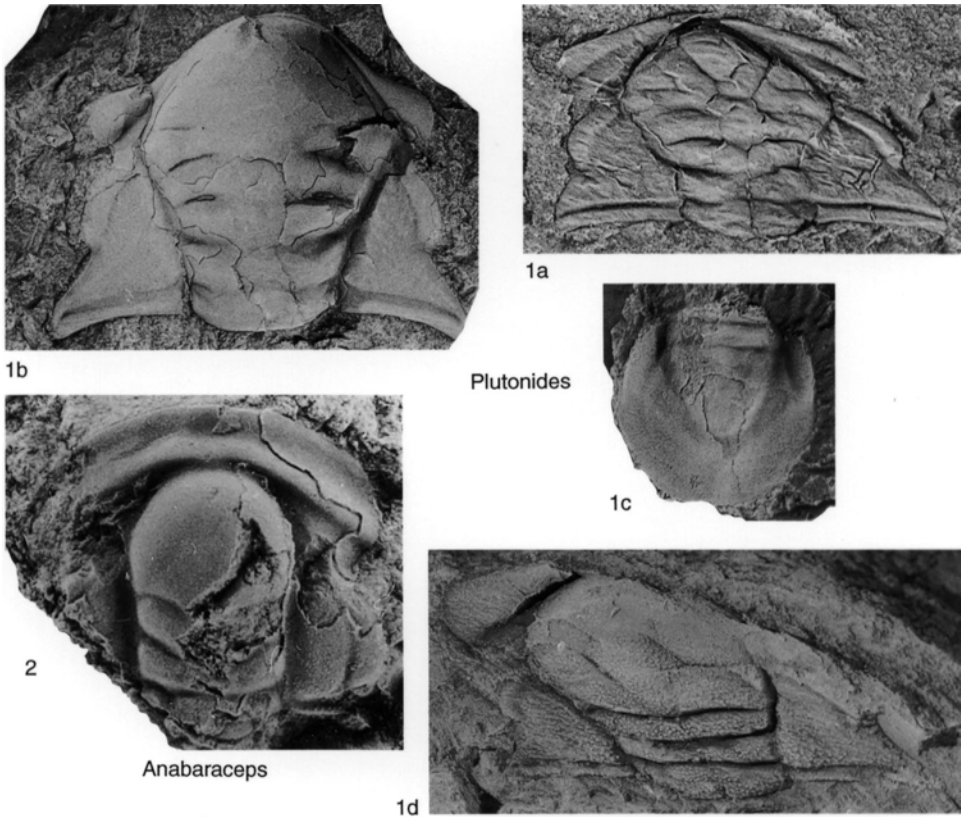
FIG. 306. Paradoxididae (p. 475–478)

almost parallel sided; S2 deep medially. Thorax in type species with 17 segments; outer pleural region wider (×1.25) than axis. Pygidium subhexagonal, widest at or behind midlength, with long, convex axis; posterior margin with 2 to 4 pairs of short spines that are progressively shorter from outermost to innermost. *lower Middle Cambrian:* Sweden, Norway, Poland, *A. (B.) oelandicus* Stage; ?western Mongolia.——FIG. 305,*1a,b.* **A. (B.) oelandicus* (SJÖGREN), Sweden (Öland); *a,* ?topotype, Borgholm, RM Ar 46245, ×1.5 (new); *b,* holotype, Borgholm or Storä Fro, RM Ar 1449, ×1 (new).

Anabaraceps REPINA, 1972, p. 29 [**A. kharaulachiensis;* OD; holotype (REPINA, 1972, p. 29, pl. 2, fig. 6–7), N383/101, CNIGR, St. Petersburg]. Glabella convex, widening anteriorly very slightly to subsemicircular frontal lobe and extending to anterior border; S2 transglabellar, shallow medially; L1 and L2 of equal size; palpebral area narrow (0.4 of glabella at S1); palpebral lobe extending from L3 almost to SO, with deep palpebral furrow; frontal area has distinctive, broad ridge subparallel to anterior border furrow; preglabellar field only slightly longer (sag.) than low anterior border; posterior

section of facial suture short; anterior section of facial suture cuts anterior margin almost in exsagittal line with outer edge of palpebral lobe. *Lower Cambrian (Toyonian):* Russia (northeastern Yakutia), *Paramicmacca* Zone.——FIG. 306,*2.* **A. kharaulachiensis;* holotype, cranidium, CNIGR N383/101, ×1.5 (new).

Anabaraspis LERMONTOVA, 1951a, p. 91 [**A. splendens;* OD; syntypes (LERMONTOVA, 1951a, pl. 13, fig. 1, 1a–1f), N120/5156, CNIGR, St. Petersburg]. Glabella subpentagonal, bluntly pointed frontally, widening gently to maximum width (tr.) across L4; S2 transglabellar, shallow medially; S3 and S4 faint; fixigena wide; palpebral lobe long, curved, extending from L1 to S3 and confluent with short eye ridge that meets glabella at or near S4; trace of parafrontal band near S4; frontal area relatively long (sag., exs.); preglabellar field and anterior border undifferentiated; frontal area large, about as wide (tr.) as distance across palpebral lobes; anterior section of facial suture long, strongly divergent; posterior section short; genal spine short, stout. Thorax with 15 to 18 segments having long, falcate spines; inner pleural region about as wide as axis. Pygidium longer than wide, subhexagonal, with long, flat

posterior area; posterior margin truncate or indented; axis short, with 1 axial ring. Surface smooth. *Lower Cambrian (Toyonian)–Middle Cambrian (lower Amgan):* Russia (northwestern and southeastern Yakutia), *A. splendens* and *Oryctocara* Zones.——Fig. 307,*2a,b.* **A. splendens; a,* lectotype, cranidium, eastern Siberia, locality not specified. Lower Cambrian ("*Protolemus* Zone"), ×1; *b,* exoskeleton lacking librigenae, Upper Toyonian to lower Amgan, north central Siberia (River Olenek), ×2 (Demokidov & Lazarenko, 1964, pl. 22, fig. 1).

Eccaparadoxides Šnajdr, 1957, p. 238 [**Paradoxides pusillus* Barrande, 1846, p. 11; OD; lectotype, meraspid cranidium (Šnajdr, 1958, p. 117), ČC 321, No. 1244, NMP, Prague] [=*Phanoptes* Hawle & Corda, 1847, p. 17, ICZN application pending; *Macrocerca* Pillet in Courtessole, Pillet, & Vizcaïno, 1988, p. 41 (type, *Eccaparadoxides macrocercus* Courtessole, 1967, p. 495; OD)]. Glabella widest across L4 or S4, well rounded frontally; S2 shallow medially; S3 and S4, if present, moderately deep, not reaching axial furrow; palpebral lobe extending from almost SO to L4; anterior section of facial suture moderately divergent in holaspis, almost transverse in meraspis; posterior section of facial suture short, cutting posterior margin almost in line (exs.) with edge of palpebral rim; preglabellar field in meraspis long (sag.), with sagittal preglabellar ridge; in holaspis preglabellar field is absent, anterior border is narrow (sag.) medially; hypostome not fused with rostral plate. Thorax with 16 to 18 segments having short to long, falcate pleural spines; inner pleural region narrow. Pygidium typically hexagonal, with terminal area short, long and spatulate, or very long; posterior margin straight or concave, ending in posterolateral angle or spine. *lower Middle Cambrian–upper Middle Cambrian:* England, Wales, France, Spain, Czech Republic, Sardinia, Sweden, Norway, northern Africa (Morocco, Algeria, Egypt), Russia (northern Siberia), western Mongolia, eastern USA (New York), eastern Canada (eastern Newfoundland, Nova Scotia, New Brunswick), Turkey.——Fig. 307,*1a,b.* **E. pusillus* (Barrande), middle Middle Cambrian (*E. pusillus* Zone), Czech Republic (Skryje); *a,* cranidium, MCZ 2754, ×1.5; *b,* pygidium, MCZ 2757b, ×4 (new).

Hydrocephalus Barrande, 1846, p. 19 [**H. carens;* SD Šnajdr, 1958, p. 129; lectotype, meraspid stage 8 or 9 (Šnajdr, 1958, pl. 24, fig. 32), ČC 210, No. 1053, NMP, Prague] [=*Phlysacium* Hawle & Corda, 1847, p. 16 (type, *P. paradoxum* Hawle & Corda, 1847, p. 16; M); *Rejkocephalus* Kordule, 1990, p. 55 (type, *Paradoxus rotundatus* Barrande, 1846, p. 11; OD)]. Glabella reaching to maximum width (tr.) across L4, about 1.5 times wider than across LO; S1 and S2 transglabellar; S3 and S4 short, shallow; in meraspis, glabella is relatively large and subcircular in front of SO; palpebral lobe moderately long, extending from L1 to S3; posterior branch of facial suture longer than in

Eccaparadoxides and *Acadoparadoxides* and cutting posterior margin at acute angle just inside genal angle; posterior border curving forward to acute inner spine angle that is not present in *Plutonides.* Hypostome not fused with rostral plate, with short spine in front of posterolateral angle. Thorax with 17 to 18 segments ending in short pleural spines; hindmost pleurae curving backwards more strongly; inner pleural region wider (tr.) than axis. Pygidium 1.6 times wider (tr.) than long, with bluntly rounded posterior margin; axis large, bluntly pointed, occupying 80% of length and more than one-half width of pygidium. [Supposed examples of genus in the United Kingdom, eastern Canada, and Scandinavia are here referred to *Plutonides* or are of uncertain generic position.] *lower Middle Cambrian–middle Middle Cambrian:* Czech Republic, Spain, Morocco.——Fig. 304,*3a.* *H. lyelli* (Barrande), middle Middle Cambrian (Jince Formation, *H. lyelli* Zone), Czech Republic (Jince); exoskeleton lacking librigenae, IRScNB 189, ×1.——Fig. 304,*3b.* **H. carens,* middle Middle Cambrian, *E. pusillus* Zone, Czech Republic (near Skryje); latex cast of left librigena, BMNH It.529b, ×1 (new).

Plutonides Hicks, 1895, p. 230, *nom. nov. pro Plutonia* Hicks, 1871, p. 399 (1869, p. 69, *nom. nud.*), *non* Stabile, 1864, p. 121 [**Plutonia Sedgwickii* Hicks, 1871, p. 399; M; lectotype, cranidium (here selected), A1086, SM, Cambridge]. Holaspis: glabella widening markedly to L4; frontal lobe long, up to 0.4 glabellar length (sag.), bluntly pointed, hanging over narrow (sag.) anterior border; S1 transglabellar, shallow medially; S2 to S4 well defined only abaxially; S3 and S4 may be effaced; preocular field small, narrower (tr.) than distance across palpebral lobes; palpebral lobe oblique, extending from L1 or S1 to about S4; posterior section of facial suture short, sigmoidal; hypostome not fused with rostral plate. Meraspis: glabella widening only slightly to broadly rounded; frontal lobe short (0.15 glabellar length); preglabellar field long (sag.), with sagittal preglabellar ridge; anterior border well defined, broadly curved, uniformly wide (sag.); S1 transglabellar; S2 to S4 deep, transverse; palpebral lobe long, well defined, confluent with eye ridge to axial furrow at or in front of S4. Thorax (where known) with 19 segments; transverse pleurae ending in short, falcate spines; inner pleural region slightly wider (tr.) than axis. Pygidium (not known for type species) subhexagonal, bluntly truncate posteriorly; axis convex, about one-half length of pygidium, with rounded tip; postaxial region slightly convex; 1 axial ring. Surface coarsely granulose or with meshlike pattern of fine, anastomosing ridges, or both. *middle Middle Cambrian:* Russia (Siberia); Mongolia; England, Wales, *T. gibbus* and *T. fissus* Zones; Sweden, *T. fissus–Pt. atavus* Zone; eastern Canada (eastern Newfoundland, Nova Scotia), *P. hicksi* Zone.——Fig. 306,*1a–c. P. hicksii* (Salter); *a,* cranidium, southwestern Wales (Solva), NMW 91.19G.2, ×4; *b,* cranidium, GSC

1a   Eccaparadoxides

1b

2a
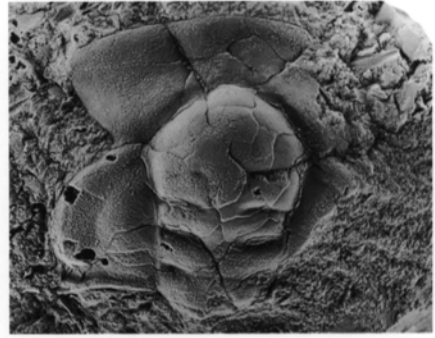
Anabaraspis

3a

3b   Schagonaria
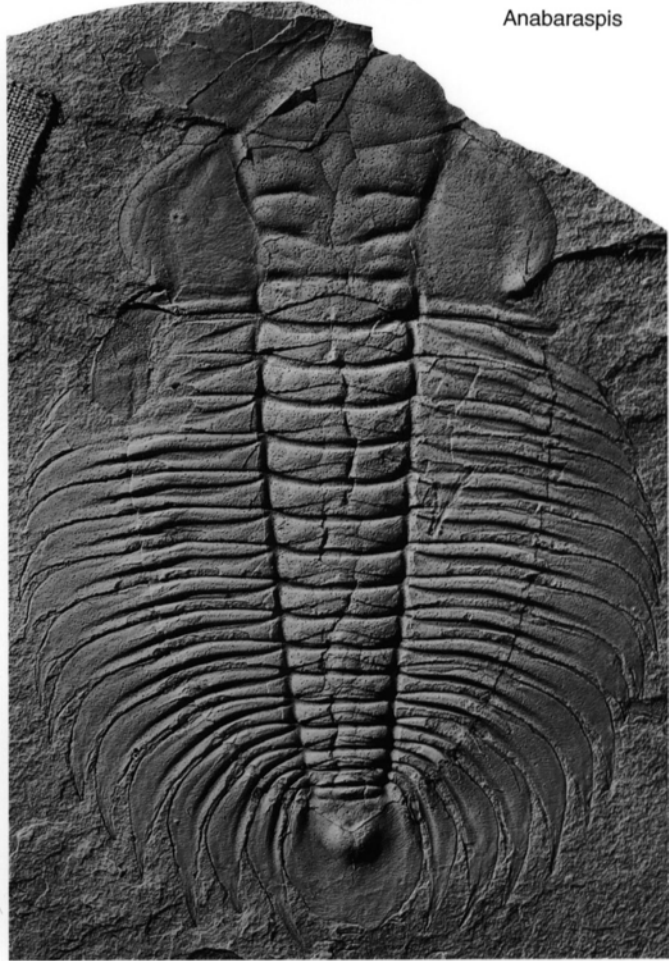
2b

Fig. 307. Paradoxididae (p. 475–478)

13070, ×1, and *c,* pygidium, GSC 101839, eastern Newfoundland (Trinity Bay and Random Island), ×2 (new).——Fig. 306,*1d.* **P. sedgwickii* (Hicks); lectotype, cranidium, southwestern Wales (St. David's), ×2.5 (new).

?Primoriella Repina, 1973, p. 170 [**P. bella;* OD; holotype (Repina, 1973, p. 171, pl. 35, fig. 1–2), 501/1551, CSGM, Novosibirsk]. Cranidium wider (tr.) than long; glabella convex, parallel sided posteriorly, expanding slightly to maximum width (tr.) at S4; frontal lobe subrounded, indenting roll-like anterior border; S1 transglabellar but faint medially; S2 transglabellar or not; S3 and S4 short (tr.), well defined; palpebral area and frontal area of equal width; eye lobe short, extending from L1 to S2 and continuous with eye ridge that ends at L4; anterior section of facial suture slightly divergent, posterior section relatively long. *uppermost Lower Cambrian:* Russia (far eastern Siberia), *Redlichina culmenica* beds.——Fig. 304,*2.* **P. bella,* Siberia (Primorye); holotype, cranidium, CSGM 501/1511, ×2 (new).

Schagonaria Poletaeva in Egorova & others, 1955, p. 111 [**S. tannuola;* OD; syntypes (Egorova & others, 1955, pl. 12, fig. 1a–1b), repository and numbers not specified]. Glabella elongate, widening anteriorly only slightly to maximum width (tr.) between S2 and preglabellar furrow; frontal lobe may reach anterior border; preglabellar ridge may be present in some specimens; S1 and S2 oblique inwards and backwards, nearly straight, meeting at sagittal line; fixigena narrow; palpebral lobe long, extending from L1 to L3 and merging with short eye ridge. Thorax with 16 segments. Pygidium poorly known but spatulate. *Middle Cambrian (Amgaian):* Russia (Ulukhema River, Tuva Region).——Fig. 307,*3a,b.* **S. tannuola; a,* dorsal exoskeleton, CSGM 296/75, ×4; *b,* cranidium, CSGM 296, ×2 (new).

Family CENTROPLEURIDAE Angelin, 1854

[Centropleuridae Angelin, 1854 in 1851–1878, p. 87]

Glabella widest (tr.) across L4; S1 transglabellar, relatively wide and deep; S2 and S3 incised, narrow, not transglabellar; S4 very oblique forwards and outwards, making large angle with S3; palpebral lobe generally long; fixigena bearing exsagittal, ridgelike baccula; anterior section of facial suture transverse or retrodivergent; genal spine long; distal end of posterior border may curve forwards to form intergenal angle; hypostome subquadrate. Thorax with 14 or 15 to 20 (?or more) segments; pleurae flat, truncate or with short spines; last 3 larger, with strongly falcate pleural spines. Pygidium transverse, with 2 to 4 pairs of mar-ginal spines; width (tr.) may be one-half to two-thirds that of cephalon; surface commonly with anastomosing ridges. *Middle Cambrian.*

Centropleura Angelin, 1854 in 1851–1878, p. 87 [**Paradoxides Loveni* Angelin, 1851 in 1851–1878, p. 2; OD; Angelin's figured specimens (1851 in 1851–1878, pl. 3, fig. 1–3) from Andrarum, Sweden, are not identified with certainty, but a syntype and topotypes were illustrated by Westergård, 1950a, pl. 1, fig. 1–3]. S2 and S3 straight, transverse; anterior section of facial suture retrodivergent; palpebral lobe narrow (tr.); fixigena with elongate (exsag.) baccula; posterior border curving forwards distally. Thorax (where known) with 16 segments; pleural tips truncate or with short spine. Pygidium transversely oval; axis slightly more than one-half length of pygidium, with about 4 pairs axial rings; 2 pairs of marginal spines. *upper Middle Cambrian:* Scandinavia, Greenland, Canada, USA, Australia, Siberia, China (Xinjiang: Tianshan), *L. laevigata* to *Centropleura* Zone (Gansu, Hunan-Guizhou border).

C. (Centropleura). Glabella with prominent frontal lobe; palpebral lobe long (extending from opposite SO or L1 to L4), curving inwards posteriorly, ending near to or well forward of posterior border; fixigena widest (tr.) opposite S1 or L2. *upper Middle Cambrian:* Sweden, Denmark, *S. brachymetopa* Zone; Greenland, *L. laevigata* Zone; Canada (Gaspé; ?western Newfoundland: Cow Head boulders); USA, Vermont (St. Alban's Shale), New York, western Nevada; Australia, *L. laevigata* Zone; Bennett Island; eastern Siberia, *P. forchhammeri* Zone; China (Xinjiang: Tianshan), *L. laevigata to Centropleura* Zone (Gansu, Hunan-Guizhou border).——Fig. 308,*2a,b.* **C. (C.) loveni* (Angelin); *a,* lectotype, small cranidium, Andrarum, Skåne, RM Ar32354, ×8; *b,* pygidium, probably same locality, RM Ar1613, ×3 (new).

C. (Beishanella) Xiang & Zhang, 1985, p. 97 [**Centropleura? beishanensis* Liu & Zhang, 1979, p. 5; M; figured syntypes (Liu & Zhang, 1979, pl. 1, fig. 15–17), XTr. 908–910, repository not ascertained]. Differs from *C. (Centropleura)* in having more weakly clavate glabella with less prominent frontal lobe; fixigena very narrow (tr.), about 0.3 of glabellar width. Thorax unknown. Pygidium similar to *C. (Centropleura).* *upper Middle Cambrian:* northwestern China (Gansu), lower part of Shuangyingshan Formation, (Tianshan), *L. laevigata–Centropleura* Zone.——Fig. 308,*3a,b.* **C. (B.) beishanensis* (Liu & Zhang), Tianshan, lower part of Shuangyingshan Formation; *a,* syntype cranidium, XTr. 908, ×1; *b,* syntype, pygidium, XTr. 909, ×2.5 (Liu & Zhang, 1979, pl. 1, fig. 15–16).

Anopolenus Salter, 1864c, p. 236 [**A. Henrici;* M; lectotype (Morris, 1988, p. 20), 42644, BMNH,
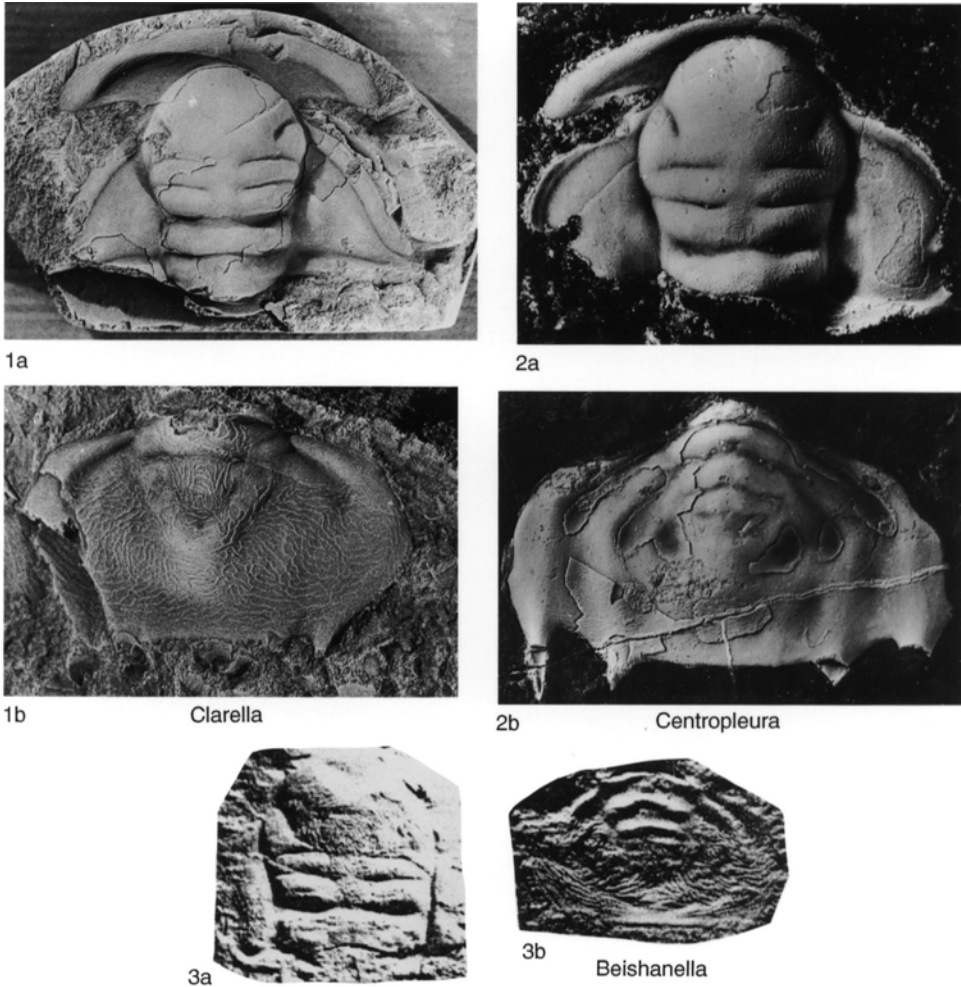
Fig. 308. Centropleuridae (p. 478–480)

London; A.5367, SM, Cambridge, Menevian Beds, St. David's, southwestern Wales]. Glabella only slightly clavat; S2 and S3 approximately transverse but slightly curved, convex forwards; anterior section of facial suture long, transverse; baccula shorter than in *Centropleura;* palpebral lobe broader than in *Centropleura,* long and evenly curved, extending from L4 to SO and reaching to posterolateral corner of cranidium; posterior margin almost straight, transverse. Thorax with 16 segments, all except last 3 having truncate pleural tips. Pygidium transversely ovate in outline, with border and 3 pairs of marginal spines; axis more than three-fourths pygidial length, with about 4 axial rings. *middle Middle Cambrian:* United Kingdom, *Pt. punctuosus* Zone; Canada (eastern Newfoundland), *P. davidis* Zone; Russia (eastern Siberia), *P. davidis* Zone.——

Fig. 309,*2a–c.* **A. henrici; a,c,* eastern Newfoundland (Manuels River); *a,* cranidium, GSC 13109, ×1.5; *c,* pygidium, GSC 13114, ×2 (new); *b,* cranidium, topotype, middle Middle Cambrian, Menevian Beds, southwstern Wales (St. David's), NMW 91.19G.3, ×3 (new).

Clarella Howell, 1933, p. 219 [*Anapolenus [sic] *venustus* Billings, 1872, p. 474; OD; lectotype selected herein, 284a, GSC, Ottawa]. Like *Anopolenus,* but glabella showing greater expansion forward of S1 and palpebral lobe broader and slightly curved sigmoidally. Thorax with 14? or 15 segments, where known; pygidium without border but with 3 to 4 pairs of short, marginal spines; axis short, with 1 to 2 axial rings. *middle Middle Cambrian–upper Middle Cambrian:* Canada (eastern Newfoundland), *P. hicksii–P. davidis* Zones; United
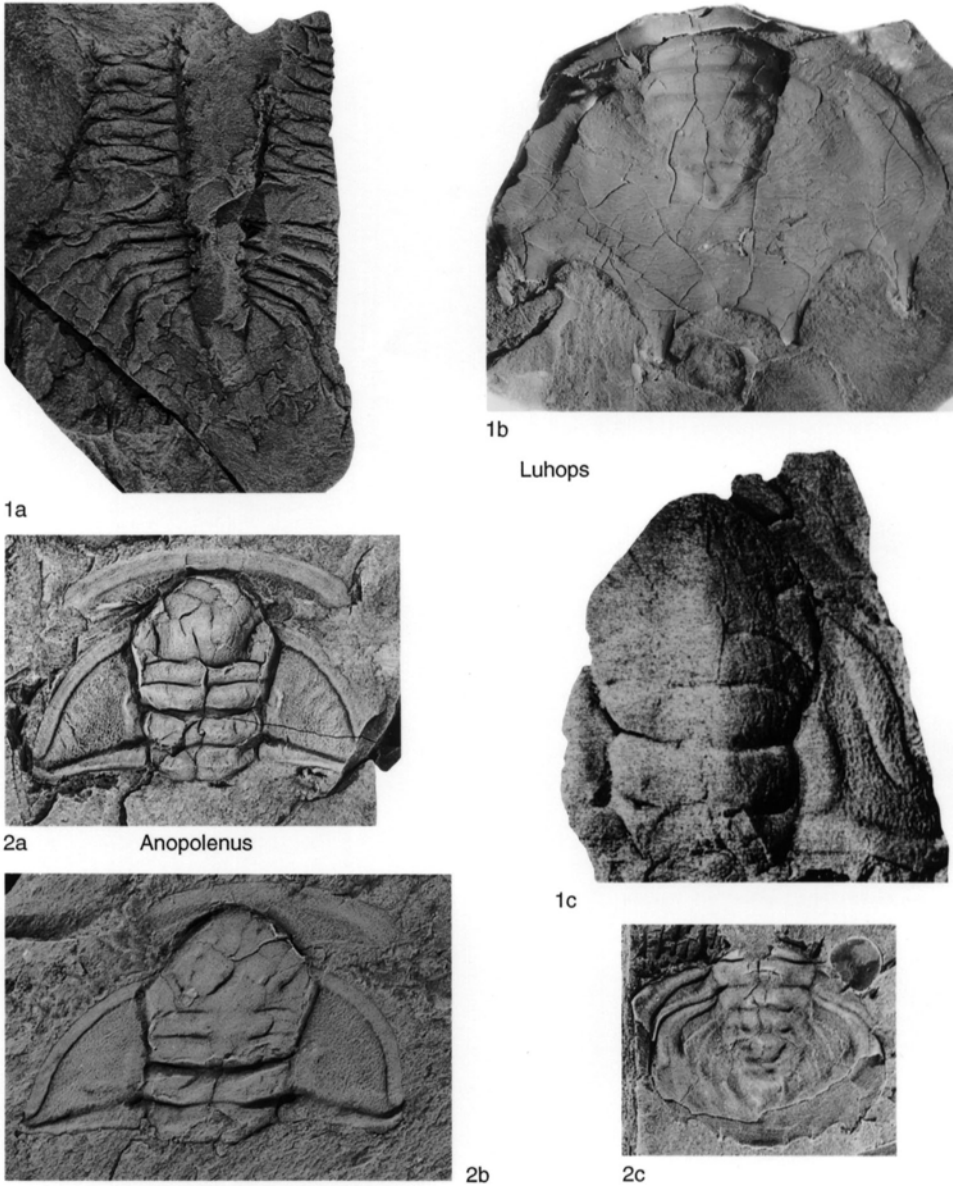
FIG. 309. Centropleuridae (p. 479–481)

Kingdom, *H. parvifrons–Pt. punctuosus* Zones; southern France, *Pt. punctuosus* Zone; Sweden, *Pt. punctuosus–S. brachymetopa* Zones.——FIG. 308,*1a,b*. **C. venusta* (BILLINGS), *P. hicksii* Zone, eastern Newfoundland; *a,* cranidium, lectotype, Manuels River Formation, Trinity Bay, GSC 284a, ×3; *b,* pygidium, St. Marys Bay, GSC 13106, ×5 (new).

Luhops ŠNAJDR, 1957, p. 239 [**Paradoxides expectans* BARRANDE, 1852, p. 918; OD; lectotype, Skryje Formation, *E. pusillus* Zone, Skryje, Czech Republic (ŠNAJDR, 1958, p. 153), ČC 313, No. 1125, NMP, Prague]. Diagnosis based on type specimens only. Thoracic pleural tips with short spines, except for posterior 3 segments; pygidium with relatively short axis having 2 to 3 axial rings and 2 pairs of

robust marginal spines. Assigned cranidium (FATKA, KORDULE, & ŠNAJDR, 1981) with S2 and S3 convex forwards, S3 oblique inwards and forwards; anterior section of facial suture relatively short; palpebral lobe broad at midlength, shorter than in *Clarella,* extending from L4 to L1, and with posterior end tapered, turned outwards, and lying well forward of posterior margin. *middle Middle Cambrian:* Czech Republic, *E. pusillus* Zone; United Kingdom, *T. fissus* or *H. parvifrons* Zones; Denmark, *Pt. punctuosus* Zone.——FIG. 309,*1a–c.* **L. expectans,* Czech Republic; *a,* thorax and pygidium, Skryje, Schary Collection, MCZ 3151, ×1.5 (Barrande, 1872, pl. 14, fig. 35); *b,* pygidium, Týřovice, NMP L.14078, ×1 (Šnajdr, 1977, pl. 1, fig. 3); *c,* cranidium, Týřovice, ×2.75 (Fatka, Kordule, & Šnajdr, 1981, pl. 2, fig. 8).

REFERENCES

Abdullaev, R. N., & O. N. Khaletskaya. 1970. Nizhniy Paleozoy Chatkalskogo Khrebta: Trilobity i Graptolity Ordovika Pskemskogo Khrebta [Lower Paleozoic of the Chatkalskiy Range: Trilobites and Graptolites of the Ordovician of the Pskemskiy Range]. Institut Geologii i Geofiziki. Tashkent. 104 p., 8 pl.

Adams, C. G., & D. V. Ager, eds. 1967. Aspects of Tethyan Biogeography. Publication no. 7. The Systematics Association. London. vi + 336 p.

Adrain, J. M., & B. D. E. Chatterton. 1990. *Odontopleura* (Trilobita, Silurian), and a method of constrained congruency analysis. Journal of Paleontology 64:600–614, fig. 1–7.

Ahlberg, Per. 1985. Lower Cambrian trilobite faunas from the Scandinavian Caledonides: A review sister group. *In* G. G. Gee & B. A. Sturt, eds., The Caledonide Orogen: Scandinavia and Related Areas. John Wiley & Sons. New York. p. 339–346.

———. 1988. Ocular structures in an Ordovician agnostid trilobite. Lethaia 21:115–120, fig. 1–3.

———. 1989. The type species of the Ordovician agnostid trilobite *Geragnostus* Howell, 1935. Palaeontologische Zeitschrift 63:309–317, fig. 1–3.

———. 1991. Trilobites in the Lower Cambrian of Scandinavia. Geologiska Foereningens i Stockholm Foerhandlingar 113:74–75, fig. 1.

Ahlberg, Per, Jan Bergström, & Jan Johansson. 1986. Lower Cambrian olenellid trilobites from the Baltic Faunal province. Geologiska Foereningens i Stockholm Foerhandlingar 108:39–56, fig. 1–16.

Alberch, Pere, S. J. Gould, G. F. Oster, & D. B. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–317, fig. 1–25.

Alberti, G. K. B. 1969. Trilobiten des jüngeren Siluriums sowie des Unter- und Mitteldevons. I. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 520:1–692, fig. 1–55, pl. 1–52.

———. 1970. Trilobiten des jüngeren Siluriums sowie des Unter- und Mitteldevons. II. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 525:1–233, fig. 1–20, pl. 1–20.

———. 1975. Zur paläozoogeographischen Verbreitung von *Warburgella rugulosa* (Alth 1874) (Trilobita, Devon-Basis). Mitteilungen der Geologisch-Paläontologisches Institut der Universität Hamburg 44:1–10, 1 pl.

———. 1981. Beziehungen zwischen "herzynischen" Trilobiten-Faunen aus NW-Marokko und Deutschland (Unter- und Mittel-Devon). Natur und Museum 111:362–369, fig. 1–4.

Alberti, Helmut. 1972. Ontogenie des Trilobiten *Phacops accipitrinus*. Neues Jahrbuch fuer Geologie und Palaeontologie, Abhandlungen 141:1–36, fig. 1–11.

Allen, P. M., A. A. Jackson, & A. W. A. Rushton. 1981. The stratigraphy of the Mawddach Group in the Cambrian succession of North Wales. Proceedings of the Yorkshire Geological Society 43:295–329, fig. 1–5, pl. 16–17.

Alpert, S. P., & J. N. Moore. 1975. Lower Cambrian trace fossil evidence for predation on trilobites. Lethaia 8:223–230, fig. 1–6.

Angelin, N. P. 1851–1878. Palaeontologia Scandinavica. Pars 1. Crustacea Formationis Transitionis [fasc. 1 (1851): Palaeontologia Suecica, p. 1–24, pl. 1–24; fasc. 2 (1854): Palaeontologia Scandinavica, p. i–ix, 21–92, pl. 25–41; republished in combined and revised form (1878): G. Lindström, ed., x + 96 p., 41 pl.]. Norstedt & Söner. Stockholm.

Apollonov, M. K. 1975. Ordovician trilobite assemblages of Kazakhstan. Fossils and Strata 4:375–380.

———. 1991. Cambrian-Ordovician boundary beds in the USSR. *In* C. R. Barnes & S. H. Williams, eds., Advances in Ordovician Geology. Geological Survey of Canada, Paper 90-9. p. 33–45, fig. 1–2.

Apollonov, M. K., & M. N. Chugaeva. 1982. Batyrbaysayskiy razrez kembriya i Ordovika v Malom Karatau (Yuzhnyy Kazakhstan) [Batyrbaisai section in the Maly Karatau (south Kazakhstan)]. Izvestiya Academii Nauk SSSR, Seriya Geologicheskaya 4:34–45.

In Russian.

Apollonov, M. K., M. N. Chugaeva, & S. V. Dubinina. 1981. The Cambrian-Ordovician boundary in the Maly Karatau Range, south Kazakhstan. *In* M. E. Taylor, ed., Short Papers for the Second International Symposium on the Cambrian System. United States Geological Survey, Open-file Report 81-743. p. 15–17.

Archinal, A. 1994. Zur Morphologie, Systematik, Stratigraphie und Ökologie der Gattung *Scutellum* (Trilobita: Devon). Senckenbergiana Lethaea 74:291–324.

Astashkin, V. A., T. V. Pegel, Yu. Ya. Shabanov, S. S. Sukhov, V. M. Sundukov, L. N. Repina, A. Yu. Rozanov, & A. Yu. Zhuravlev. 1991. The Cambrian System on the Siberian Platform. International Union of Geological Sciences, Publication 27:1–133.

Ax, Peter. 1987. The Phylogenetic System. J. Wiley & Sons. New York. 340 p., 90 fig.

Babcock, L. E. 1982. Original and diagnetic color patterns in two phacopid trilobites from the Devonian of New York. *In* Bernard Mamet & M. J. Copeland, eds., Third North American Paleontological Convention, Proceedings, vol. 1. Business and Economic Service Limited. Toronto, Ontario. p. 17–22, fig. 1–2, pl. 1.

———. 1993. Trilobite malformations and the fossil record of behavioral asymmetry. Journal of Paleontology 67:217–229, 6 fig.

———. 1994a. Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Cap Stanton formations (Middle Cambrian), North Greenland. Grønlands Geologiske Undersøgelse, Bulletin 169:79–127, 31 fig.

———. 1994b. Biogeography and biofacies patterns of Middle Cambrian polymeroid trilobites from North Greenland: Palaeogeographic and palaeooceanographic implications. Grønlands Geologiske

Undersøgelse, Bulletin 169:129–147, 7 fig.

Babcock, L. E., & S. E. Speyer. 1987. Enrolled trilobites from the Alden Pyrite Bed, Ledyard Shale (Middle Devonian) of western New York. Journal of Paleontology 61:539–548, fig. 1–5.

Baer, K. E. von. 1828. Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion. Bornträger. Königsberg. 264 p.

Balashova, E. A. 1976. Sistematika Trilobitov Asaphina i ikh Predstaviteli v SSSR [Taxomony of Trilobites Asaphina and their Representatives in the U.S.S.R. Ministerstvo Geologii SSSR, Severo-Zapadnoe Territorial'noe Geologicheskoe Upravlenie. Leningrad. 215 p.

Baldwin, C. T. 1977. Internal structures of trilobite trace fossils indicative of an open surface furrow origin. Palaeogeography, Palaeoclimatology, Palaeoecology 21:273–284, fig. 1–2, pl. 1–2.

Bancroft, B. B. 1929. Some new species of *Cryptolithus* (s.l.), from the Upper Ordovician. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 73:67–98, fig. 1–5, pl. 1–2.

Barrande, Joachim. 1846. Notice Préliminaire sur le Système Silurien et les Trilobites de Bohême. Hirschfeld. Leipzig. 96 p.

———. 1852. Système Silurien du Centre de la Bohême. I. Recherches Paléontologiques, vol. 1 (Crustacés: Trilobites). Prague & Paris. xxx + 935 p., 51 pl.

———. 1872. Système Silurien du Centre de la Bohême, I. Recherches Paléontologiques, supplément au vol. 1 (Trilobites, Crustacés divers et Poissons). Prague & Paris. 647 p., 37 pl.

Barrientos, Yolande, & M. S. Laverack. 1986. The larval crustacean dorsal organ and its relationship to the trilobite median tubercle. Lethaia 19:309–313, fig. 1–3.

Bassett, M. G., R. M. Owens, & A. W. A. Rushton. 1976. Lower Cambrian fossils from the Hell's Mouth Grits, St. Tudwal's Peninsula, North Wales. Journal of the Geological Society, London 132:623–644, fig. 1–5, pl. 1–3.

Beecher, C. E. 1893a. Larval forms of trilobites from the Lower Helderberg group. American Journal of Science (series 3) 46:142–147, pl. 2.

———. 1893b. A larval form of *Triarthrus.* American Journal of Science (series 3) 46:361–362.

———. 1895a. The larval stages of trilobites. The American Geologist 16:166–197, pl. 8–10.

———. 1895b. Structure and appendages of *Trinucleus.* American Journal of Science (series 3) 49:307–311, pl. 3.

———. 1897. Outline of a natural classification of the trilobites. American Journal of Science (series 4) 3:89–106, 181–207, pl. 3.

Belt, T. 1867. On some new trilobites from the upper Cambrian rocks of North Wales. Geological Magazine (decade 1) 4:294–295, pl. 12.

———. 1868. On the "Lingula Flags" or "Festiniog Group" of the Dolgelly District. Part 3. Geological Magazine (decade 1) 5:5–11, pl. 2.

Bengtson, Stefan, Simon Conway Morris, B. J. Cooper, P. A. Jell, & B. N. Runnegar. 1990. Early Cambrian fossils from South Australia. Association of Australasian Palaeontologists, Memoir 9. Brisbane. 364 p., 218 fig.

Bergeron, Jules. 1889. Étude géologique du Massif ancien situé au sud du plateau central. Annales des Sciences Geologiques 22:1–361, pl. 1–9.

———. 1899. Étude de quelques trilobites de Chine. Bulletin de la Société Géologique de France (series 3) 27:499–516, pl. 13.

Bergström, Jan. 1972. Appendage morphology of the trilobite *Cryptolithus* and its implications. Lethaia 5:85–94, fig. 1–3.

———. 1973a. Organization, life and systematics of trilobites. Fossils and Strata 2:1–69, fig. 1–16, pl. 1–5.

———. 1973b. Classification of olenellid trilobites and some Balto-Scandian species. Norsk Geologisk Tidsskrift 53:283–314, fig. 1–22.

———. 1973c. Palaeoecologic aspects of an Ordovician *Tretaspis* fauna. Acta Geologica Polonica 23:179–206, fig. 1–4, pl. 1–2.

———. 1973d. Trilobite segmentation. Acta Geologica Polonica 23:207–219, fig. 1–3.

———. 1976. Lower Palaeozoic trace fossils from eastern Newfoundland. Canadian Journal of Earth Sciences 13:1613–1633, fig. 1–19.

———. 1977. Proetida—a disorderly order of trilobites. Lethaia 10:95–105, fig. 1–5.

Bergström, Jan, & Per Ahlberg. 1981. Uppermost Lower Cambrian biostratigraphy in Scania, Sweden. Geologisska Foereningens i Stockholm Foerhandlingar 103(2):193–214.

Bergström, Jan, & Günther Brassel. 1984. Legs in the trilobite *Rhenops* from the Lower Devonian Hunsrück Slate. Lethaia 17:67–72, fig. 1–3.

Bergström, Jan, & Riccardo Levi-Setti. 1978. Phenotypic variation in the Middle Cambrian trilobite *Paradoxides davidis* Salter at Manuels, SE Newfoundland. Geologica et Palaeontologica 12:1–40, fig. 1–11, pl. 1–10.

Bernays, E. A. 1986. Diet-induced head allometry among foliage-chewing insects and its importance for gramnivores. Science 231:495–497, fig. 1–2.

Bernays, E. A., & J. Hamai. 1987. Head size and shape in relation to grass feeding in Acridoidea (Orthoptera). International Journal of Insect Morphology and Embryology 16:323–336.

Best, R. V. 1961. Intraspecific variation in *Encrinurus ornatus.* Journal of Paleontology 35:1029–1040, fig. 1, pl. 124.

Beyrich, E. 1845. Über einige böhmischer Trilobiten. Berlin. 47 p., 1 pl.

Billings, Elkanah. 1860. On some new species of fossils from the limestone near Point Lévi opposite Quebec. Proceedings of the Canadian Naturalist and Geologist 5:301–324, 30 fig.

———. 1865. Palaeozoic fossils, vol. 1. Geological Survey of Canada. Montreal. 426 p., 399 fig.

———. 1870. Notes on some specimens of Lower Silurian trilobites. Quarterly Journal of the Geological Society of London 26:479–486.

———. 1872. On some fossils from the Primordial rocks of Newfoundland. The Canadian Naturalist 6:465–479.

Birkenmajer, Krzysztof, & D. L. Bruton. 1971. Some

trilobite resting and crawling traces. Lethaia 4:303–319, fig. 1–14.

Blaker, M. R. 1988. A new genus of nevadiid trilobite from the Buen Formation (Early Cambrian) of Peary Land, central North Greenland. Grønlands Geologiske Undersøgelse, Rapport 137:33–41, 6 fig.

Boeck, C. 1827. Notitser til Laeren om Trilobiterne. Magazin for Naturvidenskaberne, Christiania 8(1):11–44.

Bohlin, Birger. 1949. The Asaphus Limestone in northernmost Öland. Bulletin of the Geological Institution of the University of Uppsala 33:529–570, fig. 1–10, pl. 1–2.

———. 1960. Trilobites of the genus *Megistaspis* from the Vaginatum Limestone of Scandinavia. Bulletin of the Geological Institutions of the University of Uppsala 38:155–205, fig. 1–28, pl. 1–12.

Bornemann, J. G. 1888. Die Versteinerungen des Cambrischen Schichtensystems der Insel Sardinien. Nova Acta Kaiserlich Leopoldinish-Carolinische Deutsche Akademie der Naturforscher (Halle) 56(3):427–524, pl. 35–44.

———. 1891. Die Versteinerungen des Cambrischen Schichtsystems der Insel Sardinien. Abt. 2. Nova Acta Kaiserlich Leopoldinish-Carolinische Deutsche Akademie der Naturforscher (Halle), Nova Acta 56(3):1–101 (427–528), pl. 35–40.

Boucot, A. J. 1975. Evolution and extinction rate controls. Elsevier. Amsterdam. xvi + 428 p., 44 fig., 4 pl.

———. 1988. Devonian biogeography: An update. *In* N. J. McMillan, A. F. Embry, & D. J. Glass, eds., Devonian of the World, vol. 3. Canadian Society of Petroleum Geologists. Calgary. p. 211–227, fig. 1–3.

———. 1990. Silurian and pre-Upper Devonian Bioevents. *In* E. G. Kauffman & O. H. Walliser, eds., Extinction Events in Earth History. Lecture Notes in Earth Sciences 30. p. 124–132.

Boudda, A., G. Choubert, & A. Faure-Muret. 1979. Essai de Stratigraphie de la Couverture sédimentaire de l'Anti-Atlas: Adoudounien Cambrien Inférieur. Notes et Mémoires du Service des Mines et de la Carte Géologique du Maroc 271:1–96, fig. 1–20.

Branson, C. C. 1965. New specimens of *Homotelus* from the Bromide Formation. Oklahoma Geology Notes 25:294–296, fig. 1–3.

Brasier, M. D. 1976. An Archaeocyathid-trilobite association in Sardinia and its stratigraphic significance. Rivista Italiana di Paleontologia e Stratigrafia 82(2):267–278, pl. 25.

———. 1989. Towards a biostratigraphy of the earliest skeletal biotas. *In* J. W. Cowie & M. D. Brasier, eds., The Precambrian-Cambrian Boundary. Oxford Monographs on Geology and Geophysics, vol. 12. Clarendon Press. Oxford. p. 117–165.

Brassel, Gunther, & Jan Bergström. 1978. Der Trilobit *Parahomalonotus planus* (Koch, 1883), ein Homalonotide aus dem unterdevonischen Hunsruckschiefe. Geologische Jahrbuch Hessen 106:5–11, 2 fig., 2 pl.

Brauckmann, C. 1978. Die Cyrtosymbolinae mit geblahten Wangen-Stacheln (Trilobita—Dinantium bis Namurium). Senckenbergiana Lethaea 59:137–203, 45 fig., 2 pl.

Brenchley, P. J. 1984. Late Ordovician extinctions and their relationships to the Gondwana glaciation. *In* P.

J. Brenchley, ed., Fossils and Climate. Wiley. New York. p. 291–316.

———. 1989. The late Ordovician extinction. *In* S. K. Donovan, ed., Mass Extinctions. Belhaven Press. London. p. 104–132, fig. 6.1–6.5.

Brezinski, D. K. 1986a. An opportunisitic Upper Ordovician trilobite assemblage from Missouri. Lethaia 19:315–325, fig. 1–7.

————. 1986b. Trilobite associations from the Chouteau Formation (Kinderhookian) of central Missouri. Journal of Paleontology 60:870–881, fig. 1–5.

———. 1988a. Trilobites of the Gilmore City Limestone (Mississippian) of Iowa. Journal of Paleontology 62:241–245, fig. 1–2.

———. 1988b. Appalachian Carboniferous trilobites. Journal of Paleontology 62:934–945, fig. 1–3.

———. 1992. Permian trilobites from West Texas. Journal of Paleontology 66:924–943, fig. 1–10.

Briggs, D. E. G. 1994. Giant predators from the Cambrian of China. Science 264:1283–1284.

Briggs, D. E. G., S. H. Bottrell, & Robert Raiswell. 1991. Pyritization of soft-bodied fossils: Beecher's Trilobite Bed, Upper Ordovician, New York State. Geology 19:1221–1224, fig. 1–3.

Briggs, D. E. G., & P. R. Crowther, eds. 1990. Palaeobiology: A Synthesis. Blackwell Scientific Publications. Oxford, London, Edinburgh, Boston, Melbourne. xiii + 583 p.

Briggs, D. E. G., & G. D. Edgecombe. 1993. Beecher's Trilobite bed. Geology Today (May–June 1993):97–102.

Briggs, D. E. G., & R. A. Fortey. 1992. The early radiation of the Arthropoda. *In* Jere Lipps & P. E. Signor, eds., Origin and Early Evolution of the Metazoa. Plenum. New York. p. 336–374, fig. 1–8.

Briggs, D. E. G., R. A. Fortey, & E. N. K. Clarkson. 1988. Extinction and the fossil record of the arthropods. *In* G. P. Larwood, ed., Extinction and Survival in the Fossil Record. Clarendon Press. Oxford. p. 171–209, 18 fig.

Briggs, D. E. G., R. A. Fortey, & M. A. Wills. 1992. Morphological disparity in the Cambrian. Science 256:1670–1673, fig. 1–3.

Briggs, D. E. G., & A. W. A. Rushton. 1980. An arthropod trace fossil from the Upper Cambrian Festiniog Beds of North Wales and its bearing on trilobite locomotion. Geologica et Palaeontologica 14:1–7, fig. 1, pl. 1.

Briggs, D. E. G., & H. B. Whittington. 1985. Modes of life of arthropods from the Burgess Shale, British Columbia. Transactions of the Royal Society of Edinburgh, Earth Sciences 76:149–160, fig. 1–4.

Bright, R. C. 1959. A paleoecologic and biometric study of the Middle Cambrian trilobite *Elrathia kingii* (Meek). Journal of Paleontology 33:83–98, fig. 1–8, pl. 17–18.

Brögger, W. C. 1875. Fossiler fra Øxna og Kletten. Geologiska Foereningens i Stockholm Foerhandlingar 2 (1874–1875):572–580, pl. 25.

———. 1878. Om paradoxidesskifrene ved Krekling. Nyt Magazin for Naturvidenskaberne 24:18–88, pl. 1–6.

Brongniart, A. 1822. Les Trilobites. *In* A. Brongniart

& A.-G. Desmarest, Histoire naturelle des crustacés fossiles, sous les rapports zoölogiques et géologiques. Paris & Strasbourg. p. 1–65, pl. 1–2.

Brooks, H. K. 1957. Chelicerata, Trilobitomorphia, Crustacea (exclusive of Ostracoda) and Myriapoda. *In* H. S. Ladd, ed., Treatise on Marine Ecology and Paleoecology. Vol. 2: Paleoecology. Geological Society of America, Memoir 67. p. 895–929.

Bruton, D. L. 1966. A revision of the Swedish Ordovician Odontopleuridae (Trilobita). Bulletin of the Geological Institutions of the University of Uppsala 67:1–40, fig. 1–9, pl. 1–6.

———. 1968a. The trilobite genus *Panderia* from the Ordovician of Scandinavia and the Baltic areas. Norsk Geologisk Tidsskrift 48:1–53, fig. 1–3, pl. 1–12.

———. 1968b. A revision of the Odontopleuridae (Trilobita) from the Palaeozoic of Bohemia. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Matematisk-Naturvidenskapelig Klasse (new series) 25:1–73, pl. 1–11.

———. 1976. The trilobite genus *Phillipsinella* from the Ordovician of Scandinavia and Great Britain. Palaeontology 19:699–718, fig. 1, pl. 104–108.

———. 1983. The morphology of *Celmus* (Trilobita) and its classification. Special Papers in Palaeontology 30:213–220.

Bruton, D. L., & Winfried Haas. 1997. Functional morphology of Phacopinae (Trilobita) and the mechanics of enrolment. Palaeontographica (Abt. A) 245:43 p., 25 fig., 14 pl.

Bruton, D. L., & A. W. Owen. 1988. The Norwegian Upper Ordovician illaenid trilobites. Norsk Geologisk Tidsskrift 68:241–258, fig. 1–10.

Bullard, Edward, J. E. Everett, & A. G. Smith. 1965. The fit of the continents around the Atlantic. Philosophical Transactions of the Royal Society of London (series A) 258:41–51, fig. 1–8.

Burling, L. D. 1916. *Paedeumias* and the Mesonacidae, with description of a new species, having at least 44 segments, from the Lower Cambrian of British Columbia. The Ottawa Naturalist 30:53–58, pl. 1.

Burrett, Clive. 1973. Ordovician biogeography and continental drift. Palaeogeography, Palaeoclimatology, Palaeoecology 13:161–201, fig. 1–3.

Burrett, Clive, & Robert Richardson. 1980. Trilobite biogeography and Cambrian tectonic models. Tectonophysics 63:155–192, fig. 1–6.

Busch, R. M., & F. M. Swartz. 1985. Molting and description of a new homalonotid trilobite from Pennsylvania. Journal of Paleontology 59:1062–1074, fig. 1–5.

Butterfield, N. J. 1990. Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. Paleobiology 16:272–286, fig. 1–4.

Butts, C. 1926. The Palaeozoic Rocks. *In* G. I. Adams, C. Butts, L. W. Stephanson, & W. Cooke, eds., Geology of Alabama. Geological Survey of Alabama, Special Report 14. p. 41–230, pl. 3–76.

Callaway, Charles. 1877. On a new area of Upper Cambrian rocks in South Shropshire, with a description of a new fauna. Quarterly Journal of the Geological Society of London 33:652–672, pl. 24.

Campbell, K. S. W. 1967. Trilobites of the Henryhouse Formation (Silurian) in Oklahoma. Oklahoma Geological Survey, Bulletin 115:1–68, fig. 1–7, pl. 1–19.

———. 1975. The functional morphology of *Cryptolithus.* Fossils and Strata 4:65–86, fig. 1–16, pl. 1–2.

———. 1976. The functional anatomy of phacopid trilobites: Musculature and eyes. Journal and Proceedings, Royal Society of New South Wales 108:168–188, fig. 1–12, pl. A–C.

———. 1977. Trilobites of the Haragan, Bois d'Arc and Frisco Formations (Early Devonian) Arbuckle Mountains region, Oklahoma. Oklahoma Geological Survey, Bulletin 123:1–227, fig. 1–36, pl. 1–40.

———. 1982. A note on the Haragan trilobite *Dicranurus hamatus elegantus.* Oklahoma Geology Notes 42(1):4–6, fig. 1.

Capèra, J. C., R. Courtessole, & J. Pillet. 1978. Contribution à l'étude de l'Ordovicien inférieur de la Montagne Noire. Biostratigraphie et révision des Agnostida. Annales de la Société Géologique du Nord 98:67–88.

Chang, Taiyung. 1965. A New Lower Cambrian Trilobite from Keping, western Sinkiang. Acta Palaeontologica Sinica 13(1):154–158, pl. 1.

In Chinese, with English summary.

Chang, Wentang [see also Zhang, Wentang]. 1953. Some Lower Cambrian trilobites from western Hupei. Acta Palaeontologica Sinica 1(3):121–149, pl. 1–4.

In Chinese and English.

———. 1957. Preliminary note on the Lower and Middle Cambrian stratigraphy of Poshan, Central Shantung. Acta Palaeontologica Sinica 5(1):13–32, pl. 1–2.

———. 1962. On the genus *Eoredlichia.* Acta Palaeontologica Sinica 10(1):36–44, 1 fig., pl. 1.

In Chinese, with English summary.

———. 1966. On the classification of Redlichiacea, with description of new families and new genera. Acta Palaeontologica Sinica 14(2):135–184, fig. 1–17, pl. 1–6.

In Chinese, with English summary.

———. 1980. A review of the Cambrian of China. Journal of the Geological Society of Australia 27:137–150.

———. 1988. The Cambrian System in eastern Asia. International Union of Geological Sciences, Publication 24:1–81.

Chatterton, B. D. E. 1971. Taxonomy and ontogeny of Siluro-Devonian trilobites from near Yass, New South Wales. Palaeontographica (Abt. A) 137:1–108, fig. 1–20, pl. 1–24.

———. 1980. Ontogenetic studies of Middle Ordovician trilobites from the Esbataottine Formation, Mackenzie Mountains, Canada. Palaeontographica (Abt. A) 171:1–74, fig. 1–13, pl. 1–19.

Chatterton, B. D. E., & Margaret Campbell. 1980. Silurian trilobites from near Canberra and some re-

lated forms from the Yass basin. Palaeontographica (Abt. A) 167:77–119.

———. 1993. Enrolling in trilobites: A review and some new characters. Association of Australasian Palaeontologists, Memoir 15:103–123, 8 fig.

Chatterton, B. D. E., G. D. Edgecombe, S. E. Speyer, A. S. Hunt, & R. A. Fortey. 1994. Ontogeny and relationships of Trinucleoidea (Trilobita). Journal of Paleontology 68:523–540, fig. 1–15.

Chatterton, B. D. E., Zerina Johanson, & George Sutherland. 1994. Form of the trilobite digestive system: Alimentary structures in *Pterocephalia.* Journal of Paleontology 68:294–305, fig. 1–5.

Chatterton, B. D. E., & Rolf Ludvigsen. 1976. Silicified Middle Ordovician trilobites from the South Nahanni River area, District of Mackenzie, Canada. Palaeontographica (Abt. A) 154:1–106, fig. 1–9, pl. 1–22.

Chatterton, B. D. E., & D. G. Perry. 1979. *Acanthalomina* Prantl and Pribyl, a valid subgenus of the trilobite genus *Diacanthaspis.* Journal of Paleontology 53:1327–1342, fig. 1, pl. 1–4.

———. 1983. Silicified Silurian odontopleurid trilobites from the Mackenzie Mountains. Palaeontographica Canadiana 1:1–126, 44 fig., 36 pl.

———. 1984. Silurian cheirurid trilobites from the Mackenzie Mountains, northwestern Canada. Palaeontographica (Abt. A) 184:1–78, fig. 1–22, pl. 1–35.

Chatterton, B. D. E., D. J. Siveter, G. D. Edgecombe, & A. S. Hunt. 1990. Larvae and relationships of the Calymenina (Trilobita). Journal of Paleontology 64:255–277, fig. 1–14.

Chatterton, B. D. E., & S. E. Speyer. 1989. Larval ecology, life history strategies, and patterns of extinction and survivorship among Ordovician trilobites. Paleobiology 15:118–132, fig. 1–6.

———. 1990. Applications of the study of trilobite ontogeny. *In* Short Courses in Paleontology, No. 3: Arthropod Paleobiology. Paleontological Society. Knoxville, Tennessee. p. 116–136.

Chen, Runye. 1983. A new species of *Sapushania* (Trilobita) in Lower Cambrian Chiungchussu Formation from Kunming, Yunnan. Scientia Geologica Sinica 2:203–204, pl. 1.

———. 1985. Lower Cambrian trilobites from Liangshan district of Nanzheng, Shaanxi. Acta Palaeontologica Sinica 24(3):332–336, pl. 1.

Chien, Yiyuan [see also Qian, Yiyuan]. 1958. Ontogeny of a new Upper Cambrian trilobite from Penchi, Liaoning. Palaeontologica Sinica 6:466–478.

Chlupáč, Ivo. 1977. The phacopid trilobites of the Silurian and Devonian of Czechoslovakia. Rozpravy Ústředního Ústavu Geologického 43:1–172, 26 fig., 32 pl.

———. 1983. Trilobite assemblages in the Devonian of the Barrandian area and their relations to palaeoenvironments. Geologica et Palaeontologica 17:45–73, fig. 1–5, pl. 1–3.

———. 1987. Ecostratigraphy of Silurian trilobite assemblages of the Barrandian area, Czechoslovakia. Newsletter on Stratigraphy 17:169–186, 5 fig.

Chu, Chaoling [see also Zhu, Zhaoling]. 1959. Trilo-

bites from the Kushan Formation of North and Northeastern China. Memoirs of the Institute of Palaeontology, Academica Sinica 2(2):44–128, pl. 1–7.

In Chinese and English.

Chugaeva, M. N., & M. K. Apollonov. 1982. The Cambrian-Ordovocian boundary in the Batyrbaisai section, Malyi Karatau Range, Kazakhstan, USSR. *In* M. G. Bassett & W. T. Dean, eds., The Cambrian-Ordovician boundary: Sections, fossil distributions, and correlations. National Museum of Wales, Geological Series 3. p. 77–85.

Cisne, J. L. 1971. Paleoecology of trilobites of the Kaibab Limestone (Permian) in Arizona, Utah, and Nevada. Journal of Paleontology 45:525–533, fig. 1, pl. 68.

———. 1973a. Beecher's trilobite bed revisited: Ecology of an Ordovician deepwater fauna. Postilla 160:1–25, fig. 1–5.

———. 1973b. Life history of an Ordovician trilobite *Triarthrus eatoni.* Ecology 54:135–142.

———. 1974. Trilobites and the Origin of Arthropods. Science 186:13–18, fig. 1–3.

———. 1975. Anatomy of *Triarthrus* and the relationships of the Trilobita. Fossils and Strata 4:45–63, fig. 1–13, pl. 1–2.

———. 1981. *Triarthrus eatoni* (Trilobita): Anatomy of its exoskeletal, skeletomuscular, and digestive systems. Palaeontographica Americana 9(53):95–142, fig. 1–28, pl. 17–23.

———. 1982. Origin of the Crustacea. *In* D. E. Bliss, ed., The Biology of Crustacea. Vol. 1: Systematics, the Fossil Record, and Biogeography (L. G. Abele, vol. ed.). Academic Press. New York & London. p. 65–92, fig. 1–7.

Cisne, J. L., G. O. Chandlee, B. D. Rabe, & J. A. Cowen. 1980. Geographic variation and episodic evolution in an Ordovician trilobite. Science 209:925–927, fig. 1.

Cisne, J. L., Joane Molenock, & B. D. Rabe. 1988. Evolution in a cline: The trilobite *Triarthrus* along an Ordovician depth gradient. Lethaia 13:47–59, fig. 1–9.

Clark, T. H. 1923a. New fossils from the vicinity of Boston. Proceedings of the Boston Society of Natural History 36(8):473–485, fig. 1–2.

———. 1923b. A group of new species of *Agnostus* from Lévis, Quebec. The Canadian Field-Naturalist 37(7):121–125.

Clarke, J. M. 1889. The structure and development of the visual area in the trilobite, *Phacops rana* Green. Journal of Morphology 2:253–270, pl. 1.

Clarkson, E. N. K. 1966a. Schizochroal eyes and vision of some Silurian acastid trilobites. Palaeontology 9:1–29, fig. 1–10, pl. 1–3.

———. 1966b. Schizochroal eyes and vision in some phacopid trilobites. Palaeontology 9:464–487, fig. 1–9, pl. 73–75.

———. 1966c. The life attitude of the Silurian trilobite *Phacops musheni* Salter, 1864. Scottish Journal of Geology 2:76–83, fig. 1–3, pl. 1.

———. 1967a. Fine structure of the eye in two species

of *Phacops* (Trilobita). Palaeontology 10:603–616, fig. 1–3, pl. 99.

———. 1967b. Environmental significance of eye-reduction in trilobites and Recent arthropods. Marine Geology 5:367–375, fig. 1.

———. 1969a. On the schizochroal eyes of three species of *Reedops* (Trilobita, Phacopidae) from the Lower Devonian of Bohemia. Transactions of the Royal Society of Edinburgh 68:183–205, fig. 1–6, pl. 1–3.

———. 1969b. Dimorphism of the eye in *Weberides shunnerensis* (King) (Trilobita). *In* G. E. G. Westermann, ed., Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications. E. Schweizerbart'sche Verlagsbuchhandlung. Stuttgart. p. 185–195, fig. 1–5, pl. 13.

———. 1969c. A functional study of the Silurian odontopleurid trilobite *Leonaspis deflexa* (Lake). Lethaia 2:329–344, fig. 1–7.

———. 1971. On the early schizochroal eyes of *Ormathops* (Trilobita, Zeliszkellinae). Mémoires du Bureau de Recherches Géologiques et Minières 73:51–63, fig. 1–2, pl. 1.

———. 1973a. The eyes of *Asaphus raniceps* Dalman (Trilobita). Palaeontology 16:425–444, fig. 1–4, pl. 48–50.

———. 1973b. Morphology and evolution of the eye in Upper Cambrian Olenidae (Trilobita). Palaeontology 16:735–763, fig. 1–8, pl. 91–95.

———. 1975. The evolution of the eye in trilobites. Fossils and Strata 4:7–31, fig. 1–6, pl. 1–6.

———. 1979a. The visual system of trilobites. Palaeontology 22:1–22, fig. 1–5, pl. 1.

———. 1979b. Invertebrate Palaeontology and Evolution. 1st Edition. George Allen and Unwin. London. 323 p.

Clarkson, E. N. K., Niles Eldredge, & J.-L. Henry. 1977. Some Phacopina (Trilobita) from the Silurian of Scotland. Palaeontology 20:119–142, fig. 1–6, pl. 18–20.

Clarkson, E. N. K., & Jean-Louis Henry. 1973. Structures coaptatives et enroulement chez quelques Trilobites ordoviciens et siluriens. Lethaia 6:105–132, fig. 1–18.

Clarkson, E. N. K., & Riccardo Levi-Setti. 1975. Trilobite eyes and the optics of Des Cartes and Huygens. Nature 254:663–667, fig. 1–5.

Clarkson, E. N. K., & C. M. Taylor. 1995. Ontogeny of the trilobite *Olenus wahlenbergi* Westergaard, 1922, from the Upper Cambrian Alum Shales of Andrarum, Skåne, Sweden. Transactions of the Royal Society of Edinburgh, Earth Sciences 86:13–34, 16 fig.

Clarkson, E. N. K., & X. G. Zhang. 1991. Ontogeny and structure of the Carboniferous trilobite *Paladin eichwaldi shunnerensis* (King, 1914). Transactions of the Royal Society of Edinburgh, Earth Sciences 82:277–295, 15 fig.

Cobbold, E. S. 1910. On some small trilobites from the Cambrian rocks of Comley, Shropshire. Quarterly Journal of the Geological Society of London 66:19–51, pl. 3–8.

———. 1931. Additional fossils from the Cambrian rocks of Comley, Shropshire. Quarterly Journal of the Geological Society of London 87:459–511, pl. 39–41.

Cocks, L. R. M., & R. A. Fortey. 1982. Faunal evidence for oceanic separations in the Lower Palaeozoic of Britain. Journal of the Geological Society of London 139:465–478.

———. 1988. Lower Palaeozoic facies and faunas around Gondwana. *In* A. Hallam & M. G. Audley-Charles, eds., Gondwana and Tethys. Special Publications of the Geological Society of London 37. p. 183–200.

———. 1990. Biogeography of Ordovician and Silurian faunas. *In* W. S. McKerrow & C. R. Scotese, eds., Palaeozoic palaeogeography and biogeography. Memoir of the Geological Society of London 12. p. 97–104.

Cook, H. E., & M. E. Taylor. 1975. Early Paleozoic continental margin sedimentation, trilobite biofacies, and the thermocline, western United States. Geology 3:559–562, fig. 1–4.

Cooper, G. A., & C. H. Kindle. 1936. New brachiopods and trilobites from the Upper Ordovician of Percé, Quebec. Journal of Paleontology 10:348–372, fig. 1, pl. 51–53.

Cooper, G. A., & H. B. Whittington. 1965. Use of acids in preparation of fossils. *In* Bernhard Kummel & David Raup, eds., Handbook of Paleontological Techniques. W. H. Freeman. San Francisco. p. 294–300.

Cooper, M. R. 1982. A revision of the Devonian (Emsian-Eifelian) Trilobita from the Bokkeveld Group of South Africa. Annals of the South African Museum 89:1–174, fig. 1–120.

Cossmann, M. 1902. Rectification de la nomenclature. Revista Critica Paleozoologie 16:52.

Courtessole, Robert. 1967. Contribution à la connaissance de la paléontologie et de la stratigraphie du Cambrien Moyen de la Montagne Noire (versant méridional). Bulletin de la Société d'Histoire Naturelle de Toulouse 103:491–526.

———. 1973. Le Cambrien Moyen de la Montagne Noire: Biostratigraphie. Imprimerie d'Oc. Toulouse. 248 p., fig. 1–24, 27 pl.

Courtessole, Robert, Jean-Louis Henry, & Daniel Vizcaïno. 1991. Quelques Calymenidae (Trilobita) de l'Ordovicien Inférieur (Arenig) de la Montagne Noire, France: Systématique, Évolution, et Paléoenvironments. Palaeontographica (Abt. A) 218:1–15, fig. 1–4, pl. 1–4.

Courtessole, Robert, & J. B. Jago. 1980. Biostratigraphie du Cambrien inférieur du Cabardes. Mémoire de la Société d'Études Scientifiques des l'Aude. Carcassonne, France. p. 1–26, 4 pl.

Courtessole, Robert, J. Pillet, & Daniel Vizcaïno. 1988. Stratigraphie et paléontologie du Cambrien Moyen gréseux de la Montagne Noire (versant méridional). Mémoire de la Société d'Études Scientifiques des l'Aude. Carcassonne, France. p. 1–53, pl. 1–8, unnumbered figs.

Cowie, J. W. 1971. Lower Cambrian faunal provinces. *In* F. A. Middlemiss, P. F. Rawson, & G. Newall, eds., Faunal Provinces in Space and Time. Geological Jour-

nal, Special Issue No. 4. Seal House Press. Liverpool. p. 31–46, fig. 1–4.

Cowie, John, & K. J. McNamara. 1978. *Olenellus* (Trilobita) from the Lower Cambrian strata of northwest Scotland. Palaeontology 21:615–634, fig. 1–4, pl. 69–70.

Crimes, T. P. 1970. Trilobite tracks and other trace fossils from the Upper Cambrian of North Wales. Geological Journal 7:47–68, fig. 1–7, pl. 5–13.

———. 1975. The production and preservation of trilobite resting and furrowing traces. Lethaia 8:35–48, fig. 1–7.

Daily, Brian, & J. B. Jago. 1975. The trilobite *Lejopyge* Hawle and Corda and the middle-upper Cambrian boundary. Palaeontology 18(3):527–550, fig. 1, pl. 62–63.

Daily, Brian, A. R. Milnes, C. R. Twidale, & J. A. Bourne. 1979. Geology and Geomorphology. *In* M. J. Tyler, J. K. Ling, & C. R. Twidale, eds., Natural History of Kangaroo Island. Royal Society of South Australia. p. 1–38, fig. 1–40.

Dalingwater, J. E. 1973. Trilobite cuticle microstructure and composition. Palaeontology 16:827–839, pl. 107–109.

Dalingwater, J. E., S. J. Hutchinson, Harry Mutvei, & D. J. Siveter. 1991. Cuticular ultrastructure of the trilobite *Ellipsocephalus polytomus* from the Middle Cambrian of Öland, Sweden. Palaeontology 34:205–217, fig. 1–3, pl. 1–3.

Dalingwater, Hutchinson, Mutvei, & Siveter—. 1993a. Trilobite cuticle calcification. *In* I. Kobayashi, H. Mutvei and A. Sahni, eds., Structure, Formation and Evolution of Fossil Hard Tissues. Tokai University Press. Tokyo. p. 13–20, pl. 1–2.

Dalingwater, Hutchinson, Mutvei, & Siveter—. 1993b. Cuticular ultrastructure of some Silurian calymenid trilobites from the Welsh Borderland and Gotland. Palaeontographica (Abt. A) 229: 37–49, pls. 1–10.

Dalingwater, J. E., & John Miller. 1977. The laminae and cuticular organization of the trilobite *Asaphus raniceps.* Palaeontology 20:21–32, fig. 1–2, pl. 9–10.

Dalla Salda, Luis, Carlos Cingolani, & Ricardo Varela. 1992. Early Paleozoic orogenic belt of the Andes in southwestern South America: Result of Laurentia-Gondwana collision? Geology 20:617–620, fig. 1–2.

Dalman, J. W. 1827. Om Paleaderner, eller de så kallade Trilobiterna. Kongliga Svenska Vetenskaps-Akademiens Handlingar 1826(2):113–162, 226–294, pl. 1–6.

———. 1828. Nya Svenska Palaeder. Årsberättelse om Nyare Zoologiska Arbeten och Upptäcker. Kongliga Svenska Vetenskaps-Akademiens Handlingar 1828:134–135.

Dalmatov, B. A., & L. N. Repina. 1971. A new trilobite genus from the Lower Cambrian of eastern Sayan. Paleontologicheskii Zhurnal 1971(1):115–118.

In English.

David, T. W. E. 1932. Explanatory notes to accompany a new geological map of the Commonwealth of Australia. Commonwealth Council for Scientific and Industrial Research, Australian Medical Publishing Co.,

Ltd. Sydney. 177 p.

David, T. W. E., & W. R. Browne. 1950. The Geology of the Commonwealth of Australia. 2 vol. Edward Arnold & Co. London. 747 p. (vol. 1); 618 p. (vol. 2).

Dawson, J. W. 1868. Acadian Geology: The geological structure, organic remains, and mineral resources of Nova Scotia, New Brunswick and Prince Edward Island, 2nd Edition. Macmillan. London. 694 p., 231 fig., map.

Dean, W. T. 1966. The Lower Ordovician stratigraphy and trilobites of the Landeyran Valley and the neighbouring district of the Montagne Noire, southwestern France. Bulletin of the British Museum (Natural History), Geology Series 12(6):245–353, 21 pl.

Debrenne, F. 1990. Archaeocyatha du Maroc: Essai de synthèse. Géologie Méditerranéenne 17(3–4):213–227.

Delgado, J. F. N. 1904. Faune Cambrienne du Haut-Alemtejo (Portugal). Communicacoes dos Servicos Geologicos de Portugal 5:307–374, pl. 1–6.

Demeter, E. J. 1973. Lower Ordovician pliomerid trilobites from western Utah. Brigham Young University Geology Studies 20:37–65.

Demokidov, K. K., & N. P. Lazarenko. 1964. Stratigrafiia verkhnego Dokembriia i Kembriia i Nizhnekembriiskie triloby severnoi chasti srednei sibiri i ostrovov sovetskoi Arktiki [Stratigraphy of the upper Precambrian and Cambrian and Lower Cambrian trilobites in the northern part of central Siberia and the islands of the Soviet Arctic]. Trudy Nauchno-Issledovatel'skogo Instituta Geologii Arktiki, vol. 137. Moscow. 288 p.

Dollo, Louis. 1910. La Paléontologie éthologique. Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie, Mémoires 23(1909):377–421, fig. 1–13, pl. 7–11.

Dong, Xiping. 1990. Both agnostid and conodont based Middle-Upper Cambrian boundary in Huayuan, Hunan. *In* L. N. Repina & A. Yu. Zhuravlev, eds., Third International Symposium on the Cambrian System, Novosibirsk, USSR, Abstracts. Institut Geologii i Geofiziki, Sibirskoe Otdelenie, Akademiia Nauk SSSR. p. 86–88.

Donovan, S. K. 1991. The processes of fossilization. Belhaven Press. London. ix + 303 p.

Du, W. C., & Y. T. Shao. 1963. A new Lower Cambrian trilobite from Wuting, Yunnan. Acta Paleontologica Sinica 11(2):304, 1 unnumbered fig.

Dubinina, S. V. 1982. Konodontnie assotsiatsii pogranichnykh otlozheniy Kembriya i Ordovika Malogo Karatau (Yuzhnyy Kazakhstana) [Conodont associations of Cambrian-Ordovician boundary beds in Maly Karatau (south Kazakhstan)]. Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya 4:47–54.

In Russian.

Dunbar, C. O. 1925. Antennae in *Olenellus getzi,* n. sp. American Journal of Science (series 5) 9:303–308, fig. 1–2.

Dyar, G. H. 1890. The number of moults of

lepidopterous larvae. Psyche 5:420–422.

Eckel, E. B. 1982. The Geological Society of America: Life history of a learned society. Geological Society of America, Memoir 155:167 p.

Edgecombe, G. D., & B. D. E. Chatterton. 1987. Heterochrony in the Silurian radiation of encrinurine trilobites. Lethaia 20:337–351, fig. 1–7.

———. 1990a. *Mackenziurus,* a new genus of the Silurian *"Encrinurus" variolaris plexus* (Trilobita). American Museum Novitates 2968:1–22, fig. 1–9.

———. 1990b. Systematics of *Encrinuroides* and *Curriella* (Trilobita), with a new Early Silurian encrinurine from the Mackenzie Mountains. Canadian Journal of Earth Sciences 27:820–833, fig. 1, pl. 1–4.

———. 1992. Early Silurian (Llandovery) encrinurine trilobites from the Mackenzie Mountains, Canada. Journal of Paleontology 66:52–74, fig. 1–12.

Edgecombe, G. D., & L. Ramsköld. 1991. Trilobite monophyly revisited. Historical Biology 4:267–283.

Edgecombe, G. D., S. E. Speyer, & B. D. E. Chatterton. 1988. Protaspid larvae and phylogenetics of encrinurid trilobites. Journal of Paleontology 62:779–799, fig. 1–11.

Egorova, L. I., M. N. Lomovitskaia, O. K. Poletaeva, & A. G. Sivov. 1955. Tip Arthropoda, Chlenistonogie: Klass Trilobita, Trilobiti [Trilobites]. *In* Atlas rukovodiashchikh form iskopaemykh fauny i flory zapadnoi Sibiri, I [Atlas of index forms of fossil faunas and floras of western Siberia, I]. Gosgeoltexizdat. Moscow. p. 102–145.

Egorova, L. I., & V. E. Savitskii. 1969. Stratigrafiia i biofatsii kembriia Sibirskoi platformy (Zapadnoe Prianabar'e) [Stratigraphy and biofacies of the Cambrian of the Siberian Platform (western Pre-Anabar)]. Sibirskogo Nauchno-issledovatel'skogo Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya, Seriya Paleontologiya i stratigrafiya 43. 407 p.

In Russian.

Eldredge, Niles. 1970. Observations on burrowing behavior in *Limulus polyphemus* (Chelicerata, Merostomata), with implications on the functional anatomy of trilobites. American Museum Novitates 2436:1–18, fig. 1–4.

———. 1971. Patterns of cephalic musculature in the Phacopina (Trilobita) and their phylogenetic significance. Journal of Paleontology 45:52–67, 7 fig., pl. 13–14.

———. 1973. Systematics of Lower and lower Middle Devonian species of the trilobite *Phacops* Emmrich in North America. Bulletin of the American Museum of Natural History 151:285–338, fig. 1–37.

———. 1977. Trilobites and evolutionary patterns. *In* Anthony Hallam, ed., Patterns of Evolution. Elsevier. Amsterdam. p. 305–332, fig. 1–13.

———. 1980. An extravagance of species. Natural History 89(7):45–5l.

Eldredge, Niles, & L. Braniša. l980. Calmoniid trilobites of the Lower Devonian *Scaphiocoelia* Zone of Bolivia, with remarks on related species. Bulletin of the American Museum of Natural History 165:185–289, fig. 1–39.

Eldredge, Niles, & A. R. Ormiston. 1979. Biogeography of Silurian and Devonian trilobites of the Malvinokaffric Realm. *In* Jane Gray & A. J. Boucot, eds., Historical Biogeography, Plate Tectonics and the changing environment: Proceedings of the 37th Annual Biology Colloquium and Selected Papers. Oregon State University Press. Corvallis. p. 147–167, pl. 1.

Emmons, Ebenezer. 1844. The Taconic System: Based on observations in New York, Massachusetts, Maine, Vermont and Rhode Island. Albany, New York. 653 p.

———. 1855. American Geology, Containing a Statement of the Principles of the Science, with Full Illustrations of the Characteristic Fossils. Vol. 1, Parts I–III. New York State Publisher. Albany, New York. 17 pl.

Endo, R. 1939a. Description of *Blackwelderia quadrata* n. sp. and its post-embryonic development. Bulletin of the Central National Museum of Manchoukuo 1:1–6, pl. 1–2.

———. 1939b. The post-embryonic development of *Blackwelderia quadrata* Endo. Proceedings of the Imperial Academy, Tokyo 15:131–134, fig. 1–14.

Erben, H. K. 1961. Blinding and extinction of certain *Proetidae* (Tril.). Journal of the Palaeontological Society of India 3:82–104, 5 fig.

———. 1964. Facies developments in the marine Devonian of the Old World. Proceedings of the Ussher Society 1(3):92–118.

Ergaliev, G. Kh. 1965. K stratigrafiya venda i kembriya Baykonur-Karatau-Dzhabaglinskoy zony [Towards the stratigraphy of the Vendian and Cambrian of the Baikonur-Karatau-Dzhebaglinsk zones]. Izvestiya Akademii Nauk Kazakhskoy SSR, Seriya Geologicheskaya 6:12–25.

———. 1980. Trilobity Srednego i Verkhnego Kenbriya Malogo Karatau. Nauka. Alma-Ata. 211 p., 20 pl.

———. 1983. Nekotorye trilobity Verkhnego Kembriya i Nizhnego Ordovika Bolyshogo Karatau i Ulutau [Some trilobites from the Upper Cambrian and Lower Ordovician of the Greater Karatau and Ulutau]. *In* M. K. Apollonov, S. M. Bandeletov, & N. K. Ivshin, eds., Stratigrafiya i Paleontologiya Nizhnego Paleozoya Kazakhstana. Nauka. Alma-Ata. p. 35–66, pl. 1–6.

———. 1990. Kyrshabakty section in Maly Karatau as a stratotype for stage and zonal subdivision of the Middle and Upper Cambrian. *In* L. N. Repina & A. Yu. Zhuravlev, eds., Third International Symposium on the Cambrian System, Novosibirsk, USSR, Abstracts. Institut Geologii i Geofiziki, Sibirskoe Otdelenie, Akademiia Nauk SSSR. p. 90.

Esker, G. C., III. 1968. Colour markings in *Phacops* and *Greenops* from the Devonian of New York. Palaeontology 11:498–499, pl. 96.

Etheridge, R., Jr. 1902. Official Contributions to the Palaeontology of South Australia. No. 13: Evidence of further Cambrian trilobites. South Australian Parliamentary Papers, p. 3–4, pl. 2.

Evitt, W. R. 1953. Observations on the trilobite *Ceraurus.* Journal of Paleontology 27:33–48, 1 fig.,

pl. 5–8.

———. 1961. Early ontogeny in the trilobite family Asaphidae. Journal of Paleontology 35:986–995, fig. 1–6, pl. 117–118.

Evitt, W. R., & R. P. Tripp. 1977. Silicified Middle Ordovician trilobites from the families Encrinuridae and Staurocephalidae. Palaeontographica (Abt. A) 157:109–174, fig. 1–19, pl. 1–24.

Evitt, W. R., & H. B. Whittington. 1953. The exoskeleton of *Flexicalymene* (Trilobita). Journal of Paleontology 27:49–55, 1 fig., pl. 9–10.

Fatka, Oldřich, Vratislav Kordule, & Milan Šnajdr. 1981. New Middle Cambrian trilobites from the Barrandian. Věstník Ústředního Ústavu Geologického 56:367–370, pl. 1–2.

Feist, Raimund. 1970. *Breviscutellum* (*Meridioscutellum*) n. sg. (Trilobite) et son développement larvaire. Geobios 3(4):41–73.

———. 1991. The late Devonian trilobite crises. Historical Biology 5:197–214.

———. 1995. Effect of paedomorphosis in eye reduction on patterns of evolution and extinction in trilobites. *In* K. J. McNamara, ed., Evolutionary Change and Heterochrony. John Wiley & Sons. New York. p. 226–244.

Feist, Raimund, & E. N. K. Clarkson. 1989. Environmentally controlled phyletic evolution, blindness and extinction in Late Devonian tropidocoryphine trilobites. Lethaia 22:359–373, fig. 1–9.

Feist, Raimund, & Eberhard Schindler. 1994. Trilobites during the Frasnian Kellwasser crisis in European Late Devonian cephalopod limestones. Courier Forschungsinstitut Senckenberg, Frankfurt am Main 169:195–223, 7 fig., 5 pl.

Fisher, D. C. 1975. Swimming and burrowing in *Limulus* and *Mesolimulus.* Fossils and Strata 4:281–290.

Foote, Mike. 1989. Perimeter-based Fourier analysis: A new morphometric method applied to the trilobite cranidium. Journal of Paleontology 63:880–885, fig. 1–5.

———. 1991. Morphologic patterns of diversification: Examples from trilobites. Palaeontology 34:461–485, fig. 1–4.

Ford, S. W. 1872. Descriptions of some new species of primordial fossils. American Journal of Science (series 3) 3:419–422, fig. 1–2.

———. 1873. Remarks on the distribution of the fossils in the Lower Potsdam rocks at Troy, N.Y., with descriptions of a few new species. American Journal of Science (series 3) 6:134–140, fig. 1–2.

———. 1877. On some embryonic forms of trilobites from the primordial rocks at Troy, N.Y. American Journal of Science (series 3) 13:265–273, pl. 4.

———. 1881. On additional embryonic forms of trilobites from the primordial rocks of Troy, N.Y., with observations on the genera *Olenellus, Paradoxides,* and *Hydrocephalus.* American Journal of Science (series 3) 22:250–259, fig. 1–12.

Fordyce, David, & T. W. Cronin. 1989. Comparison of fossilized schizochroal compound eyes of phacopid trilobites with eyes of modern marine crustaceans and other arthropods. Journal of Crustacean Biology 9:554–569, fig. 1–5.

———. 1993. Trilobite vision: A comparison of schizochroal and holochroal eyes with compound eyes of modern arthropods. Paleobiology 19:288–303, 7 fig.

Fortey, R. A. 1974a. A new pelagic trilobite from the Ordovician of Spitsbergen, Ireland, and Utah. Palaeontology 17:111–124, fig. 1–4, pl. 13–14.

———. 1974b. The Ordovician trilobites of Spitsbergen. I. Olenidae. Norsk Polarinstitutt Skrifter 160:1–181, fig. 1–12, pl. 1–24.

———. 1975a. Early Ordovician trilobite communities. Fossils and Strata 4:331–352, fig. 1–6.

———. 1975b. The Ordovician trilobites of Spitsbergen. II. Asaphidae, Nileidae, Raphiophoridae and Telephinidae of the Valhallfonna Formation. Norsk Polarinstitutt Skrifter 162:1–207, fig. 1–15, pl. 1–41.

———. 1979. Early Ordovician trilobites from the Catoche Formation (St. George Group), western Newfoundland. Geological Survey of Canada, Bulletin 321:61–114, fig. 10–13, pl. 23–37.

———. 1980a. Generic longevity in Lower Ordovician trilobites: Relation to environment. Paleobiology 6:24–31, fig. 1–4.

———. 1980b. The Ordovician trilobites of Spitsbergen. III. Remaining trilobites of the Valhallfonna Formation. Norsk Polarinstitutt Skrifter 171:1–163, fig. 1–8, pl. 1–25.

———. 1980c. *Basilicus tyrannus* (Murchison) and the glabellar structure of the asaphid trilobites. Bulletin of the British Museum (Natural History), Geology 34(4):255–264, 12 fig.

———. 1983. Cambrian–Ordovician trilobites from the boundary beds in Western Newfoundland and their phylogenetic significance. *In* D. E. G. Briggs & P. D. Lane, eds., Trilobites and Other Early Arthropods: Papers in Honour of Professor H. B. Whittington, F. R. S. Special Papers in Palaeontology 30:179–211, fig. 1–3, pl. 23–27.

———. 1985. Pelagic trilobites as an example of deducing the life habits of extinct arthropods. Transactions of the Royal Society of Edinburgh, Earth Sciences 76:219–230, fig. 1–11.

———. 1986. The type species of the Ordovician trilobite *Symphysurus:* Systematics, functional morphology and terrace ridges. Palaeontologische Zeitschrift 60:255–275, fig. 1–12.

———. 1989. There are extinctions and extinctions: Examples from the Lower Palaeozoic. Philosphical Transactions of the Royal Society of London (B, Biological Sciences) 325:327–355, fig. 1–9.

———. 1990a. Ontogeny, hypostome attachment and trilobite classification. Palaeontology 33:529–576, fig. 1–19, pl. 1.

———. 1990b. Trilobite evolution and systematics. Short Courses in Paleontology, Paleontological Society 3:44–65.

Fortey, R. A., & B. D. E. Chatterton. 1988. Classification of the trilobite suborder Asaphina. Palaeontology 31:165–222, fig. 1–27, pl. 17–19.

Fortey, R. A., & E. N. K. Clarkson. 1976. The function of the glabellar "tubercle" in *Nileus* and other trilobites. Lethaia 9:101–106, fig. 1–4.

Fortey, R. A., & R. P. S. Jefferies. 1982. Fossils and

phylogeny: A compromise approach. *In* K. A. Joysey & A. E. Friday, eds., Problems of Phylogenetic Reconstruction, Systematics Association Special Volume 21. Academic Press. London & New York. p. 197–234, fig. 1–17.

Fortey, R. A., & S. F. Morris. 1978. Discovery of nauplius-like trilobite larvae. Palaeontology 21:823–833, fig. 1–3, pl. 94.

———. 1982. The Ordovician trilobite *Neseuretus* from Saudi Arabia, and the palaeogeography of the *Neseuretus* fauna related to Gondwanaland in the earlier Ordovician. Bulletin of the British Museum (Natural History), Geology 36:63–75, fig. 1–11.

Fortey, R. A., & R. M. Owens. 1975. Proetida: A new order of trilobites. Fossils and Strata 4:227–239.

———. 1978. Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales. Bulletin of the British Museum (Natural History) Geology 30:225–294, fig. 1–12, pl. 1–11.

———. 1979. Enrollment in the classification of trilobites. Lethaia 12:219–226, fig. 1–2.

———. 1987. The Arenig Series in South Wales: Stratigraphy and Palaeontology. I. The Arenig Series in South Wales. Bulletin of the British Museum (Natural History), Geology 41:67–307, fig. 1–146.

———. 1990a. Trilobites. *In* K. J. McNamara, ed., Evolutionary Trends. Belhaven Press. London. p. 121–142, 7 fig.

———. 1990b. Evolutionary radiations in the Trilobita. *In* P. D. Taylor & G. P. Larwood, eds., Major Evolutionary Radiations. Systematics Association Special Vol. 42. Clarendon Press. Oxford. p. 139–164, 8 fig.

———. 1991. A trilobite fauna from the highest Shineton Shales in Shropshire, and the correlation of the latest Tremadoc. Geological Magazine 128(5): 437–464, 13 fig.

Fortey, R. A., & A. W. A. Rushton. 1980. *Acanthopleurella* Groom, 1902: Origin and life-habits of a miniature trilobite. Bulletin of the British Museum (Natural History), Geology 33:79–89, fig. 1–21.

Fortey, R. A., & J. H. Shergold. 1984. Early Ordovician trilobites, Nora Formation, central Australia. Palaeontology 27:315–366, fig. 1–17, pl. 38–46.

Fortey, R. A., & H. B. Whittington. 1989. The Trilobita as a natural group. Historical Biology 2:125–138.

Fortey, R. A., & N. V. Wilmot. 1991. Trilobite cuticle thickness in relation to palaeoenvironment. Palaeontologische Zeitschrift 65:141–151, fig. 1–5.

Fowler, G. H. 1909. Biscayan plankton. Part 12: The Ostracoda. Transactions of the Linnaean Society of London, Zoology 10:219–336.

Frey, R. C. 1989. Paleoecology of a well-preserved nautiloid assemblage from a late Ordovician shale unit, southwestern Ohio. Journal of Paleontology 63:604–620, fig. 1–9.

Fritz, W. H. 1972. Lower Cambrian trilobites from the Sekwi Formation type section, Mackenzie Mountains, northwestern Canada. Geological Survey of Canada, Bulletin 212:1–90, pl. 1–20.

———. 1973. Medial Lower Cambrian trilobites from the Mackenzie Mountains northwestern Canada.

Geological Survey of Canada, Paper 73-24:1–43, fig. 1, pl. 1–8.

———. 1976. Ten stratigraphic sections from the Lower Cambrian Sekwi Formation, Mackenzie Mountains, northwestern Canada. Geological Survey of Canada, Paper 76-22:1–42.

———. 1978. Fifteen stratigraphic sections from the Lower Cambrian of the Mackenzie Mountains, northwestern Canada. Geological Survey of Canada, Paper 77-33:1–19, pl. 1–7.

———. 1979. Eleven stratigraphic sections from the Lower Cambrian of the Mackenzie Mountains, northwestern Canada. Geological Survey of Canada, Paper 78-23:1–19, fig. 1, pl. 1–7.

———. 1980. Two new formations in the Lower Cambrian Atan Group, Cassiar Mountains, north-central British Columbia. Current Research, Part B, Geological Survey of Canada, Paper 80-1B:217–225, fig. 25.1–25.3, pl. 25.1.

———. 1991. Lower Cambrian trilobites from the Illtyd Formation, Wernecke Mountains, Yukon Territory. Geological Survey of Canada, Bulletin 409:1–76, fig. 1–5, pl. 1–17.

———. 1992. Walcott's Lower Cambrian olenellid trilobite collection 61k, Mount Robson area, Canadian Rocky Mountains. Geological Survey of Canada, Bulletin 432:1–64, fig. 1–7, pl. 1–17.

———. 1993. New Lower Cambrian olenelloid trilobite genera *Cirquella* and *Geraldinella* from southwestern Canada. Journal of Paleontology 67:856–868, fig. 1–13.

———. 1995. *Esmeraldina rowei* and associated Lower Cambrian trilobites (1f fauna) at the base of Walcott's Waucoban Series, southern Great Basin, U.S.A. Journal of Paleontology 69:708–723, 10 fig.

Fritz, W. H., & E. L. Yochelson. 1988. The status of *Salterella* as a Lower Cambrian index fossil. Canadian Journal of Earth Sciences 25:403–416.

Gaines, R. B., Jr. 1951. Statistical study of *Irvingella,* Upper Cambrian trilobite. Texas Journal of Science 3:606–616.

Geyer, Gerd. 1983. Biostraigraphische und systematisch-paläontologische Untersuchungen in Grenzbereich Unter-/Mittelkambrium von Marokko. Ph.D. thesis. Universitäts Würzburg. 229 p., 19 pl.

———. 1988. Agnostida aus dem höheren Unterkambrium und der Mittelkambrium von Marokko. Teil 2: Eodiscina. Neues Jahrbuch für Geologie und Palaeontologie, Abhandlungen 177:93–133, fig. 1–112.

———. 1990a. Revised Lower to lower Middle Cambrian biostratigraphy of Morocco. Newsletters in Stratigraphy 22:53–70, 2 pl.

———. 1990b. Die marokkanischen Ellipsocephalidae (Trilobita: Redlichiida). Beringeria 3:1–363, 69 fig., pl. 1–56.

———. 1993. The giant Cambrian trilobites of Morocco. Beringeria 8:71–107, 4 fig., 11 pl.

———. 1996. The Moroccan fallotaspid trilobites revisited. Beringeria 18:89–199, 69 fig.

Geyer, Gerd, & A. R. Palmer. 1995. Neltneriidae and Holmiidae (Trilobita) from Morocco and the prob-

lem of Early Cambrian intercontinental correlation. Journal of Paleontology 69:459–474.

Gill, E. D. 1949. *Prosopon,* a term proposed to replace the biologically erroneous term *ornament.* Journal of Paleontology 23:572.

Ginatzy, W., & F. Romer. 1984. Cuticle formation, moulting and control. *In* J. Berelter-Hahn, A. Matalsky, & K. Richards, eds., Biology of the integument. Springer. Berlin. p. 638–684.

Goldring, Roland. 1985. The formation of the trace fossil *Cruziana.* Geological Magazine 122:65–72, fig. 1–4.

Goryanskii, V. Yu., L. I. Egorova, & V. E. Savitskii. 1964. O faune nizhnego kembriia severnogo sklona Anabarskogo shchita [Lower Cambrian fauna from the northern slope of the Anabar shield]. Uchenye Zapiski, Seriia Paleontologiia i Biostratigrafiia 4:5–32.

In Russian.

Gould, S. J. 1977. Ontogeny and phylogeny. Belknap Press. Cambridge, Massachusetts. 510 p.
———. 1985. The paradox of the first tier: An agenda for paleobiology. Paleobiology 11:2–12.

Grabau, A. W. 1931. Palaeozoic centers of faunal evolution and dispersal. Bulletin of the Geological Society of China 11(3):227–239.
———. 1937. Palaeozoic Formation in the Light of the Pulsation Theory. Cambrian Pulsation, vol. 3, pt. 2. Peiping University Press. Peking. 850 p., 58 fig., 4 pl., 6 correlation charts.

Green, J. 1834. Descriptions of some new North American trilobites. American Journal of Science (series 1) 25:334–337.

Grönwall, K. A. 1902. Bornholms Paradoxideslag og deres Fauna. Danmarks Geologiske Undersøgelse (series 2) 13:1–230, pl. 1–4.

Gunther, L. F., & V. G. Gunther. 1981. Some Middle Cambrian fossils of Utah. Brigham Young University Studies 28:87 p.

Guo, Hongjun, & Jiye Duan. 1978. Cambrian and Early Ordovician trilobites from northeastern Hebei and Western Liaoning. Acta Palaeontologica Sinica 17(4):439–460, pl. 1–3.

Gürich, G. 1907. Versuch einer Neueinteilung Trilobiten. Zentralblatt fuer Mineralogie, Geologie und Palaeontologie, Stuttgart 1907:129–133.

Haack, S. C. 1987. The evolution and acuity of the schizochroal eye in trilobites. Evolutionary Theory 8:69–72, fig. 1–2.

Haas, Winfried. 1969. Lower Devonian trilobites from central Nevada and northern Mexico. Journal of Paleontology 43:641–659, fig. 1–6, pl. 81–84.
———. 1981. Tastsinnesorgane bei *Trimerus* (*Dipleura*)—Trilobita, Homalonotidae—Ein Beitrag zum Bau und Leben der Trilobiten. Natur und Museum 111:347–355, fig. 1–14.

Hahn, Gerhard. 1990. Palaeobiogeographic distribution and biostratigraphic significance of Lower Carboniferous trilobites: A review. Courier Forschungs-Institut Senckenberg 130:199–205.

Hahn, Gerhard, & Renate Hahn. 1981. Kulmtrilobiten und ihr Lebensraum. Natur und Museum 111:355–361, fig. 1–8.
———. 1988. The biostratigraphical distribution of Carboniferous Limestone trilobites in Belgium and adjacent areas. Bulletin de la Société Belge de Géologie 97(1):77–93.

Hall, J. 1847. Palaeontology of New York, vol. 1. *In* Natural History of New York, Part 4. Carroll & Cook. Albany, New York. xxiii + 338 p., 87 pl.
———. 1859. Trilobites of the shales of the Hudson River Group. *In* 12th Annual Report of the New York State Cabinet for Natural History. Albany, New York. p. 59–62.
———. 1861. Supplementary note to the thirteenth report of the Regents of the State Cabinet. *In* 15th Annual Report of the New York State Cabinet for Natural History. Albany, New York. p. 113–119.

Appeared as a preprint in 1861 and then published in 1862.

———. 1863. Preliminary notice of the fauna of the Potsdam Sandstone; with remarks upon the previously known species of fossils and descriptions of some new ones, from the sandstone of the Upper Mississippi Valley. New York State Cabinet of Natural History, 16th Annual Report, Appendix D, Contributions to Palaeontology, p. 119–184, pl. Va–X1.

Hall, J., & R. P. Whitfield. 1877. Paleontology. United States Geological Exploration of the Fortieth Parallel 4(2):198–302.

Hallam, Anthony. 1973. Atlas of Palaeobiogeography. Elsevier Scientific Publishing Company. Amsterdam. xii + 531 p.

Hammann, Wolfgang. 1983. Calymenacea (Trilobita) aus dem Ordovizium von Spanien; ihre Biostratigraphie, Okologie und Systematik. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 542:1–177, fig. 1–50, pl. 1–25.
———. 1985. Life habit and enrolment in Calymenacea (Trilobita) and their significance for classification. Transactions of the Royal Society of Edinburgh, Earth Sciences 76:307–318, fig. 1–4.

Hammann, Wolfgang, R. Laske, & G.-L. Pillola. 1990. *Tariccoia arrusensis* n. g. n. sp., an unusual trilobite-like arthropod: Rediscovery of the "phyllocarid" beds of Taricco (1922) in the Ordovician "Puddinga" sequence of Sardinia. Bolletina della Societa Paleontologica Italiana 29:163–178, 3 pl.

Hammann, Wolfgang, & Isabel Rabano. 1987. Morphologie und Lebensweise der Gattung *Selenopeltis* (Trilobita) und ihre Vorkommen im Ordovizium von Spanien. Senckenbergiana Lethaea 68:91–137, 11 fig., 3 pl.

Han, Nairen. 1978. Panderian organs of *Cyclopyge rotundata* Lu (Trilobita). Acta Palaeontologica Sinica 17:351–356, 2 fig., 2 pl.

In Chinese, with English summary.

Harkness, R., & H. Hicks. 1871. On the ancient rocks of the St. David's Promontory, south Wales, and their fossil contents. Quarterly Journal of the Geological Society of London 27:384–402, fig. 1, pl. 15–16.

Harrington, H. J. 1938. Sobre las faunas del ordoviciano inferior del norte Argentino. Revista del

Museo de la Plata (new series) 1:109–289, pl. 1–14.

———. 1956. Olenellidae with advanced cephalic spines. Journal of Paleontology 30:56–61, fig. 1, pl. 15.

Harrington, H. J., & A. F. Leanza. 1957. Ordovician trilobites of Argentina. Department of Geology, University of Kansas, Special Publication 1:1–276, 140 fig.

Harrington, H. J., R. C. Moore, & C. J. Stubblefield. 1959. Morphological terms applied to Trilobita. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology, Part O, Arthropoda 1. Geological Society of America & University of Kansas Press. New York & Lawrence, Kansas. p. 117–126.

Hartnoll, R. G. 1969. Mating in Brachyura. Crustaceana 16:161–181.

———. 1982. Growth. *In* D. E. Bliss & L. G. Abele, eds., The Biology of Crustacea. Vol. 2: Embryology, Morphology, and Genetics. Academic Press. New York & London. p. 11–196.

Havlíček, Vladimír, & Jiří Vaněk. 1990. Ordovician invertebrate communities in black-shale lithofacies (Prague Basin, Czechoslovakia). Věstník Ústředního Ústavu Geologického 65:223–236, fig. 1–3.

Havlíček, Vladimír, Jiří Vaněk, & Oldřich Fatka. 1993. Floating algae of the genus *Krejciella* as probable hosts of epiplanktonic organisms (Dobrotivá Series, Ordovician: Prague basin). Journal of the Czech Geological Society 38:79–87, 1 fig., pl. 1–4.

Hawle, Ignaz, & A. J. C. Corda. 1847. Prodrom einer Monographie der böhmischen Trilobiten. Abhandlungen Koeniglichen Boehmischen Gesellschaft der Wissenschaften. J. G. Calve. Prague. 176 p., 7 pl.

Hayes, A. O., & B. J. Howell. 1937. Geology of the Saint John, New Brunswick. Geological Society of America, Special Paper 5:1–146.

Henningsmoen, Gunnar. 1951. Remarks on the classification of trilobites. Norsk Geologisk Tidsskrift 29:174–217.

———. 1957a. The trilobite family Olenidae: With description of Norwegian material and remarks on the Olenid and Tremadocian Series. Skrifter Utgitt av det Norske Videnskaps-Akademi i Oslo, I, Matematisk-naturvidenskapelig Klasse 1957(1):1–303, fig. 1–19, pl. 1–31.

———. 1957b. Los trilobites de las capas *Saukianda,* Cambrico inferior, en Andalucia. Estudios Geologicos 14 (memoir 35–36):251–269, pl. 36–39.

———. 1958. The Upper Cambrian faunas of Norway with descriptions of non-olenid invertebrate fossils. Norsk Geologisk Tidsskrift 38:179–195, pl. 1–7.

———. 1959. Rare Tremadocian trilobites from Norway. Norsk Geologisk Tidsskrift 39:153–174, fig. 1, pl. 1–2.

———. 1960. The Middle Ordovician of the Oslo Region, Norway. 13: Trilobites of the family Asaphidae. Norsk Geologisk Tidsskrift 40:203–257, fig. 1–5, pl. 1–14.

———. 1975. Moulting in trilobites. Fossils and Strata 4:179–200, fig. 1–14.

Henry, Jean-Louis. 1980a. Trilobites ordoviciens du Massif Armoricain. Mémoires de la Société Géologique et Mineralogique de Bretagne 22:1–250,

95 fig., 48 pl.

———. 1980b. Evolution and classification of some Ordovician Calymenina (Trilobita). Geological Magazine 117:351–362, fig. 1–4, pl. 1–2.

———. 1985. New information on the coaptative devices in the Ordovician trilobites *Placoparia* and *Crozonaspis,* and its significance for their classification and phylogeny. Transactions of the Royal Society of Edinburgh, Earth Sciences, 76:319–324, fig. 1–6.

———. 1989. Paléoenvironnements et dynamique de faunes de trilobites dans l'Ordovicien (Llanvirn supérieur–Caradoc basal) du massif Armoricain (France). Palaeogeography, Palaeoclimatology, Palaeoecology 73:139–153, fig. 1–7.

———. 1996. Classification de quelques Calymenina (Trilobita) Ordoviciens: Calymenidae ou Homalonotidae? Geobios 29:331–340, 3 fig., pl. 45.

Henry, J.-L., & E. N. K. Clarkson. 1975. Enrollment and coaptations in some species of the Ordovician trilobite genus *Placoparia.* Fossils and Strata 4:87–96, fig. 1–3, pl. 1–3.

Henry, J.-L., & Jacques Destombes. 1991. Un biofacies à trilobites Homalonotidae dans l'Ordovicien de la marge nord-gondwanienne: Implications paléobiologiques et paléogéographiques. Lethaia 24:249–253, fig. 1–3.

Hesselbo, S. P. 1987. The biostratinomy of *Dikelocephalus* sclerites: Implications for the use of trilobite attitude data. Palaios 2:605–608, 3 fig.

Hessin, W. A. 1988. *Leviceraurus,* a new cheirurine trilobite from the Cobourg Formation (Middle–Upper Ordovician), southern Ontario, Canada. Journal of Paleontology 62:87–93, 5 fig.

Hessler, R. R. 1964. The Cephalocarida: Comparative skeletomusculature. Memoirs of the Connecticut Academy of Arts and Sciences 16:1–97, 47 fig.

———. 1965. Lower Mississippian trilobites of the Family Proetidae in the United States. Part II. Journal of Paleontology 39:248–264, 1 fig., pl. 37–40.

———. 1982. The structural morphology of walking mechanisms in eumalacostracan crustaceans. Philosophical Transactions of the Royal Society of London (series B) 296:245–298, fig. 1–41.

Hicks, Henry. 1869. On some recent discoveries of fossils in the Cambrian rocks. Report of the British Association for the Advancement of Science for 1868, Transactions of Sections, p. 68–69.

———. 1871. Descriptions of new species of fossils from the Longmynd rocks of St. David's. Quarterly Journal of the Geological Society of London 27:399–402, pl. 15–16.

———. 1875. On the succession of the Ancient Rocks in the vicinity of St. David's, Pembrokeshire, with special reference to those of the Arenig and Llandeilo Groups, and their fossil contents. Quarterly Journal of the Geological Society of London 31:167–195, pl. 8–11.

———. 1895. On the genus *Plutonides* (non *Plutonia*) from the Cambrian rocks of St. David's. Geological Magazine (decade 4) 2:230–231.

Hill, D., G. Playford, & J. T. Woods. 1971. Cambrian fossils of Queensland. Queensland Palaeontographical Society. Brisbane. 32 p., 15 pl.

Hintze, L. F. 1953. Lower Ordovician trilobites from western Utah and eastern Nevada. Utah Geological and Mineralogical Survey, Bulletin 48:vi + 249 p., 1 fig., 28 pl.

Date on cover November 1952, but for evidence of publication date see H. B. Whittington, 1953, American Journal of Science 251:766–767.

Ho, Xinyi, & Jinseng Li. 1959. Discovery of fossils from the Late Cambrian Sanyoudong Limestone, NW Hubei and its stratigraphical significance. Short Papers for the First All-China Conference on Stratigraphy 1. Beijing Geological College. p. 153–160, pl. 1.

In Chinese.

Hoffman, Antoni, & Wolf-Ernst Reif. 1994. Rudolf Kaufmann's work on iterative evolution in the Upper Cambrian trilobite genus *Olenus:* A reappraisal. Palaeontologische Zeitschrift 68:71–87, 6 fig.

Hofmann, H. J. 1979. Chazy (Middle Ordovician) trace fossils in the Ottawa-St. Lawrence lowlands. Geological Survey of Canada, Bulletin 321:27–59, fig. 5–9, pl. 9–22.

Hohensee, S. R., & J. H. Stitt. 1989. Redeposited *Elvinia* Zone (Upper Cambrian) trilobites from the Collier Shale, Ouachita Mountains, west-central Arkansas. Journal of Paleontology 63:857–869, fig. 1–6.

Holloway, D. J. 1980. Middle Silurian trilobites from Arkansas and Oklahoma, U.S.A. Palaeontographica (Abt. A) 170:1–85, fig. 1–10, pl. 1–20.

———. 1981. Silurian dalmanitacean trilobites from North America, and the origins of the Dalmanitinae and Synphoriinae. Palaeontology 24:695–731, fig. 1–5, pl. 96–103.

Holm, G., & A. H. Westergård. 1930. A Middle Cambrian fauna from Bennett Island. Zapiski Akademii Nauk Soyuza SSR, po Otdeleniyu Fiziko-Matematicheskikh Nauk 21(8):1–25, pl. 1–4.

Holub, K. 1908. Příspěvek ku poznání fauny pásma Dd₁γ. Rozpravy České Akademie Věd Císare Frantiska Josefa Vědy, Slovesnost a Umeni, Třídy 2, Matematico-prírodovědecké 17(10):1–19, 1 pl.

———. 1912. Doplňky ku fauně Eulomového horizontu v okolí Rokycan. Rozpravy České Akademie Věd Císare Frantiska Josefa Vědy, Slovesnost a Umění, Třídy 2, Matematico-přírodovědecké 21(33):1–2, 2 pl.

Horný, Radvan, & František Bastl. 1970. Type specimens of fossils in the National Museum, Prague. Volume 1, Trilobita. Museum of Natural History. Prague. 354 p., 20 pl.

Horváth, Gábor, & E. N. K. Clarkson. 1993. Computational reconstruction of the probable change of form of the corneal lens and maturation of optics in the post-ecdysial development of the schizochroal eye of the Devonian trilobite *Phacops rana milleri.* Journal of Theoretical Biology 160:343–374, 15 fig.

Horváth, Gábor, E. N. K. Clarkson, & W. Pix. 1997. Survey of modern counterparts of schizochroal eyes: Structural and functional similarities and differences. Historical Biology 12:229–264.

House, M. R. 1971. Devonian faunal distributions. *In* F. A. Middlemiss, P. F. Rawson, & G. Newall, eds., Faunal Provinces in Space and Time. Geological Journal Special Issue 4:77–94.

———. 1979. Devonian in the eastern hemisphere. *In* R. A. Robison & C. Teichert, eds., Treatise on Invertebrate Paleontology, Part A, Introduction. Geological Society of America & the University of Kansas. Boulder, Colorado & Lawrence, Kansas. p. 183–217.

Howell, B. F. 1933. The classification of the trilobite Subfamily Centropleurinae. Meddelelser fra Dansk Geologisk Forening 8:215–219.

———. 1935a. New Middle Cambrian agnostian trilobites from Vermont. Journal of Paleontology 9:218–221, pl. 22.

———. 1935b. Cambrian and Ordovician trilobites from Hérault, southern France. Journal of Paleontology 9:222–238, pl. 22–23.

———. 1935c. Some New Brunswick Cambrian agnostians. Bulletin of the Wagner Free Institute of Science 10(2):13–16, 1 pl.

———. 1937. Cambrian *Centropleura vermontensis* fauna of northwestern Vermont. Geological Society of America, Bulletin 48:1147–1210, 6 pl.

———. 1955. *Phalagnostus,* a new genus for trilobite *Battus nudus* Beyrich. Journal of Paleontology 29:925–926.

Howell, B. F., J. Bridge, C. F. Deiss, I. Edwards, C. Lochman, G. O. Raasch, & C. E. Resser. 1944. Correlation of the Cambrian formations of North America. Bulletin of the Geological Society of America 55:993–1003.

Howell, B. F., E. A. Frederickson, Christina Lochman, G. O. Raasch, & Franco Rasetti. 1947. Terminology for describing Cambrian trilobites. Journal of Paleontology 21:72–76, fig. 1.

Hu, Chunghung. 1963. The dimorphism and ontogeny of *Norwoodella halli* Resser. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 52:129–132.

———. 1964a. Ontogeny and dimorphism of the trilobite *Peltura scarabeoides* (Wahlenberg) from the Upper Cambrian of Norway. Journal of the Palaeontological Society of India 5–9:39–44, 1 pl.

———. 1964b. The ontogeny and dimorphism of *Welleraspis lata* Howell (Trilobita). Journal of Paleontology 38:95–97, pl. 24.

———. 1968. Notes on the ontogeny and sexual dimorphism of Upper Cambrian trilobites of the *Welleraspis* faunule from Pennsylvania. Journal of Nanyang University 2:321–357, 8 fig., 5 pl.

———. 1969. Ontogeny and sexual dimorphism of three Upper Cambrian trilobites. Journal of Nanyang University 3:438–462, 6 fig., 3 pl.

———. 1970. Ontogenies and sexual dimorphisms of two Upper Cambrian trilobites. Proceedings of the Geological Society of China 13:143–155.

———. 1971. Ontogeny and sexual dimorphism of Lower Palaeozoic Trilobita. Palaeontographica Americana 7(44):29–155, fig. 1–59, pl. 7–26.

———. 1972. Ontogeny of three *Cedaria* Zone trilobites from the Upper Cambrian, Montana.

Transactions and Proceedings of the Palaeontological Society of Japan (new series) 85:245–259.

———. 1973. Description of basal Ordovician trilobites from the Deadwood Formation, northern Black Hills, South Dakota. Proceedings of the Geological Society of China 16:85–95.

———. 1974a. Ontogenies of two Middle Ordovician trilobites from the Edinburg Formation, Virginia. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 95:353–363.

———. 1974b. Ontogenies of a few Middle Ordovician trilobites from the Edinburg Formation of Virginia, U.S.A. Bulletin of the Geological Survey of Taiwan 24:51–67.

———. 1975a. Ontogenies of two species of silicified trilobites from the Middle Ordovician of Virginia. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 97:32–47.

———. 1975b. Ontogenies of four species of silicified Middle Ordovician trilobites from Virginia. Proceedings of the Geological Society of China 18:115–127, 3 fig., 2 pl.

———. 1976. Ontogenies of three species of silicified Middle Ordovician trilobites from Virginia. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 101:247–263, 3 fig., pl. 26–28.

———. 1978. Ontogenies of four Upper Cambrian trilobites from the Bonneterre Dolomite, Missouri. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 111:348–357.

———. 1979. Ontogenic studies of a few Upper Cambrian trilobites from the Deadwood Formation, South Dakota. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 114:49–63.

———. 1980. Ontogenies of a few Upper Cambrian trilobites from the Deadwood Formation, South Dakota. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 119:371–387.

———. 1981. Studies on the ontogenic and phylogenic development of two Upper Cambrian trilobites from South Dakota. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 123:159–167, 2 fig., pl. 20–21.

———. 1983. Ontogenic and phylogenic development of two Upper Cambrian trilobites from the Nolichucky Formation, Tennessee. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 129:26–34, 4 fig., pl. 10–11.

———. 1984. Ontogenesis of *Ehmaniella burgessensis* Rasetti (Trilobita) from the Burgess Shale, Middle Cambrian, Yoho Park, British Columbia. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 135:395–400, 1 fig., pl. 76.

———. 1985a. Ontogenies of two Middle Cambrian corynexochid trilobites from the Canadian Rocky Mountains. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 138:138–147.

———. 1985b. Ontogenic development of Cambrian trilobites from British Columbia and Alberta, Canada

(part 1). Journal of Taiwan Museum 38:121–158, 10 fig., 9 pl.

———. 1986. Ontogenic development of Cambrian trilobites from British Columbia and Alberta, Canada (part 2). Journal of Taiwan Museum 39:1–44, fig. 11–20, pl. 10–20.

Hu, Chunghung, & I. L. Li. 1971. Ontogenies of four proparian trilobites from Upper Cambrian, Montana, U.S.A. (with a description of *Vernaculina lushihi*, n. sp.). Proceedings of the Geological Society of China 14:165–184.

Hu, Chunghung, & L. L. Tan. 1971. Ontogenies of two Upper Cambrian trilobites from northern Black Hills, South Dakota. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 82:61–72.

Hughes, C. P. 1969. The Ordovician trilobite faunas of the Builth-Llandrindod Inlier, Central Wales, part 1. Bulletin of the British Museum (Natural History), Geology 18:39–103, fig. 1–6, pl. 1–14.

———. 1970. Statistical analysis and presentation of trinucleid (Trilobita) fringe data. Palaeontology 13:1–9, fig. 1.

———. 1971. The Ordovician trilobite faunas of the Builth-Llandrindod Inlier, Central Wales, part 2. Bulletin of the British Museum (Natural History), Geology 20:117–182, fig. 1–13, pl. 1–16.

———. 1975. Redescription of *Burgessia bella* from the Middle Cambrian Burgess Shale, British Columbia. Fossils and Strata 4:415–435, pl. 1–13.

———. 1979. The Ordovician trilobite faunas of the Builth-Llandrindod Inlier, Central Wales, part 3. Bulletin of the British Museum (Natural History), Geology 32:109–181, fig. 1–177.

Hughes, C. P., J. K. Ingham, & R. Addison. 1975. The morphology, classification and evolution of the Trinucleidae (Trilobita). Philosophical Transactions of the Royal Society of London (series B) 272:537–604, fig. 1–123.

Hughes, N. C. 1993. Distribution, taphonomy and functional morphology of the Upper Cambrian trilobite *Dikelocephalus*. Milwaukee Public Museum, Contributions in Biology and Geology 84:1–49, 6 fig., 7 pl.

Hunt, A. S. 1966. Submarginal suture and ventral plate of an agnostid trilobite. Journal of Paleontology 40:1238–1240, 1 fig.

———. 1967. Growth, variation, and instar development of an agnostid trilobite. Journal of Paleontology 41:203–208, fig. 1–2, pl. 22.

Hupé, Pierre. 1945. Les organes de Pander des Trilobites asaphidés. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 221:705–706.

———. 1950. Étude statistique de l'évolution du cephalon des trilobites *Proparia* et *Opistoparia*. Bulletin de la Société Géologique de France (series 5) 20:9–24, fig. 1–8.

———. 1951. Sur les affinités des trilobites. Bulletin de la Société Géologique de France (series 6) 1:469–486, fig. 1–6.

———. 1952. Sur les Zones de Trilobites du Cambrien inférieur marocain. Comptes Rendus des

Séances de l'Académie des Sciences, Paris 235:480–481.

———. 1953a. Contribution à l'étude du Cambrien inférieur et du Précambrian III de l'Anti-Atlas Marocain. Direction de la Production Industrielle et des Mines, Division des Mines et de la Géologie, Service Géologique, Notes et Mémoires 103:1–402, fig. 1–99, pl. 1–24.

Dated 1952 on cover, published 1953.

———. 1953b. Classe des trilobites. *In* Jean Piveteau, ed., Traité de Paléontologie, vol. 3. Les formes ultimes d'Invertébrés: Morphologie et évolution: Onychophores—Arthropodes—Échinodermes—Stomocordés. Masson. Paris. p. 44–246, fig. 1–140.

———. 1953c. Quelques remarques sur la croissance et la segmentation des trilobites. Bulletin de la Société Géologique de France (series 6) 3:3–11, fig. 1–4.

———. 1954. Classification des trilobites. Annales de Paleontologie 39:61–168, fig. 1–92.

Dated 1953, but printed in 1954.

———. 1955a. Classification des trilobites. Annales de Paléontologie 41:91–325, fig. 93–247.

———. 1955b. À propos des organes de Pander des trilobites. Bulletin de la Société Géologique de France (series 6) 4(1954):701–711, fig. 1–8, pl. 29, pl. 30, fig. 1.

———. 1960. Sur le Cambrien inférieur du Maroc. *In* Report of the 21st International Geological Congress, Norden, Part 8, Late Precambrian and Cambrian Stratigraphy, p. 75–85.

Hupé, Pierre, & J. Abadie. 1950. Sur l'existence de Trilobites du Cambrien inférieur marocain. Comptes Rendus des Séances de l'Académie des Sciences 230:2112–2113.

Hutchinson, R. D. 1962. Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. Geological Survey of Canada, Bulletin 88:1–156, pl. 1–25.

ICZN. 1985. International Code of Zoological Nomenclature. 3rd edition. International Trust for Zoological Nomenclature, British Museum (Natural History) & University of California Press. London & Berkeley. xx + 338 p.

Illing, V. C. 1916. The Paradoxidian fauna of a part of the Stockingford Shales. Quarterly Journal of the Geological Society 71:386–450, pl. 28–38.

Ingham, J. K. 1968. British and Swedish Ordovician species of *Cybeloides* (Trilobita). Scottish Journal of Geology 4:300–316, fig. 1–3, pl. 1–2.

———. 1970. The Upper Ordovician trilobites from the Cautley and Dent district of Westmorland and Yorkshire, Part 1. Palaeontographical Society, London, Monograph, vol. 124. p. 1–58, pl. 1–9.

Ivshin, N. K. 1953. Srednekembriyskie trilobity Kazakhstana, Chast 1. Boshchekulskiy faunisticheskiy gorizont [Middle Cambrian trilobites of Kazakhstan, Part 1. Boshchekul faunal horizon]. Institut Geologicheskikh Nauk, Akademiya Nauk, Alma-Ata. 226 p.

———. 1956. Verkhnekembriyskie trilobity Kazakh-stana, Chast 1. Kuyandinskiy faunisticheskiy gorizont mezhdurechiya Olenty-Shiderty [Upper Cambrian trilobites of Kazakhstan, Part 1. Kuyandinsk faunal horizon between the Olenty and Shiderty Rivers]. Institut Geologicheskikh Nauk, Akademiya Nauk, Kazakhskoy SSR. Alma-Ata. 98 p., 9 pl.

———. 1960. New biostratigraphical scale for the Upper Cambrian of the Sayan-Altai geosynclinal region. Trudy Instituta geologicheskikh nauk Akademii nauk Kazakhskoy SSR 3:1–62.

———. 1962. Verkhnekembriyskie trilobity Kazakhstana, Chast 2. Seletinskiy Gorizont Kuyandinskogo Yarusa tsentralnogo Kazakhstana [Upper Cambrian trilobites of Kazakhstan, Part 2. Seletinsk horizon of the Kuyandinsk Stage of central Kazakhstan]. Institut Geologicheskikh Nauk, Akademii Nauk Kazakhskoy SSR. Alma-Ata. 412 p., 21 pl.

Ivshin, N. K., & N. V. Pokrovskaya. 1968. Stage and zonal subdivision of the Upper Cambrian. Proceedings of the 23rd International Geological Congress, Prague. p. 97–108.

Jaanusson, Valdar. 1953a. Untersuchungen über baltoskandische Asaphiden. Revision der mittelordovizischen Asaphiden des Siljan-Gebietes in Dalarna. Arkiv foer Mineralogi och Geologi 1(14):377–464, 15 fig., 10 pl.

———. 1953b. Untersuchungen über baltoskandische Asaphiden. II. Revision der *Asaphus* (*Neoasaphus*)-Arten aus dem Geschiebe des sudbottnischen Gebietes. Arkiv foer Mineralogi och Geologi 1(15):465–499, 6 fig., 6 pl.

———. 1954. Zur Morphologie und Taxonomie der Illaeniden. Arkiv foer Mineralogi och Geologi 1(20):545–583, 19 fig., 3 pl.

———. 1956a. On the trilobite genus *Celmus* Angelin, 1854. Bulletin of the Geological Institutions of the University of Uppsala 36:35–49, fig. 1–2, pl. 1.

———. 1956b. Untersuchungen über baltoskandische Asaphiden. III. Über die Gattungen *Megistaspis* n. nom. und *Homalopyge* n. gen. Bulletin of the Geological Institutions of the University of Uppsala 36:59–77, fig. 1–3, pl. 1.

———. 1975. Evolutionary processes leading to the trilobite suborder Phacopina. Fossils and Strata 4:209–218, fig. 1–5.

———. 1979. Ordovician. *In* R. A. Robison & Curt Teichert, eds., Treatise on Invertebrate Paleontology, Part A, Introduction. Geological Society of America & The University of Kansas. Boulder, Colorado & Lawrence, Kansas. p. 136–166.

Jaekel, O. 1909. Über die Agnostiden. Zeitschrift der Deutschen Geologischen Gesellschaft 61:380–401, 23 fig.

Jago, J. B. 1973. Cambrian agnostid communities in Tasmania. Lethaia 6:405–421, fig. 1–3.

———. 1976. Late Middle Cambrian agnostid trilobites from north-western Tasmania. Palaeontology 19:133–172, fig. 1, pl. 21–26.

———. 1987. Idamean (Late Cambrian) trilobites from the Denison Range, south-west Tasmania. Palaeontology 30:207–231, fig. 1–3, pl. 24–27.

Jahnke, H. 1969. *Phacops zinkeni* F. A. Roemer 1843—ein Beispiel für eine ontogenetische Entwicklung bei Phacopiden (Trilobitae, Unterdevon). Neues Jahrbuch für Geologie und Palaeontologie, Abhandlungen 133:309–324, pl. 32.

Jefferies, R. P. S. 1986. The Ancestry of the Vertebrates. British Museum (Natural History), London & Syndicates of the University of Cambridge. viii + 376 p.

Jegla, T. 1982. A review of the molting physiology of the trilobite larva of *Limulus. In* J. Bonaventura, C. Bonaventura, & S. Tesh, eds., Physiology and Biology of Horseshoe Crabs. Alan R. Liss, Inc. New York. p. 83–101.

Jell, P. A. 1970. *Pagetia ocellata,* a new Cambrian trilobite from northwestern Queensland. Memoirs of the Queensland Museum 15(4):303–313, pl. 23–24.

———. 1974. Faunal provinces and possible planetary reconstruction of the Middle Cambrian. Journal of Geology 82:319–350, 11 fig.

———. 1975a. Australian Middle Cambrian eodiscoids with a review of the superfamily. Palaeontographica (Abt. A) 150:1–97, fig. 1–22, pl. 1–29.

———. 1975b. The abathochroal eye of *Pagetia,* a new type of trilobite eye. Fossils and Strata 4:33–43, fig. 1–5.

———. 1978a. Trilobite respiration and genal caeca. Alcheringa 2:251–260, 6 fig.

———. 1978b. *Asthenopsis* Whitehouse, 1939 (Trilobita, Middle Cambrian) in northern Australia. Memoirs of the Queensland Museum 18:219–231, pl. 31–38, 2 fig.

———. 1989. Some aberrant exoskeletons from fossil and living arthropods. Memoirs of the Queensland Museum 27:491–498, 7 fig.

Jell, P. A., & L. N. Repina. 1992. Olenellid trilobites of the Botomian Stage, Siberian Platform. Paleontologicheskii Zhurnal 1992:118–122.

Jell, P. A., & R. A. Robison. 1978. Revision of a late Middle Cambrian trilobite faunule from northwestern Queensland. University of Kansas Paleontological Contributions, Paper 90:1–21, fig. 1–2, pl. 1–4.

Jensen, Sören. 1990. Predation by early Cambrian trilobites on infaunal worms—evidence from the Swedish Mickwitzia Sandstone. Lethaia 23:29–42, fig. 1–10.

Johnson, M. E., D. F. Skinner, & K. G. Macleod. 1988. Ecological zonation during the carbonate transgression of a late Ordovician rocky shore (northeastern Manitoba, Hudson Bay, Canada). Palaeogeography, Palaeoclimatology, Palaeoecology 65:93–114, fig. 1–15.

Johnson, T. T. 1985. Trilobites of the Thomas T. Johnson collection: How to find, Prepare and Photograph Trilobites. Litho-Print Incorporated. Dayton, Ohio. 176 p.

Jones, P. J., J. H. Shergold, & E. C. Druce. 1971. Late Cambrian and Early Ordovician Stages in western Queensland. Journal of the Geological Society of Australia 18(1):1–32.

Kácha, Petr, & Radko Šaríč. 1991. Ontogeny of the trilobite *Kosovopeltis svobodai* Šnajdr from the Bohe-mian Silurian. Věstník Ústředního Ústavu Geologického 66:257–273, 11 fig., pl. 1–6.

Kauffman, R. 1933. Variations statistische Untersuchungen über die "Artabwandlung" und "Artumbildung" an der Oberkambrischen Trilobitengattung *Olenus* Dalm. Abhandlungen aus dem Geologisch-palaeontologischen Institut der Universitaet Greifswald 10:1–54.

Kautsky, F. 1945. Die Unterkambrische Fauna vom Aistjakk in Lappland (Die Larven von *Strenuella*). Geologiska Foereningens i Stockholm Foerhandlingar 67:129–211, fig. 1–5, pl. 9–18.

Keller, B. M., & N. V. Pokrovskaya. 1965. Novye dannye o vozraste fosforitov Karatau [New information about the age of the phosphorites in Karatau]. Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya 6:78–91, pl. 1.

Kennedy, R. J. 1989. Ordovician (Llanvirn) trilobites from S.W. Wales. Palaeontographical Society, London, Monograph, vol. 141(1987). p. 1–55, 4 fig., 14 pl.

Khalfin, L. L., ed. 1960. Biostratigrafiya Paleozoya Sayano-Altayskoy Gornoy Oblasti. Tom 1: Nizhniy Paleozoy [Biostratigraphy of the Paleozoic of the Sayan-Altai mountain range. Vol. 1: Lower Paleozoic]. Trudy Sibirskogo Nauchno-Issledovatelskogo Instituta Geologii, Geofiziki i Mineralnogo Syrya 19:498 p., 69 fig., pl. 1–33; pl. 1–20.

Khomentovskii, V. V. 1976. Vend [Vendian]. Trudy Instituta Geologii i Geofiziki 243:271 p.

In Russian

Khomentovskii, V. V., & L. N. Repina. 1965. Nezhnii Kembrii Stratotipicheskogo razreza Sibiri [The Lower Cambrian Stratotype section of Siberia]. Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Akadmeiia Nauk SSSR:1–196, pl. 1–14.

Kiaer, J. 1917. The Lower Cambrian *Holmia* fauna at Tømten in Norway. Videnskapsselskapets Skrifter. 1. Matematisk-naturvidenskapelig Klasse 10:1–140, 15 fig., pl. 1–14.

Although cover says 1916, p. 112 says printed on Apr. 20, 1917.

Kielan, Zofia. 1960. Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia. Palaeontologia Polonica 11:vi + 191, 50 fig., 36 pl.

King, W. B. R. 1941. The Cambrian fauna of the Salt Range of India. Records of the Geological Survey of India 75(1940), Professional Paper 9:1–15, pl. 1–5.

Kir'ianov, V. V., & N. E. Tchernysheva. 1967. O nizhnekembriiskikh otdozheniiakh severo-zapadnoi volini i nakhodke drevneishego trilobita [About Lower Cambrian deposits of northwestern Volini and the discovery of an ancient trilobite]. Izvestiia Akademii Nauk SSSR, Seriia Geologicheskaia 1967(7):119–125.

Kobayashi, Teiichi. 1935. The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology. Part 3: Cambrian faunas of South Chosen with a special study on the Cambrian trilo-

bite genera and families. Journal of the Faculty of Science, Imperial University of Tokyo, Section II, 4(2):49–344, fig. 1–33, pl. 1–24.

———. 1937a. Restudy of the Dames' Types of the Cambrian trilobites from Liaotung. Transactions and Proceedings of the Palaeontological Society of Japan 12(7):70–86, pl. 17.

———. 1937b. The Cambro-Ordovician shelly faunas of South America. Journal of the Faculty of Science, Imperial University of Tokyo, Section II, 4(4):369–522, pl. 1–8.

———. 1938. Upper Cambrian fossils from British Columbia with a discussion on the isolated occurrence of the "Olenus" Beds of Mt. Jubilee. Journal of Japanese Geology and Geography 15:149–192, pl. 15–16.

———. 1939a. On the Agnostids (part 1). Journal of the Faculty of Science, Imperial University of Tokyo, Section II, Geology, Mineralogy, Geography, Seismology 5(5):69–198.

———. 1939b. Supplementary notes on the Agnostida. Journal of the Geological Society of Japan 46:577–580.

———. 1941a. Studies on Cambrian trilobite genera and families (I). Japanese Journal of Geology and Geography 18(1–2):25–40, pl. 1–2.

———. 1941b. Studies on Cambrian trilobite genera and families (II). Japanese Journal of Geology and Geography 18(1–2):41–51, pl. 3.

———. 1941c. Studies of the genera and families of the Trilobita (III). Japanese Journal of Geology and Geography 18(1–2):59–70, pl. 5–6.

———. 1942a. On the Dolichometopinae. Journal of the Faculty of Science, Imperial University of Tokyo, Section II, 6(10):141–206, pl. 1–4.

———. 1942b. Studies on Cambrian trilobite genera and families (IV). Japanese Journal of Geology and Geography 18(4):197–212, pl. 20–21.

———. 1942c. Two Cambrian trilobites from the Parara limestone in the Yorke's Peninsula, South Australia. Proceedings of the Imperial Academy, Tokyo 18:492–498, fig. 1–10.

———. 1943. Brief notes on the eodiscids 1, their classification with a description of a new species and a new variety. Proceedings of the Imperial Academy, Tokyo 19:37–42, fig. 1–5.

———. 1944a. On the eodiscids. Journal of the Faculty of Science, Imperial University of Tokyo, Section II, 7(1):1–74, pl. 1–2, table 1–4.

———. 1944b. The zoopalaeogeographic province in the Upper Cambrian and Lower Ordovician periods. Japanese Journal of Geology and Geography 19:19–26.

———. 1944c. On the Cambrian formations in Yunnan and Haut-Tonkin and the trilobites contained. Japanese Journal of Geology and Geography 19:107–138, pl. 9–10.

———. 1949. The *Glyptagnostus* hemera, the oldest world-instant. Japanese Journal of Geology and Geography 21(1–4):1–6, pl. 1.

———. 1955. The Ordovician fossils from the McKay Group in British Columbia, western Canada, with a note on the Early Ordovician palaeogeography. Journal of the Faculty of Science, University of Tokyo, Section II, 9(3):355–493, pl. 1–9.

———. 1962. The Cambro-Ordovician formations and faunas of South Korea, Part 9. Palaeontology 8: The Machari fauna. Journal of the Faculty of Science, University of Tokyo, Section II, 14(1):1–152, pl. 1–8.

Kobayashi, Teiichi, & T. Hamada. 1971. Agnostoid trilobites in a Devonian formation in west Malaysia. Proceedings of the Japan Academy 47(4):396–400.

———. 1974. Silurian trilobites of Japan. In comparison with Asian, Pacific and other faunas. Palaeontological Society of Japan, Special Papers 18:viii + 155 p., 12 pl.

———. 1978. Upper Ordovician trilobites from the Langkawi Islands, Malaysia. Geology and Palaeontology of Southeast Asia 19:1–27, pl. 1–2.

Kobayashi, Teiichi, & F. Kato. 1951. On the ontogeny and the ventral morphology of *Redlichia chinensis*, with description of *Alutella nakamurai* n. gen. n. sp. Journal of the Faculty of Science, University of Tokyo, Section II, 8(3):99–143, 9 fig., pl. 1–5.

Kolobova, I. M. 1981. *Granulatagnostus*—novyy rod trilobitov iz Ordovika Kazakhstana [*Granulatagnostus*—a new genus of trilobites from the Ordovician of Kazakhstan]. Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva 24:257–260. Nauka, Leningrad.

Kopaska-Merkel, D. C. 1981. Ontogeny of *Ehmaniella:* Implications for trilobite ecology. United States Geological Survey, Open-file Report 81-743:111–114.

———. 1987. Ontogeny and evolution of an Ordovician trilobite. Society of Economic Paleontologists and Mineralogists Mid Year Meeting, Abstracts 4:43–44.

Kordule, V. 1990. *Rejkocephalus,* a new paradoxid genus from the Middle Cambrian of Bohemia (Trilobita). Věstník Ústředního Ústavu Geologického 65:55–60.

Korobeinikova, T. V. 1966. O novom rode Sem. Redlichiidae iz otlozhenij nizhnego Kembriya vostochnogo Cayana [On a new genus of the family Redlichiidae from the Lower Cambrian deposits of eastern Sayan]. Trudy Tomskogo Gosudarstvennogo Universiteta Imeni V. V. Kuibysheva 184:75–82, pl. 1.

Korobov, M. N. 1980. Biostratigrafiia i miomernye triloby nizhnego kembriia Mongolii [Biostratigraphy and miomerid trilobites from the Lower Cambrian of Mongolia]. The Joint Soviet-Mongolian Scientific-Research Geological Expedition, Transactions 26:5–108, fig. 1–12, pl. 1–11, table 1–2.

———. 1989. Biostratigrafiia i polimernye triloby nizhnego kembriia Mongolii [Biostratigraphy and Lower Cambrian Polymera trilobites of Mongolia]. The Joint Soviet-Mongolian Scientific-Research Geological Expedition, Transactions 48:1–208, pl. 1–13.

Koroleva, M. N. 1982. Triloby Ordovika severo-vostochnogo Kazakhstana. Nedra. Moscow. 192 p., 26 pl.

Kraevsky, B. G. 1965. Nekotorye nizhnekembrijskie

trilobity khrebta Iolgo (Gornyj Altaj) [Some Lower Cambrian trilobites from Khrebta Iolgo (Gorno Altai)]. Trudy SNIIGGIMS 34:47–56, pl. 1.

Křiž, Jiří, & Ilja Pek. 1974. *Dysplanus, Nobilasaphus,* and *Petrbokia* (Trilobita) in the Llandeilo of Bohemia. Věstník Ústředního Ústavu Geologického 49:19–27, pl. 1–4, 1 fig.

Kruse, P. D. 1990. Cambrian palaeontology of the Daly Basin. Northern Territory Geological Survey, Report 7:1–58.

Kuo, Zhenming. 1965. New material of Late Cambrian trilobite fauna from the Yehli area, Kaiping Basin, Hopei. Acta Palaeontologica Sinica 13(4):629–643, pl. 1.

Kushan, Bijan. 1973. Stratigraphie und trilobiten fauna in der Mila-Formation (Mittelkambrium-Tremadoc) im Alborz-gebirge (N-Iran). Palaeontographica (Abt. A) 144:113–165, fig. 1–18, pl. 26–34.

Labandeira, C. C., & N. C. Hughes. 1994. Biometry of the late Cambrian trilobite genus *Dikelocephalus* and its implications for trilobite systematics. Journal of Paleontology 68:492–517, 15 fig.

Lake, P. 1906. A Monograph of the British Cambrian Trilobites, Part 1. Palaeontographical Society, London, Monograph, 1906. p. 1–28, pl. 1–2.

Lalicker, C. G. 1935. Larval stages of trilobites from the Middle Cambrian of Alabama. Journal of Paleontology 9:394–399, pl. 47.

Landing, Ed. 1992. Lower Cambrian of SE Newfoundland: Epeirogeny and Lazarus faunas, lithofacies-biofacies linkages. *In* Jere Lipps & P. E. Signor, eds., Origin and Early Evolution of the Metazoa. Plenum Press. New York & London. p. 283–309.

———. 1993. Precambrian-Cambrian boundary GSSP, SE Newfoundland: Biostratigraphy and geochronology. *In* G. S. Odin, ed., Phanerozoic Time Scale. IUGS Subcommission on Geochronology, Bulletin de Liaison et Informations 11. p. 6–8.

Landing, Ed, Paul Myrow, A. P. Benus, & G. M. Narbonne. 1989. The Placentian Series: Appearance of the oldest skeletized faunas in southeastern Newfoundland. Journal of Paleontology 63:739–769, fig. 1–12.

Lane, P. D. 1971. British Cheiruridae (Trilobita). Palaeontographical Society, London, Monograph, vol. 125. p. 1–95, 13 fig., 16 pl.

———. 1972. New trilobites from the Silurian of north-east Greenland, with a note on trilobite faunas in pure limestones. Palaeontology 15:336–364, fig. 1, pl. 59–64.

Lane, P. D., & A. T. Thomas. 1978. Family Scutelluidae Richter & Richter, 1955. *In* A. T. Thomas, British Wenlock Trilobites, Part 1. Palaeontographical Society, London, Monograph, vol. 132. p. 8–29.

———. 1983. A review of the trilobite suborder Scutelluina. *In* D. E. G. Briggs & P. D. Lane, eds., Trilobites and Other Early Arthropods: Papers in Honour of Professor H. B. Whittington, F. R. S. Special Papers in Palaeontology 30:141–160, fig. 1–7.

Lask, P. B. 1993. The hydrodynamic behavior of scler-ites from the trilobite *Flexicalymene meeki.* Palaios 8:219–225, 6 fig.

Laudon, L. R. 1939. Unusual occurrence of *Isotelus gigas* DeKay in the Bromide Formation (Ordovician) of southern Oklahoma. Journal of Paleontology 13:211–213, fig. 1–2.

Laurie, J. R. 1988. Revision of some Australian Ptychagnostinae (Agnostida, Cambrian). Alcheringa 12:169–205.

———. 1989. Revision of species of Goniagnostus Howell and Lejopyge Corda from Australia (Agnostida, Cambrian). Alcheringa 13:175–191.

———. 1990. On the Middle Cambrian agnostoid species *Agnostus fallax* Linnarsson 1869. Alcheringa 14:317–324.

Lauterbach, K.-E. 1980. Schlüsselereignisse in der Evolution des Grundplans der Arachnata (Arthropoda). Abhandlungen des Naturwissenschaften Vereins in Hamburg 23:163–327.

———. 1983. Synapomorphien zwischen Trilobiten- und Cheliceratenzweig der Arachnata. Zoologischer Anzeiger 210:213–238.

Laverack, M. S., & Yolande Barrientos. 1985. Sensory and other superficial structures in living marine Crustacea. Transactions of the Royal Society of Edinburgh, Earth Sciences 76:123–136, fig. 1–12.

Laverock, W. 1927. On the casting of the shell in *Limulus.* Proceedings and Transactions of the Biological Society of Liverpool 41:13–26.

Lazarenko, N. P. 1962. Novye nizhnekembriiskie trilobity Sovetskoi Arktiki [New Lower Cambrian trilobites from the Soviet Arctic]. Sborník Statey po Paleontologii i biostratigrafii 29:29–77.

———. 1966. Biostratigrafiya i nekotorye novye trilobity Verkhnego Kembriya Oleneksogo podnyatiya i Kharaulakhskikh Gor. Uchenye Zapiski [The biostratigraphy and some new trilobites of the Upper Cambrian of the Olenck uplift and Kharanlakh hills]. Paleontologiya i Biostratigrafiya 11:33–78, pl. 1–8.

Leanza, A. F. 1949. *Olenopsis* Ameghino 1889 (un roedor) versus *Olenopsis* Bornemann 1891 (un trilobite). Asociacion Geologia Argentina (Buenos Aires), Revista 4(1):36.

Lee, Shanchi [see Li, Shanji].

Lermontova E. V. 1940. Klass trilobity [Class Trilobita]. *In* A. G. Vologdin, ed., Atlas rukovodyashchikh form iskopaemykh faun SSSR. 1. Kembriy [Atlas of the leading forms of the fossil faunas of the USSR. 1. Cambrian]. State Editorial Office for Geological Literature. Moscow & Leningrad. p. 112–162, pl. 35–49.

———. 1951a. Nizhnekembriiskie trilobity i brakhiopody Vostochnoi Sibiri [Lower Cambrian trilobites and brachiopods from Eastern Siberia]. Vsesoiuznyj Nauchno-Issledovatel'skij Geologicheskij Institut (VSEGEI), Gosudarstvennoe Izdatel'stvo. Moscow. 218 p.

———. 1951b. Verkhnekembriyskie trilobity i brakhiopody Boshche-Kulya (severo-vostochnyy Kazakhstan) [Upper Cambrian trilobites and brachiopods from Boshchekul (west Pavlodar oblast), N.E. Kazakh]. Vsesoiuznyj Nauchno-Issledovatel'skij

Geologicheskij Institut (VSEGEI), Gosudarstvennoe Izdatel'stvo. Moscow. 49 p., 6 pl.

Lespérance, P. J. 1990. Cluster analysis of previously described communities from the Ludlow of the Welsh Borderland. Palaeontology 33:209–224, fig. 1–4.

———. 1991. Vincular furrows in some early Silurian and Devonian Phacopidae (Trilobita), predominantly from North America. Journal of Paleontology 65:276–294, fig. 1–6.

Levi-Setti, R. 1975. Trilobites: A Photographic Atlas. University of Chicago Press. Chicago & London. 213 p.

Li, Jinseng, & Suseng Hao. 1959. Discovery of fossils from the Qinjiamiao Limestone, Ichang Gorge, W. Hubei, and its stratigraphical significance. Short Papers for the 1st All-China Conference on Stratigraphy 1:129–138, pl. 1.

In Chinese.

Li, Shanji [Lee Shanchi]. 1978. Trilobita. *In* Palaeontological Atlas of SW China, Sichuan Vol. 1: Sinian to Devonian. Geological Publishing House. Beijing. p. 179–284, 568–583 (explanation of plates), pl. 89–114.

———. 1980. Trilobites from the Chiulaotung Formation (Lower Cambrian) in Emei area, western Sichuan. Acta Palaeontologica Sinica 19:42–50, pl. 1–3.

Li, Shanji, Chenglin Kang, Xiguang Zhang. 1990. Sedimentary environment and trilobites of Lower Cambrian Yuxiansi formation in Leshan district, Sichuan. Chengdu Institute of Geology and Mineral Resources, Chinese Academy of Geological Science 12:37–56, pl. 1–4.

Li, Yaoxi, Lisheng Song, Ziqiang Zhou, & Jingyao Yang. 1975. Lower Palaeozoic Stratigraphy of Western Dabashan. Geological Publishing House. Beijing. 232 p., 70 pl.

Liñan, E., & J. Fernández-Carrasco. 1984. La Formación Torreábolos y la paleogeografía del límite Precámbrico-Cámbrico en Ossa Morena (Flanco norte de la alineación Olivenza-Monesterio). Cuadernos do Laboratorio Xeolóxico de Laxe 8:315–328.

Liñan, E., A. Perejon, & K. Sdzuy. 1993. The Lower–Middle Cambrian stages and stratotypes from the Iberian Peninsula: A revision. Geological Magazine 130(6):817–833.

Lindström, G. 1901. Researches on the visual organs of the trilobites. Kongliga Svenska Vetenskaps-Akademiens Handlingar 34(8):1–86, 12 fig., 6 pl.

Linnarsson, J. G. O. 1869. Om Vestergötlands Cambriska och Siluriska aflagringar. Kongliga Svenska Vetenskaps-Akademiens Handlingar 8(2):1–89, pl. 1–2.

———. 1873. Om några forsteningar från Sveriges och Norges "Primordialzon." Kongliga Svenska Vetenskaps-Akadamiens Förhandlingar 6(1871): 789–796, pl. 16.

———. 1879. Om faunen i kalken med *Conocoryphe exsulans* ("coronatuskalken"). Sveriges Geologiska Undersökning (series C) 35:1–31, pl. 1–3.

———. 1883. De undre paradoxideslagren vid Andrarum. Sveriges Geologiska Undersökning (series C) 54:1–47, pl. 1–4.

Lipcius, R. N., & W. F. Herrnkind. 1982. Molt cycle alterations in behavior, feeding and diet rhythms of a decapod crustacean, the spiny lobster *Panulirus argus.* Marine Biology 68:241–252.

Lisogor, K. A., S. N. Rozov, & A. V. Rozova. 1988. Korrelyatsiya srednekembriyskikh otlozheniy Malogo Karatau i Sibirskoy Platformy po trilobitam. Trudy Instituta Geologii i Geofiziki 720:54–82, pl. 4–7.

Liu, Yiren. 1975. *Spinoredlichia,* a new Early Cambrian trilobite genus from Kueichou Province. Acta Geologica Sinica 1:14–16, pl. 1.

Liu—. 1982. Trilobita. *In* The Palaeontological Atlas of Hunan. Ministry of Geology and Mineral Resources, Geological Memoirs (series 2), vol. 1. Geological Publishing House. Beijing. p. 290–346, pl. 207–242.

In Chinese.

Liu, Yiren, & Tairong Zhang. 1979. Discovery of Middle Cambrian *Centropleura* (Trilobita) in China. Geological Review 25(2):1–6, 1 pl.

In Chinese.

Lochman, Christina. 1952. *In* G. A. Cooper & others, eds., Cambrian stratigraphy and paleontology near Caborca, northwestern Sonora, Mexico. Miscellaneous Collections of the Smithsonian Museum 119:60–161.

———. 1956. Stratigraphy, paleontology, and paleogeography of the *Elliptocephala asaphoides* strata in Cambridge and Hoosick quadrangles, New York. Geological Society of America, Bulletin 67:1331–1396.

Lochman, Christina, & D. Duncan. 1944. Early Upper Cambrian faunas of central Montana. Geological Society of America, Special Papers 54:181 p., 19 pl.

Lochman-Balk, Christina, & J. L. Wilson. 1958. Cambrian biostratigraphy in North America. Journal of Paleontology 32:312–350, fig. 1–18.

Lockwood, A. P. M. 1968. Aspects of the Physiology of Crustacea. Oliver and Boyd. Edinburgh. 328 p.

Loeblich, A. R., Jr. 1940. An occurrence of *Isotelus gigas* DeKay in the Arbuckle Mountains, Oklahoma. Journal of Paleontology 14:161–162.

Lotze, F. 1961. Das Kambrium Spaniens. Teil 1: Stratigraphie. Akademie der Wissenschaften und der Literatur Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse 6:285–501.

Lu, Yenhao. 1940. On the ontogeny and phylogeny of *Redlichia intermedia* Lu (sp. nov.). Bulletin of the Geological Society of China 20:333–342, pl. 1.

———. 1941. Lower Cambrian stratigraphy and trilobite fauna of Kunming, Yunnan. Bulletin of the Geological Society of China 21(1):71–90, pl. 1.

———. 1942. Some Lower Cambrian trilobites from Chintingshan, N. Kueichou. Bulletin of the Geological Society of China 22(3–4):177–188, 2 pl.

———. 1946. Early Middle Cambrian faunas from Meitan. Bulletin of the Geological Society of China 25:185–199, pl. 1.

———. 1950. On the genus *Redlichia* with description of its new species. Geological Review 15:157–169, pl. 1.

In Chinese.

———. 1961. New Lower Cambrian trilobites from eastern Yunnan. Acta Palaeontologica Sinica 9(4):299–328, pl. 1–3.

In Chinese, with English summary.

Lu, Yenhao, Wentang Chang, Yiyuan Qian, Zhaoling Zhu, Huanling Lin, Zhiyi Zhou, Sengui Zhang, & Jinliang Yuan. 1974. Cambrian trilobites. *In* Nanjing Institute of Geology & Paleontology, A Handbook of the Stratigraphy and Palaeontology of Southwest China. Science Press. Beijing. p. 82–107, pl. 31–42.

Lu, Yenhao, Wentang Chang, Zhaoling Zhu, Yiyuan Qian, & Liwen Xiang. 1965. Fossils of Each Group of China: Chinese Trilobites. Science Press. Beijing. 766 p., 135 pl. (2 vol.)

In Chinese.

Lu, Yenhao, & N. T. Dong. 1952. Revision of the Cambrian type sections of Shantung. Acta Geologica Sinica 32(3):164–201, fig. 1–11.

Lu, Yenhao, & Huanling Lin. 1981. Zonation of Cambrian faunas in western Zhejiang and their correlation with faunas in North China, Australia, and Sweden. *In* M. E. Taylor, ed., Short Paper for the Second International Symposium on the Cambrian System 1981. United States Geological Survey, Open-file Report 81-743:118–120.

———. 1989. The Cambrian trilobites of western Zhejiang. Palaeontologia Sinica 178:1–287, pl. 1–28.

Lu, Yenhao, & Yiyuan Qian. 1983. Cambro-Ordovician trilobites from eastern Guizhou. Palaeontologia Cathayana 1:1–105, 3 fig., 12 pl.

Lu, Yenhao, & Hongji Wu. 1982. The ontogeny of *Platycoryphe sinensis* and its bearing on the phylogeny of the Homalonotidae. Acta Palaeontologica Sinica 21:37–56.

———. 1983. Ontogeny of the trilobite *Dalmanitina (Dalmanitina) nanchangensis* Lu. Palaeontologia Cathayana 1:123–154.

Lu, Yenhao, Zhaoling Zhu, Yiyuan Quian, Huanling Lin, Zhiyi Zhou, & Kexing Yuan. 1974. The Bioenvironmental control hypothesis and its application to the Cambrian biostratigraphy and palaeozoogeography. Nanjing Institute of Geology & Palaeontology, Academia Sinica, Memoir 5:27–110, pl. 1–4.

In Chinese.

Ludvigsen, Rolf. 1978a. The trilobites *Bathyurus* and *Eomonorachus* from the Middle Ordovician of Oklahoma and their biofacies significance. Life Sciences Contributions, Royal Ontario Museum 114:1–18, 5 fig.

———. 1978b. Middle Ordovician trilobite biofacies, Southern Mackenzie Mountains. *In* C. R. Stelck, & B. D. E. Chatterton, eds., Western and Arctic Canadian Biostratigraphy, Geological Association of Canada Special Paper 18:1–37, 15 fig., 3 pl.

———. 1979a. Fossils of Ontario. Part 1: The trilobites. Life Sciences Miscellaneous Publications. Royal Ontario Museum. Ontario. p. 1–96, 58 fig.

———. 1979b. The Ordovician trilobite *Pseudogygites* Kobayashi in eastern and arctic North America. Life Sciences Contributions, Royal Ontario Museum 120:1–41, 13 fig.

———. 1982. Upper Cambrian and Lower Ordovician Biostratigraphy of the Rabbitkettle Formation, Western District of Mackenzie. Life Sciences Contributions, Royal Ontario Museum 134:1–188, 70 fig.

Ludvigsen, Rolf, & B. D. E. Chatterton. 1980. The ontogeny of *Failleana* and origin of the Bumastinae (Trilobita). Geological Magazine 117:471–478.

———. 1982. Ordovician Pterygometopidae (Trilobita) of North America. Canadian Journal of Earth Sciences 19:2179–2206, fig. 1–9, pl. 1–7.

———. 1991. The peculiar Ordovician trilobite *Hypodicranotus* from the Whittaker Formation, District of Mackenzie. Canadian Journal of Earth Sciences 28:616–622, fig. 1–4, pl. 1.

Ludvigsen, Rolf, & S. R. Westrop. 1983a. Trilobite biofacies of the Cambrian-Ordovician interval in North America. Alcheringa 7:301–319, 23 fig.

———. 1983b. Franconian trilobites of New York State. Memoirs of the New York State Museum 23:1–45, pl. 1–19.

———. 1985. Three new Upper Cambrian stages for North America. Geology 13:139–143, fig. 1–4.

Ludvigsen, Rolf, S. R. Westrop, & C. H. Kindle. 1989. Sunwaptan (Upper Cambrian) trilobites of the Cow Head Group, western Newfoundland, Canada. Palaeontographica Canadiana 6:175 p., 50 pl.

Ludvigsen, Rolf, S. R. Westrop, B. R. Pratt, P. A. Tuffnell, & G. A. Young. 1986. Paleoscene #3. Dual biostratigraphy: Zones and biofacies. Geoscience Canada 13:139–154, 19 fig.

Lütke, F. 1980. Zur evolution der altpaläozoischen Proetina (Trilobita). Senckenbergiana Lethaia 61:73–144.

MacArthur, R. H., & E. O. Wilson. 1967. The theory of island biogeography. Monographs in Population Biology 1, Princeton University Press. Princeton, New Jersey. 203 p.

Männil, R. 1982. Wenlock and late Silurian trilobite associations of the East Baltic area and their stratigraphical value. *In* D. Kaljo & E. Klaaman, eds., Ecostratigraphy of the East Baltic Silurian. Academy of Sciences of the Estonian S. S. R., Institute of Geology. Valgus, Tallinn. p. 63–69.

Mansuy, H. 1912. Étude géologique du Yunnan oriental. Part 2: Paléontologie. Mémoires du Service Géologique de l'Indochine 1 (fasc. 2):1–146, pl. 1–25.

Manton, S. M. 1977. The Arthropoda. Habits, Functional Morphology, and Evolution. Clarendon Press. Oxford. xxii + 527.

Marek, Ladislav. 1961. The trilobite family Cyclopygidae Raymond in the Ordovician of Bohemia. Rozpravy Ústředního Ústavu Geologického 28:1–84, 25 fig., 6 pl.

In English with Czech summary.

Martin, F., & W. T. Dean. 1988. Middle and Upper Cambrian acritarch and trilobite zonation at Manuels

River and Random Island, eastern Newfoundland. Geological Survey of Canada, Bulletin 381:1–91, fig. 1–10, pl. 1–18.

Martinsson, A. 1974. The Cambrian of Norden. *In* C. H. Holland, ed., Lower Palaeozoic Rocks of the World. Vol. 2: Cambrian of the British Isles, Norden and Spitsbergen. John Wiley & Sons. London & New York. p. 185–283.

Matthew, G. F. 1886. Illustrations of the fauna of the St. John Group continued. III. Descriptions of new genera and species (including a description of a new species of Solenopleura by J. F. Whiteaves). Transactions of the Royal Society of Canada 3 (section 4):29–84, pl. 5–7.

———. 1888. Illustrations of the fauna of the St. John Group. II. The smaller trilobites with eyes (Ptychoparidae and Ellipsocephalidae). Transactions of the Royal Society of Canada 5 (section 4):123–166.

———. 1889. Sur le développement des premiers Trilobites. Mémoires de la Société Royale Malacologique de Belgique 23:351–362.

———. 1890. On Cambrian organisms in Acadia. Proceedings and Transactions of the Royal Society of Canada 7 (section 4):135–162.

———. 1896. Faunas of the Paradoxides Beds in eastern North America, no. 1. Transactions of the New York Academy of Sciences 15:192–247, pl. 14–17.

———. 1897. What is the Olenellus fauna? The American Geologist 19:396–407.

———. 1899a. The Etcheminian fauna of Smith Sound, Newfoundland. Transactions of the Royal Society of Canada 5 (section 4):97–119.

———. 1899b. A new Cambrian trilobite. Bulletin of the Natural History Society of New Brunswick 17:137–142, pl. 3.

Mauchline, J. 1976. The Hiatt growth line for Crustacea. Marine Biology 35:79–84.

Maximova, Z. A. 1955. Trilobity sretsnego i verkhnego Devona urala i severnykh Mugodzhar [Trilobites of the Middle and Upper Devonian of the Urals and northern Mugodzhar Hills. Trudy Vsesoyuznogo Nauchnogo-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI) 3:1–263, 44 fig., pl. 1–18.

In Russian.

———. 1968. Srednepaleozoiskie trilobity tsentral'nogo Kazakhstana. Trudy Vsesoyuznogo Nauchnogo-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI) 165:1–208, 35 pl.

McAllister, J. E., & Uwe Brand. 1989. Primary and diagenetic microstructures in trilobites. Lethaia 22:101–111, fig. 1–7.

McKerrow, W. S., & C. R. Scotese, eds. 1990. Palaeozoic Palaeogeography and Biogeography. Geological Society of London, Memoir 12:1–435.

McKerrow, W. S., C. R. Scotese, & M. D. Brasier. 1992. Early Cambrian continental reconstructions. Journal of of the Geological Society, London 149:599–606, fig. 1–3.

McKinney, M. L. 1986. Ecological causation of heterochrony: A test and implications for evolutionary theory. Paleobiology 12:282–289, fig. 1–3.

McNamara, K. J. 1978. Paedomorphosis in Scottish olenellid trilobites (early Cambrian). Palaeontology 21:635–655, fig. 1–7, pl. 71.

———. 1980. Evolutionary trends and their functional significance in chasmopine trilobites. Lethaia 13:61–78, fig. 1–11.

———. 1981a. Paedomorphosis in Middle Cambrian xystridurine trilobites from northern Australia. Alcheringa 5:209–224, 9 fig.

———. 1981b. The role of paedomorphosis in the evolution of Cambrian trilobites. United States Geological Survey, Open-file Report 81-743:126–129.

———. 1982. Heterochrony and phylogenetic trends. Paleobiology 8:130–142, fig. 1–6.

———. 1983. Progenesis in trilobites. *In* D. E. G. Briggs & P. D. Lane, eds., Trilobites and Other Early Arthropods: Papers in Honour of Professor H. B. Whittington, F.R.S. Special Papers in Palaeontology 30:59–68.

———. 1986a. The role of heterochrony in the evolution of Cambrian trilobites. Biological Reviews 6:121–156.

———. 1986b. A guide to the nomenclature of heterochrony. Journal of Paleontology 60:4–13, fig. 1–4.

———. 1986c. Techniques of exuviation in Australian species of the Cambrian trilobite *Redlichia.* Alcheringa 10:403–412, fig. 1–5.

———. 1988. The abundance of heterochrony in the fossil record. *In* M. L. McKinney, ed., Heterochrony in Evolution: A Multidisciplinary Approach. Topics in Paleobiology, Vol. 7. Plenum Press. New York & London. p. 287–325.

McNamara, K. J., & D. M. Rudkin. 1984. Techniques of trilobite exuviation. Lethaia 17:153–173, fig. 1–13.

M'Coy, F. 1846. A Synopsis of the Silurian Fossils of Ireland. Dublin. 72 p., 5 pl.

———. 1849. On the classification of some British fossil Crustacea with notices of some new forms in the University collection at Cambridge. Annals and Magazine of Natural History (series 2) 4:161–179, 330–335, 392–414.

Meneghini, G. 1881. Fauna primordiale in Sardegna. Atti Academia, Lincei Transunti 5 (series 3):305–307.

———. 1882. Fauna Cambriana dell'Iglesiente in Sardegna. Atti Soc. Toscana Scienze Naturali, Processi Verbali 1–2(1878–1881):158–166.

———. 1888. Paleontologia dell'Iglesiente in Sardegna. Fauna Cambriana: Trilobiti. Memoria per Servier alla Descrizione della Carta Geologica, d'Italia (Roma) 3(2):1–53, pl. 1–7.

Mens, K., J. Bergström, & K. Lendzion. 1990. The Cambrian System of the East European Platform. International Union of Geological Sciences, Publication 25:1–73.

Mikulic, D. G. 1981. Trilobites in Paleozoic carbonate buildups. Lethaia 14:45–56, fig. 1.

Mikulic, D. G., & Rodney Watkins. 1981. Trilobite ecology in the Ludlow Series of the Welsh Borderland. *In* Jane Gray, A. J. Boucot, & W. B. N. Berry, eds., Communities of the Past. Hutchinson Ross. Stroudsburg. p. 101–117, 10 fig.

Miller, John. 1975. Structure and function of trilobite terrace lines. Fossils and Strata 4:155–178, fig. 1–21.

———. 1976. The sensory fields and life mode of

Phacops rana (Green, 1832) (Trilobita). Transactions of the Royal Society of Edinburgh 69(16):337–367, 6 fig., 4 pl.

Miller, John, & E. N. K. Clarkson. 1980. The postecdysial development of the cuticle and the eye of the Devonian trilobite *Phacops rana milleri* Stewart 1927. Philosophical Transactions of the Royal Society of London (series B) 288:461–480, fig. 1–47.

Missarzhevsky, V. V. 1983. Stratigraphy of the oldest Phanerozoic units in the Anabar Massif. Sovetskaya Geologiya 1983(9):62–73.

Moberg, J. C. 1899. Sveriges älsta kända Trilobiter. Geologiska Foereningens i Stockholm Foerhandlingar 21:309–348, fig. 1, pl. 13–15.

Moberg, J. C., & C. O. Segerberg. 1906. Bidrag till Kannedomen om *Ceratopyge*-regionen med sarskild hänsyn till dess utveckling i Fogelsångtrakten. Meddelande fran Lunds Geologiska Faltklubb (series B) 2:1–113, pl. 1–7.

Monke, H. 1903. Beitrage zur Geologie von Schantung. Part 1: Obercambrische trilobiten von Yen-tsy-yai. Jahrbuch Königliche Preussische Geologische Landesanstalt, Berlin 23:103–151.

Moore, R. C., ed. 1959. Treatise on Invertebrate Paleontology, Part O, Arthropoda 1. Geological Society of America & University of Kansas Press. Lawrence, Kansas & Boulder, Colorado. xix + 560 p., 415 fig.

Morris, S. F. 1988. A Review of British Trilobites, Including a Synoptic Revision of Salter's Monograph. Palaeontographical Society, London, Monograph, vol. 140. p. 1–316.

Morris, S. F., & R. A. Fortey. 1985. Catalogue of the Type and Figured Specimens of Trilobita in the British Museum (Natural History). British Museum (Natural History). London. 183 p., 8 pl.

Morzadec, Pierre. 1983. Trilobites du Devonien (Emsien-Famennien) de la rade de Brest (Massif Armoricain). Palaeontographica (Abt. A) 181:103–184, fig. 1–39, pl. 1–32.

———. 1988. Le genre *Psychopyge* (Trilobita) dans le Devonien inférieur du nord de l'Afrique et l'ouest de l'Europe. Palaeontographica (Abt. A) 200:153–161, fig. 1–2, pl. 1–2.

Müller, K. J. 1981. Arthropods with phosphatized soft parts from the Upper Cambrian "Orsten" of Sweden. Short Papers for the Second International Symposium on the Cambrian System, 1981. United States Geological Survey, Open-file Report 81-743:147–151.

———. 1985. Exceptional preservation in calcareous nodules. Philosophical Transactions of the Royal Society of London (series B) 311:67–73, 1 fig., 1 pl.

Müller, K. J., & Dieter Walossek. 1986. Arthropod larvae from the Upper Cambrian of Sweden. Transactions of the Royal Society of Edinburgh, Earth Sciences 77:157–179.

———. 1987. Morphology, ontogeny and life-habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. Fossils and Strata 19:1–124, 28 fig., 33 pl.

Mutvei, Harry. 1981. Exoskeletal structure in the Ordovician trilobite *Flexicalymene*. Lethaia 14:225–234, fig. 1–6.

Neben, W., & H. H. Kreuger. 1971. Fossilien ordovischer Gescheibe. Staringia 1:5 p., 50 pl.

Nelson, C. A. 1976. Late Precambrian–Early Cambrian stratigraphic and faunal succession of eastern California and the Precambrian–Cambrian boundary. *In* J. N. Moore & A. E. Fritsche, eds., Depositional Environments of Lower Paleozoic Rocks in the White-Inyo Mountains, Inyo County, California. Society of Economic Paleontologists and Mineralogists, Pacific Section. Los Angeles. p. 31–41.

Neltner, L., & N. Poctey. 1949. Quelques faunes géorgiennes du Maroc. Notes et Mémoires du Service Géologique du Maroc 74:53–83, fig. 1–5, pl. 1–7.

Nicholas, T. C. 1916. Notes on the trilobite fauna of the Middle Cambrian of the St. Tudwal's peninsula, Carnarvonshire. Quarterly Journal of the Geological Society, London 71:451–472, pl. 39.

Nicoll, R. S., & J. H. Shergold. 1991. Revised Late Cambrian (pre-Payntonian–Datsonian) conodont biostratigraphy at Black Mountain, Georgina Basin, western Queensland, Australia. BMR Journal of Australian Geology & Geophysics 12:93–118.

Nicosia, M. L., & Franco Rasetti. 1970. Revisione dei trilobiti del Cambriano dell'Iglesiente (Sardegna) descrittida Meneghini. Accademia Nazionale Lincei, Memorie Classe Scienze Fisiche Matematiche e Naturali (series 8) (section 2, fascile 1) 10:1–18, pl. 1–3.

Nikolaisen, Frank. 1983. The Middle Ordovician of the Oslo Region, Norway. Part 32: Trilobites of the family Remopleuridida. Norsk Geologisk Tidsskrift 62 (1982):231–329, fig. 1–14, pl. 1–15.

Nikolaisen, Frank, & Gunnar Henningsmoen. 1985. Upper Cambrian and lower Tremadoc olenid trilobites from the Digermul peninsula, Finnmark, northern Norway. Norges Geologiske Undersøkelse, Bulletin 400:1–49, 18 fig.

———. 1990. Lower and Middle Cambrian trilobites from the Digermul peninsula, Finnmark, northern Norway. Norges Geologiske Undersøkelse, Bulletin 419:55–95, 10 fig.

Novák, Otomar. 1883. Zur Kenntnis der böhmischen Trilobiten. Beitraege zur Palaeontologie Oesterreich-Ungarns und des Orients 3(1/2):23–63, pl. 8–12.

Öpik, A. A. 1958. The Cambrian trilobite *Redlichia*: Organization and generic concept. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 42:1–51, 9 fig., 6 pl.

———. 1959. Genal caeca of agnostids. Nature 183:1750–1751, fig. 1.

———. 1961a. Alimentary caeca of agnostids and other trilobites. Palaeontology 3:410–438, fig. 1–16, pl. 68–70.

———. 1961b. The Geology and palaeontology of the headwaters of the Burke River, Queensland. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 53:1–249, 59 fig., pl. 1–24.

———. 1963. Early Upper Cambrian fossils from Queensland. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 64:1–133, 40 fig., 9 pl.

———. 1967. The Mindyallan fauna of north-west-

ern Queensland. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 74, vol. 1(text):1–404, fig. 1–149; vol. 2(appendices, plates and index):1–166, 67 pl.

———. 1968. The Ordian Stage of the Cambrian and its Australian Metadoxididae. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Department of National Development, Bulletin 92:133–168, pl. 19–20.

———. 1970a. Nepeid trilobites of the Middle Cambrian of Northern Australia. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 113:1–48, 15 fig., 17 pl.

———. 1970b. *Redlichia* of the Ordian (Cambrian) of Northern Australia and New South Wales. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 114:1–66, 3 fig., 14 pl.

———. 1975a. Templetonian and Ordian xystridurid trilobites of Australia. Australian Government Publishing Service, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 121:84 p., 13 fig., 32 pl.

———. 1975b. Cymbric Vale fauna of New South Wales and Early Cambrian biostratigraphy. Australian Government Publishing Service, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 159:1–78, 14 fig., 7 pl.

———. 1979. Middle Cambrian agnostids: Systematics and biostratigraphy. Australian Government Publishing Service, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 172:1–188, 54 fig., 67 pl. (2 vol.).

———. 1982. Dolichometopid trilobites of Queensland, Northern Territory, and New South Wales. Australian Government Publishing Service, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 175:1–85, 33 fig., 32 pl.

Orlowski, Stanislaw. 1985. Lower Cambrian and its trilobites in the Holy Cross Mts. Acta Geologica Polonica 35:231–250, fig. 1–18, pl. 1–7.

Ormiston, A. R. 1967. Lower and Middle Devonian trilobites of the Canadian Arctic Islands. Geological Survey of Canada, Bulletin 153:1–148, fig. 1–7, pl. 1–17.

———. 1971. Silicified specimens of the Gedinnian trilobite, *Warburgella rugulosa canadensis* Ormiston, from the Northwest Territories, Canada. Palaeontologische Zeitschrift 45:173–180, fig. 1–2, pl. 19–21.

Osgood, R. G. 1970. Trace Fossils of the Cincinnati area. Palaeontographica Americana 6(41):279–444, fig. 1–29, pl. 57–83.

———. 1975. The Paleontological significance of trace fossils. *In* R. W. Frey, ed., The Study of Trace Fossils. Springer-Verlag. New York. p. 87–108.

Osmólska, Halszka. 1963. On some Famennian Phacopinae (Trilobita) from the Holy Cross Mountains. Acta Palaeontologica Polonica 8:495–519, 7 fig., 3 pl.

———. 1975. Fine morphological characters of some Upper Palaeozoic trilobites. Fossils and Strata 4:201–207, pl. 1–2.

Owen, A. W. 1980. The trilobite *Tretaspis* from the Upper Ordovician of the Oslo region, Norway. Palaeontology 23: 715–747, fig. 1–9, pl. 89–93.

———. 1981. The Ashgill trilobites of the Oslo Region, Norway, Palaeontographica (Abt. A) 175:1–88, fig. 1–3, pl. 1–17.

———. 1985. Trilobite abnormalities. Transactions of the Royal Society of Edinburgh, Earth Sciences 76:255–272, fig. 1–5.

———. 1986. The uppermost Ordovician (Hirnantian) trilobites of Girvan, southwest Scotland, with a review of coeval trilobite faunas. Transactions of the Royal Society of Edinburgh 77:231–239, 2 fig., 2 tables.

———. 1987a. The Scandinavian Middle Ordovician trinucleid trilobites. Palaeontology 30:75–103, fig. 1–4, pl. 11–14.

———. 1987b. The trilobite *Tretaspis* at the Middle-Upper Ordovician boundary in Västergötland. Geologiska Foereningens i Stockholm Foerhandlingar 109:259–266, fig. 1–2.

Owen, A. W., & D. L. Bruton. 1980. Late Caradoc-early Ashgill trilobites of the central Oslo Region, Norway. Paleontological Contributions from the University of Oslo 245:62 p., 4 fig., 10 pl.

Owen, A. W., & J. K. Ingham. 1988. The stratigraphical distribution and taxonomy of the trilobite *Onnia* in the type Onnian Stage of the uppermost Caradoc. Palaeontology 31:829–855, fig. 1–8, pl. 74–77.

Owens, R. M. 1973. British Ordovician and Silurian Proetidae (Trilobita). Palaeontographical Society, London, Monograph, vol. 127. 98 p., 12 fig., 15 pl.

———. 1974. The affinities of the trilobite genus *Scharyia,* with a description of two new species. Palaeontology 17:685–697, fig. 1–3, pl. 98–99.

———. 1983. A review of Permian trilobite genera. *In* D. E. G. Briggs & P. D. Lane, eds., Trilobites and Other Early Arthropods: Papers in Honour of Professor H. B. Whittington, F. R. S. Special Papers in Palaeontology 30:15–41, fig. 1–2, pl. 1–5.

———. 1986. The Carboniferous Trilobites of Britain, Part 1. Palaeontographical Society, London, Monograph, vol. 138. p. 1–26, pl. 1–7, fig. 1–4.

———. 1994. Pseudoextinctions in late Devonian proetide trilobites. Historical Biology 9:207–221, fig. 1–8.

Owens, R. M., R. A. Fortey, J. C. W. Cope, A. W. A. Rushton, & M. G. Bassett. 1982. Tremadoc faunas from the Carmarthen district, South Wales. Geological Magazine 119:1–38, fig. 1–4, pl. 1–8.

Owens, R. M., & G. Hahn. 1993. Biogeography of Carboniferous and Permian trilobites. Geologica et Palaeontologica 27:165–180, fig. 1–7.

Owens, R. M., & Wolfgang Hammann. 1990. Proetide trilobites from the Cystoid Limestone (Ashgill) of NW Spain, and the suprageneric classification of related forms. Palaeontologische Zeitschrift 64:221–244, fig. 1–20.

Owens, R. M., & J. W. Tilsley. 1995. An atheloptic trilobite assemblage from the Carboniferous of North Devon. Geological Magazine 132:713–728, 8 fig.

Pabian, R. K., & J. A. Fagerstrom. 1972. Late Paleozoic trilobites from southeastern Nebraska. Journal of

Paleontology 46:789–816, fig. 1–19, pl. 1.

Pack, P. D., & H. B. Gayle. 1971. A new olenellid trilobite, *Biceratops nevadensis,* from the Lower Cambrian near Las Vegas, Nevada. Journal of Paleontology 45:893–898, 2 fig., pl. 102.

Palmer, A. R. l951. *Pemphigaspis,* a unique Upper Cambrian trilobite. Journal of Paleontology 25:762–764, pl. 105.

———. 1955. Upper Cambrian Agnostidae of the Eureka district, Nevada. Journal of Paleontology 29:86–101, fig. 1–2, pl. 19–20.

———. 1957. Ontogenetic development of two olenellid trilobites. Journal of Paleontology 31:105–128, fig. 1–9, pl. 19.

———. 1958. Morphology and ontogeny of a Lower Cambrian ptychoparioid trilobite from Nevada. Journal of Paleontology 32:154–170, fig. 1–7, pl. 25–26.

———. 1960. Trilobites of the Upper Cambrian Dunderberg Shale, Eureka district, Nevada. United States Geological Survey, Professional Paper 334C:1–109, 11 pl.

———. 1962a. *Glyptagnostus* and associated trilobites in the United States. United States Geological Survey, Professional Paper 374F:1–63, 6 pl.

———. 1962b. Comparative ontogeny of some opisthoparian, gonatoparian and proparian Upper Cambrian trilobites. Journal of Paleontology 36:87–96, fig. 1–2, pl. 19.

———. 1964. An unusual Lower Cambrian Trilobite fauna from Nevada. United States Geological Survey, Professional Paper 483F:1–12, 2 fig., 3 pl.

———. 1965a. Biomere—a new kind of stratigraphic unit. Journal of Paleontology 39:149–153, fig. 1–2.

———. 1965b. Trilobites of the late Cambrian pterocephaliid biomere in the Great Basin, United States. United States Geological Survey, Professional Paper 493:iv + 1–105, 16 fig., 20 pl.

———. 1968. Cambrian Trilobites of East-Central Alaska. United States Geological Survey, Professional Paper 559B:1–115, fig. 1–6, pl. 1–16.

———. 1971. The Cambrian of the Great Basin and adjacent areas, western United States. *In* C. H. Holland, ed., Lower Palaeozoic Rocks of the World. Vol. 1: Cambrian of the New World. John Wiley & Sons. London & New York. p. 1–78.

———. 1972. Problems of Cambrian Biogeography. 24th International Geological Congress, Montreal, Canada, Section 7 (Paleontology). p. 310–315, 5 fig.

———. 1977. Biostratigraphy of the Cambrian System—a progress report. Annual Review of Earth and Planetary Science 5:13–33.

———. 1984. The biomere problem: Evolution of an idea. Journal of Paleontology 58:599–611, fig. 1–14.

Palmer, A. R., & C. G. Gatehouse. 1972. Early and Middle Cambrian trilobites from Antarctica. United States Geological Survey, Professional Paper 456D:1–37, 3 fig., 6 pl.

Palmer, A. R., & R. B. Halley. 1979. Physical stratigraphy and trilobite biostratigraphy of the Carrara Formation (Lower and Middle Cambrian) in the southern Great Basin. United States Geological Survey, Professional Paper 1047:1–131, 36 fig., 18 pl.

Palmer, A. R., & N. P. James. 1979. The Hawke Bay event: A circum-Iapetus regression near the lower Middle Cambrian boundary. *In* D. R. Wones, ed., The Caledonides in the U.S.A., Proceedings. Virginia Polytechnic Institute and State University Department of Geology, Memoir 2. Blacksburg, Virginia. p. 15–18.

Palmer, A. R., & L. N. Repina. 1993. Through a glass darkly: Taxonomy, phylogeny, and biostratigraphy of the Olenellina. The University of Kansas Paleontological Contributions (new series) 3:1–35, fig. 1–13.

Peach, B. N. 1894. Additions to the fauna of the *Olenellus*-zone of the Northwest Highlands. Quarterly Journal of the Geological Society of London 50:661–676, pl. 29–32.

Peel, J. S., ed. 1988. Stratigraphy and Palaeontology of the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddelelser om Grønland, Geoscience 20:1–168.

Pek, Ilja. 1970. *Granuloagnostus* g. n. (Trilobita) from the Sarka formation of the Barrandian area. Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium 29:129–131.

———. 1977. Agnostid trilobites of the central Bohemian Ordovician. Sborník Geologických Věd, Paleontologie 19:5–44, 11 fig., 12 pl.

Pek, Ilja, & Martin Smola. 1989. *Leiagnostus ariel* sp. nov. (Trilobita) from the Klabava Formation (Ordovician, Barrandian). Casopis pro Mineralogii a Geologii 34(2):195–7, 1 pl.

Pek, Ilja, & Jiří Vaněk. 1971. Revision of the genera *Peronopsis* Hawle et Corda, 1847 and *Diplorrhina* Hawle et Corda, 1847 (Trilobita) from the Middle Cambrian of Bohemia. Věstník Ústředního Ústavu Geologického 46:269–275, pl. 1–2.

Peng, Shanchi. 1992. Upper Cambrian biostratigraphy and trilobite faunas of the Cili-Taoyuan area, northwestern Hunan, China. Association of Australasian Palaeontologists, Memoir 13. p. 1–119, fig. 1–63.

Perejon, A. 1986. Bioestratigrafia de los Arqueociatos en España. Cuadernos Geologia Iberica 9:213–265.

Petrunina, Z. E. 1966. Trilobity i biostratigrafiya Tremadoka zapadnoy chast Sayano-Altayskoy Gornoy oblasti. Institut Geologicheskikh Nauk, Akademiya Nauk Kazakhskoy SSR. Alma-Ata. 30 p.

Pillola, G.-L. 1991. Trilobites du Cambrien inférieur du SW de la Sardaigne, Italie. Palaeontographica Italica 78:1–174, 56 fig., 32 pl.

Pocock, K. J. 1970. The Emuellidae, a new family of trilobites from the Lower Cambrian of South Australia. Palaeontology 13:522–562, fig. 1–9, pl. 106–110.

Pokrovskaya, N. V. 1958. Agnostidy Srednego Kembriya Yakutii, Chast I [Agnostida from the Middle Cambrian of Yakutia, part 1]. Akademii Nauk SSSR, Trudy Geologicheskogo Instituta 16:1–96, pl. 1–5.

———. 1959. Trilobitovaya fauna i Stratigrafiya Kembrijskikh otlochenij Tuvy [Trilobite fauna and stratigraphy of Cambrian deposits from Tuva]. Akademia Nauk SSSR, Trudy Geologicheskogo Instituta 27:1–199, pl. 1–11.

———. 1960. Otriad Miomera Jaekel, 1909 [Order Miomera Jaekel, 1909]. *In* Yu. A. Orlov, ed., Osnovy

Paleontologii, N. E. Chernysheva, ed., v. 8, Chlenistonogie trilobitoobraznye i rakoobraznye [Fundamentals of Paleontology, v. 8, Arthropoda trilobites and crustaceans]. Akademiia Nauk SSSR. Moscow. p. 54–61, fig. 31, pl. 1–2.

———. 1967. [Generic description]. *In* I. T. Zhuravleva, N. M. Zadorozhnaia, D. V. Osadchaia, N. V. Pokrovskaya, N. M. Rodionova, & V. D. Fonin, eds., Fauna nizhnego Kembriia Tuvy [Lower Cambrian fauna from Tuva]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Moscow. p. 115–116, fig. 18–19, pl. 15.

Pompeckj, J. F. 1896. Die fauna des Cambrium von Tejrovic und Skrej in Böhmen. Jahrbuch der Kaiserlich-koeniglichen Geologishe Reichanstalt, Wien 45:495–614, 1 fig., pl. 13–17.

Pospelov, A. G., & E. V. Romanenko. 1980. Drevniaia rannekembriiskaia fauna altaia i Kuznetskogo Altaia [Early Cambrian fauna from Altai and Kuznetsk Alatau]. *In* I. T. Zhuravleva, ed., Kembrii Altae-Saianskoi skladchatoi oblasti [Cambrian of the Altai-Sayan Folded Region]. Institute of Geology and Geophysics, Siberian Branch of Academy of Sciences SSSR. Nauk Publishing House. Moscow. p. 58–82, pl. 11–14.

Poulsen, C. 1923. Bornholms Olenslag og deres Fauna. Danmarks Geologiske Undersøgelse (series 2) 40:83 p., pl. 1–3.

———. 1927. The Cambrian, Ozarkian, and Canadian faunas of northwest Greenland. Meddelelser om Grønland 70:233–343, pl. 14–21.

———. 1932. The Lower Cambrian faunas of East Greenland. Meddelelser om Grønland 87(6):1–66.

———. 1960. Fossils from the late Middle Cambrian *Bolaspidella* Zone of Mendoza, Argentina. Matematisk-fysiske Meddelelser, Det Kongelige Danske Videnskabernes Selskab 32(11):1–42, pl. 1–3.

Poulsen, V. 1974. Olenellacean trilobites from eastern North Greenland. Geological Society of Denmark, Bulletin 23:79–101.

Pratt, B. 1992. Trilobites of the Marjuman and Steptoean Stages (Upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. Palaeontographica Canadiana 9:1–179, 34 pl.

Prentice, J. E. 1967. Lower Carboniferous trilobites of North Devon and related species from northern England. Bulletin of the British Museum (Natural History), Geology 14:209–241, fig. 1–3, pl. 1–7.

Přibyl, Alois, & Jiří Vaněk. 1969. Trilobites of the family Trinucleidae Hawle et Corda, 1847, from the Ordovician of Bohemia. Sborník Geologických Věd, Paleontologie 11:85–137, 15 fig., 16 pl.

———. 1976. Palaeoecology of Berounian trilobites from the Barrandian area. Rozpravy Československé Akademie Věd, Řada Matematických a Přírodních Věd 86(5):1–40, pl. 1–8.

———. 1980. Ordovician trilobites of Bolivia. Rozpravy Československé Akademie Věd, Řada Matematických a Přírodních Věd 90(2):3–90, 22 fig., pl. 1–26.

———. 1986. A study of the morphology and phylogeny of the Family Harpetidae Hawle and Corda, 1847 (Trilobita). Sborník Narodního Muzea v Praze 42B(1–2):1–51, fig. 1–17, pl. 1–10.

Price, D., & P. M. Magor. 1984. The ecological significance of variation in the generic composition of Rawtheyan (late Ordovician) trilobite faunas from North Wales. Geological Journal 19:187–200.

Przibram, H. 1929. Quanta in biology. Proceedings of the Royal Society of Edinburgh 49:224–231.

Qian, Yiyuan [see also Chien, Yiyuan]. 1982. Ontogeny of *Pseudagnostus benxiensis* sp. nov. (Trilobita). Acta Palaeontologica Sinica 21(6):632-644, 1 pl.

In Chinese, with English summary.

Qian, Yiyuan, & Zemin Zhou. 1984. Middle and early Upper Cambrian trilobites from Kunshan, Jiansu, with reference to their distribution in the lower Yangtze region. Acta Palaeontologica Sinica 23(2):170–184, pl. 1–2.

Qiu, Hongan, Yanhao Lu, Zhaoling Zhu, Dechang Bi, Tianrui Lin, Zhiyi Zhou, Quanzhong Zhang, Yiyuan Qian, Tianyin Ju, Nairen Han, & Xus Wei. 1983. Trilobita. *In* Paleontological Atlas of East China. Part 1: Early Paleozoic. Nanjing Institute of Geology and Mineral Resources. Geological Publishing House. Beijing. p. 1–657, pl. 1–176.

In Chinese.

Rabano, Isabel. 1989. El genero *Uralichas* Delgado, 1892 (Trilobita, Lichaida) en el Ordovicico de la peninsula Iberica. Boletin Geológico y Minero 1989:21–47, 6 fig., pl. 1–4.

———. 1990. Trilobites del Ordovicico Medio del sector meridional de la zona Centroibérica española. Publicaciones Especiales del Boletin Geologico y Minero. 233 p.

Ramsköld, Lars. 1985. Silurian phacopid and dalmanitid trilobites from Gotland. Acta Universitatis Stockholmiensis—Stockholm Contributions in Geology 40:1–62, 8 fig., 12 pl.

———. 1986. Silurian Encrinurid trilobites from Gotland and Dalarna, Sweden. Palaeontology 29:527–575, fig. 1–9, pl. 37–49.

———. 1988. Heterochrony in Silurian phacopid trilobites as suggested by the ontogeny of *Acernaspis*. Lethaia 21:307–318, fig. 1–4.

———. 1991a. The perforated trilobite *Laethoprusia* gen. nov., and the phylogeny of *Koneprusia* and *Isoprusia* (Odontopleuridae, Koneprusiinae). Transactions of the Royal Society of Edinburgh, Earth Sciences 82:125–141, fig. 1–7.

———. 1991b. Pattern and process in the evolution of the Odontopleuridae (Trilobita): The Selenopeltinae and Ceratocephalinae. Transactions of the Royal Society of Edinburgh, Earth Sciences 82:143–181, fig. 1–12.

Ramsköld, Lars, & B. D. E. Chatterton. 1991. Revision of the polyphyletic "*Leonaspis*" (Trilobita). Transactions of the Royal Society of Edinburgh, Earth Sciences 82:333–371, 11 fig., 1 table.

Ramsköld, Lars, Chen Jun-Yuan, G. D. Edgecombe, & Zhou Gui-Qing. 1996. Preservational folds stimulating tergite junctions in tegopeltid and naraoiid

arthropods. Lethaia 29:15–20, 2 fig.

Ramsköld, Lars, & G. D. Edgecombe. 1991. Trilobite monophyly revisited. Historical Biology 4:264–283.

Ramsköld, Lars, & Lars Werdelin. 1991. The phylogeny and evolution of some phacopid trilobites. Cladistics 7:29–74, fig. 1–8.

Rasetti, Franco. 1944. Upper Cambrian trilobites from the Lévis Conglomerate. Journal of Paleontology 18:229–258, pl. 36–39.

———. 1945a. New Upper Cambrian trilobites from the Lévis Conglomerate. Journal of Paleontology 19:462–478, pl. 60–62.

———. 1945b. Fossiliferous horizons in the 169 "Sillery Formation" 170 near Lévis, Quebec. American Journal of Science 243:305–319, pl. 1–2.

———. 1948a. Lower Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). Journal of Paleontology 22:1–24, pl. 1–6.

———. 1948b. Middle Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). Journal of Paleontology 22:315–339, pl. 45–52.

———. 1952a. Revision of the North American trilobites of the family Eodiscidae. Journal of Paleontology 26:434–451, pl. 51–54.

———. 1952b. Cephalic sutures in the Upper Cambrian trilobite *Entomaspis*. Journal of Paleontology 26:797–802, fig. 1–5, pl. 117.

———. 1952c. Ventral cephalic sutures in Cambrian trilobites. American Journal of Science 250:885–898, 1 pl.

———. 1954. Phylogeny of the Cambrian trilobite family Catellicephalidae and the ontogeny of *Welleraspis*. Journal of Paleontology 28:599–612, fig. 1–4, pl. 62.

———. 1966a. New Lower Cambrian trilobite faunule from the Taconic sequence of New York. Smithsonian Miscellaneous Collections 148(9):1–52, 12 pl.

———. 1966b. Revision of the North American species of the Cambrian trilobite genus *Pagetia*. Journal of Paleontology 40:502–511, pl. 59–60.

———. 1967. Lower and Middle Cambrian faunas from the Taconic sequence of New York. Smithsonian Miscellaneous Collections 152(4):1–111, 14 pl.

———. 1972. Cambrian trilobite faunas of Sardinia. Atti della Accademia Nazionale dei Lincei, Memorie (series 8) 11 (section IIª, fasc. 1):1–100, pl. 1–19.

Rasetti, Franco, & George Theokritoff. 1967. Lower Cambrian agnostid trilobites of North America. Journal of Paleontology 41:189–196, pl. 20.

Ratte, F. 1886. Note on some trilobites new to Australia. Proceedings of the Linnaean Society of New South Wales 1:1065–1066.

Raw, Frank. 1925. The development of *Leptoplastus salteri* (Callaway), and of other trilobites (Olenidae, Ptychoparidae, Conocoryphidae, Paradoxidae, Phacopidae, and Mesonacidae). Quarterly Journal of the Geological Society of London 81:223–324, pl. 25–28.

———. 1927. The ontogenies of trilobites and their significance. American Journal of Science (series 5) 14:7–35, 131–149, fig. 1–25.

———. 1936. Mesonacidae of Comley in Shropshire, with a discussion of classification within the family. Quarterly Journal of the Geological Society of London 92:236–293, pl. 16–23.

———. 1953. The external morphology of the trilobite and its significance. Journal of Paleontology 27:82–129, fig. 1–7.

Raymond, P. E. 1913a. Some changes in the names of genera of trilobites. The Ottawa Naturalist 26:137–142.

———. 1913b. On the genera of the Eodiscidae. The Ottawa Naturalist 27:101–106.

———. 1914a. Notes on the ontogeny of *Paradoxides*, with a description of a new species from Braintree, Massachusetts. Bulletin of the Museum of Comparative Zoology at Harvard College 58:225–244.

———. 1914b. Notes on the ontogeny of *Isotelus gigas* DeKay. Bulletin of the Museum of Comparative Zoology at Harvard College 58:247–264.

———. 1920. The appendages, anatomy and relationships of trilobites. Memoirs of the Connecticut Academy of Arts and Sciences 7:1–169, 46 fig., 11 pl.

———. 1922. A trilobite retaining color-markings. American Journal of Science (series 5) 4:461–464, 1 fig.

———. 1924. New Upper Cambrian and Lower Ordovician trilobites from Vermont. Proceedings of the Boston Society for Natural History 37:389–466, pl. 12–14.

———. 1931. Notes on invertebrate fossils, with descriptions of new species. Bulletin of the Museum of Comparative Zoology at Harvard College 55(6):165–213, 5 pl.

———. 1935. Protaspides of trilobites. Journal of Paleontology 9:400–401.

Redlich, K. 1899. The Cambrian fauna of the eastern Salt Range. Memoirs of the Geological Survey of India, Palaeontologica Indica (new series) 1:1–13, pl. 1.

Reed, F. R. C. 1903. The Lower Palaeozoic Trilobites of the Girvan District, Ayrshire. Palaeontological Society Monograph:1–48, pl. 1–6.

Reimann, I. G. 1943. *Terataspis* gets remodeling: New find yields new knowledge. Hobbies, Buffalo Museum of Science 23(4):75–77, 4 fig.

Repina, L. N. 1956. Trilobity rod *Bulaiaspis* [Trilobite genus *Bulaiaspis*]. *In* Materialy po paleontologii, novye semeistav i rody [Materials for Paleontology, New families and genera]. Trudy Vsesoyuznogo Nauchnogo-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI) (new series) 12:145–147.

———. 1960. Kompleksy trilobitov nizhnego i srednego kembriya zapadnoj chast Vostochnogo Sayana [Lower and Middle Cambrian trilobites of western part of eastern Sayan]. *In* Regionalnaya Stratigrafya SSSR, vyp. 4 [Regional Stratigraphy of the USSR, vol. 4]. Izdatel'stvo Akademii Nauk SSSR. Moscow. p. 171–225.

———. 1961. O hakhodke olenellid v lenskom iaruse Batenevskogo kriazha [On the discovery of olenellids in the Lena Stage of Batenevskiy Ridge]. Doklady Akademii Nauk USSR 136(4):40–45.

———. 1966. Trilobity nezhnego kembriya yuga Sibiri (Nadsemejstvo Redlichioidea), Chast 1 [Trilo-

bites of the Lower Cambrian of Southern Siberia (Superfamily Redlichioidea)]. Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Akademiia Nauk SSSR. p. 1–176, pl. 1–27.

———. 1972. K voprosu o razvitii trilobitov semeistva Protolenidae (Sibir') [Problems concerning the evolution of the Family Protolenidae (Siberia)]. *In* I. T. Zhurnoleva, ed., Problemy biostratigrafii i paleontologii nizhnego kembriia Sibiri [Problems of Biostratigraphy and Palaeontology of the Lower Cambrian of Siberia]. Nauka. Moscow. p. 15–30.

———. 1973. Trilobity [Trilobites]. *In* O. G. Okuneva & L. N. Repina, Biostratigrafiia I Fauna Kembriia primor'ia [Biostratigraphy and fauna of the Cambrian of Primorye]. "NAUKA" Siberian Branch. Novosibirsk. p. 155–209.

———. 1979. Zavisimost morfologicheskikh priznakov ot uslovii obitaniia trilobitov i otsenka ikh znacheniia dlia sistematiki nadsemeistva Olenelloidea [The dependence of morphological features upon the living conditions of trilobites and an evaluation of their importance in the classification of the Superfamily Olenelloidea]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofizikii 431:11–30, 13 fig., pl. 1–2.

In Russian.

———. 1986. Planetarnaia korreliatsiia iarusnikh podrazdeleniia nizhnego kembriia po trilobitam [Global correlation of stage subdivisions of the Lower Cambrian according to trilobites]. *In* I. T. Zhuravleva, ed., Biostratigrafiya i paleontologiya kembriya severnoy Azii [Biostratigraphy and paleontology of the Cambrian of central Asia]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofizikii 669. p. 4–25.

———. 1990a. Evoliutsiia trilobitov no nachal'nykh etapakh ikh istoricheskogo razvitiia [Evolution of trilobites in their early stages of historical development]. *In* O. A. Betekntina & I. T. Zhuravleva, eds., Sreda i zhizn' v geologicheskom proshlom [Environment and life of the geologic past]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofizikii 764. p. 34–44.

———. 1990b. Evoliutsiia soobshchestv trilobitov v rannekembriiskikh basseinakh [Evolution of trilobite associations in Early Cambrian basins]. *In* V. N. Dubamolov & A. T. Mosalenko, eds., Printsip razvitiia i istorizma v geologii i paleobiologii [Principles of Development and Historicity in Geology and Paleontology]. Nauka, Sibirskoe Otdelenie. Novosibirsk. p. 206–212.

Repina, L. N., G. V. Belyaeva, & L. P. Sobolev. 1976. Novy danny po nizhnemu kembriiu basseina R. Shevli [New data on the Lower Cambrian in the basin of the River Shevli]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofizikii 296:151–161, pl. 14–16.

Repina, L. N., V. V. Khomentovskii, I. T. Zhurvavleva, & A. Yu. Rozanov. 1964. Biostratigrafiia nizhnego kembriia Sayano-Altaiskoi skladchatoi oblasti [Biostratigraphy of the Lower Cambrian of the Sayan-Altay fold region]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki. Moscow. 364 p., 48 pl.

Repina, L. N., N. P. Lazarenko, N. P. Meshkova, V. I. Korshunov, N. I. Nikiforov, & N. A. Aksarina. 1974. Biostratigrafiia i fauna nizhnego kembriia Kharaulakha (Khr. Tuora-Sis) [Biostratigraphy and fauna of the Lower Cambrian of Kharaulakh (Tuora-Sis ridge)]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofizikii 235:1–299.

Repina, L. N., & V. S. Pereladov. 1988. O trilobitakh roda *Lenadiscus* Repina [The trilobite genus *Lenadiscus* Repina]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofizikii 720:176–179, pl. 25.

Repina, L. N., Z. E. Petrunina, & T. I. Hajrullina. 1975. Trilobity [Trilobites]. *In* L. N. Repina, B. V. Yaskovich, N. A. Aksarina, Z. E. Petrunina, I. A. Poniklenko, D. A. Rubanov, G. V. Bolgova, A. N. Golikov, T. I. Hajrullina, & M. M. Posokhova, Stratigrafiia i fauna nizhnego paleozoia cevernykh predgorii Turkestanskogo n Alaiskogo Khrebtov (iuzhnyi Tian'-Shan') [Stratigraphy and fauna of the Lower Paleozoic of the northern submontane belt of Turkestan and Alai Ridges (southern Tian-shan)]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofizikii 278:100–248, pl. 7–48.

Repina, L. N., & E. V. Romanenko. 1978. Trilobity i stratigrafiia nizhnego kembriia Altaia [Trilobites and stratigraphy of the Lower Cambrian of Altay]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofizikii 382:1–304, fig. 1–17, pl. 1–32.

Resser, C. E. 1928. Cambrian fossils from the Mojave Desert. Smithsonian Miscellaneous Collections 81:1–14.

———. 1937. Third contribution to nomenclature of Cambrian trilobites. Smithsonian Miscellaneous Collections 95(22):1–29.

———. 1938. Cambrian System (restricted) of the Southern Appalachians. Geological Society of America, Special Paper 15:1–140, 16 pl.

———. 1939. The Ptarmigania strata of the northern Wasatch Mountains. Smithsonian Miscellaneous Collections 98(24):1–72, pl. 1–14.

Resser, C. E., & B. F. Howell. 1938. Lower Cambrian *Olenellus* Zone of the Appalachians. Geological Society of America, Bulletin 49:195–248, 13 pl.

Reyment, R. A. 1976. Göran Wahlenberg's collection. Illustrated Catalogue of the Type Collections of the Palaeontological Museum of the University of Uppsala 3:2–11.

Reynolds, S. E. 1980. Integration of behaviour and physiology in ecdysis. *In* M. J. Berridge, J. E. Treherne, & V. B. Wigglesworth, eds., Advances in Insect Physiology 15. Academic Press. London. p. 476–595.

Riccio, J. F. 1952. The Lower Cambrian Olenellidae of the Southern Marble Mountains, California. Southern California Academy of Science, Bulletin 51(2):25–49.

Richter, Rudolf. 1921. Beitrage zur Kenntnis

devonischer Trilobiten. III. Uber die Organisation von Harpes. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 37:179–218, 3 fig., pl. 16–17.

———. 1932. Crustacea (Paläontologie). *In* R. Dittler, G. Joos, E. Korschelt, G. Linek, F. Oltmanns, K. Schaum, eds., Handwörterbuch der Naturwissenschaften, 2nd ed. Gustav Fisher. Jena. p. 840–864, fig. A, 1–64.

This volume was published in 9 parts, which were not dated. The final part contains the title page (dated 1933) and list of contents. All parts were received together by the University Library, Cambridge, United Kingdom, on 23 March, 1933. An offprint of Crustacea (Paläontologie) sent by Richter to Professor O. M. B. Bulman (Sedgwick Museum, Cambridge) is dated 1932 on the cover in Richter's handwriting. Stubblefield (1936) and subsequent authors date the article 1932.

———. 1937. Von Bau und Leben der Trilobiten, 8: Die "Salter'sche Einbettung" als Folge und Kennzeichen des Hautungs-Vorgangs. Senckenbergiana 19:413–431, 3 fig.

———. 1942. Die Einkippungsregel. Senckenbergiana 25:181–206, 404, 1 fig.

Richter, Rudolph, & Emma Richter. 1926. Die Trilobiten des Oberdevons: Beitrage zur Kenntnis devonischer Trilobiten, IV. Abhandlungen der Preussischen Geologischen Landesanstalt (new series) 99:1–314, 18 fig., 12 pl.

———. 1940. Studien im Paläozoikum der Mittelmeer-Länder, 5: Die Saukianda-Stufe von Andalusien, eine fremde Fauna im europäischen Ober-Kambrium. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 450:1–81, pl. 1–5.

———. 1941a. Die Fauna des Unter-Kambriums von Cala in Andalusien. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 455:1–90, fig. 1, pl. 1–4.

———. 1941b. Das Kambrium am Toten Meer und die älteste Tethys. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 460:1–50, fig. 1–3, pl. 1–2.

Robison, R. A. 1964. Late Middle Cambrian faunas from western Utah. Journal of Paleontology 38:510–566, fig. 1–4, pl. 79–92.

———. 1967. Ontogeny of *Bathyuriscus fimbriatus* and its bearing on the affinities of the corynexochid trilobites. Journal of Paleontology 41:213–221, fig. 1–5, pl. 24.

———. 1971. Additional Middle Cambrian trilobites from the Wheeler Shale of Utah. Journal of Paleontology 45:796–804, fig. 1, pl. 89–91.

———. 1972a. Mode of life of agnostid trilobites. 24th International Geological Congress, Montreal, Canada, Section 7 (Paleontology). p. 33–40, 2 fig.

———. 1972b. Hypostoma of agnostid trilobites. Lethaia 5:239–248, fig. 1–4.

———. 1978. Origin, taxonomy, and homeomorphs of *Doryagnostus* (Cambrian Trilobita). The University of Kansas Paleontological Contributions, Paper 91:1–

Robison—. 1982. Some Middle Cambrian agnostoid trilobites from western North America. Journal of Paleontology 56:132–160, fig. 1–2, pl. 1–6.

———. 1984. Cambrian Agnostida of North America and Greenland. Part 1: Ptychagnostidae. The University of Kansas Paleontological Contributions, Paper 109:1–59, 32 fig.

———. 1988. Trilobites of the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddelelser om Grønland, Geoscience 20:23–103, 27 fig.

Robison, R. A., & D. P. Campbell. 1974. A Cambrian corynexochoid trilobite with only two thoracic segments. Lethaia 7:273–282, fig. 1–3.

Robison, R. A., & Jerjes Pantoja-Alor. 1968. Tremadocian trilobites from the Nochixtlán Region, Oaxaca, Mexico. Journal of Paleontology 42:767–800, fig. 1–4, pl. 97–104.

Robison, R. A., A. V. Rosova, A. J. Rowell, & T. P. Fletcher. 1977. Cambrian boundaries and divisions. Lethaia 10:257–262, fig. 1–2.

Robison, R. A., & A. J. Rowell, eds. 1976. Paleontology and depositional environments: Cambrian of western North America. Brigham Young University, Geology Studies 23(2):iii + 1–227.

Romanenko, E. V. 1985. Trilobity iz pogranichnykh otlozheniy Srednego i Verkhnego Kembriya Altaya. Paleontologicheskiy Zhurnal 1985(4):54–63, pl. 5.

Romanenko, E. V., & M. F. Romanenko. 1967. Nekotorye voprosy paleogeografii i trilobity kembriia Gornogo Altaia [On some questions of the paleogeography and Cambrian trilobites of Gorny Altay]. Izvestiya Altayskogo Otdela Geograficheskogo Obshchestva Soyuza SSR 8:62–96, pl. 1–3.

Romanenko, M. F., & E. V. Romanenko. 1962. Trilobity suiarykskoi svity srednego kembriia Gornogo Altaia [Trilobites of the Suyarksky suite of the Middle Cambrian of Gorny Altai]. Materialy Geologii Zapadnos Sibirskogo Kraya Tomsk 63:16–29, fig. 1, pl. 1–3.

Romano, M. 1976. The trilobite genus *Placoparia* from the Ordovician of the Valongo area, north Portugal. Geological Magazine 113:11–28.

Ross, R. J., Jr. 1951a. The ontogenies of three Garden City (early Ordovician) trilobites. Journal of Paleontology 25:578–586, pl. 81–84.

———. 1951b. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. Peabody Museum of Natural History, Yale University Bulletin 6:1–161, 4 fig., 36 pl.

———. 1953. Additional Garden City (Early Ordovician) trilobites. Journal of Paleontology 27:633–646, fig. 1, pl. 62–64.

———. 1967. Calymenid and other Ordovician trilobites from Kentucky and Ohio. United States Geological Survey, Professional Paper 583B:1–18, 3 fig., 5 pl.

———. 1975. Early Paleozoic trilobites, sedimentary facies, lithospheric plates, and ocean currents. Fossils and Strata 4:307–329, fig. 1–9.

———. 1979. Additional trilobites from the Ordovician of Kentucky. *In* John Pojeta, Jr., ed., Contribu-

tions to the Ordovician Paleontology of Kentucky and nearby States. United States Geological Survey, Professional Paper 1066A-G:D1–13, 6 pl.

Rowell, A. J., & D. J. McBride. 1972. Faunal variation in the *Elvinia* Zone of the Upper Cambrian of North America—a numerical approach. 24th International Geological Congress, Montreal, Canada, Section 7 (Paleontology). p. 246–253, 3 fig.

Rowell, A. J., D. J. McBride, & A. R. Palmer. 1973. Quantitative study of Trempealeauian (Latest Cambrian) trilobite distribution. Geological Society of America, Bulletin 84:3429–3442, 11 fig.

Roy, Kaustuv, & L. E. Fåhraeus. 1989. Tremadocian (Early Ordovician) nauplius-like larvae from the Middle Arm Point Formation, Bay of Islands, western Newfoundland. Canadian Journal of Earth Sciences 26:1802–1806, fig. 1–2, pl. 1.

Rozanov, A. Yu., & B. S. Sokolov, eds. 1984. Iarusnoe raschlenenie nizhnego kembriia—stratigrafiia [Stage subdivision of the Lower Cambrian—stratigraphy]. Nauka. Moscow. 184 p.

Rozanov, A. Yu., & A. Yu. Zhuravlev. 1992. The Lower Cambrian fossil record of the Soviet Union. *In* Jere Lipps & P. E. Signor, eds., Origin and Early Evolution of the Metazoa. Plenum Press. New York & London. p. 205–282.

Rozova, A. V. 1960. Verkhnekembriyskie trilobity Salaira [Upper Cambrian Trilobites of Salair]. Trudy Instituta Geologii i Geofiziki 5:116 p.

———. 1964. Biostratigrafiya i opisanie trilobitov srednego i verkhnego kembriya severo-zapada Sibirskoy platformy [Biostratigraphy and description of trilobites of the Middle and Upper Cambrian of the northwest Siberian Platform]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki. Izdatelstvo "Nauka," Moscow. 106 p., 19 pl.

Rudkin, D. M. 1985. Exoskeletal abnormalities in four trilobites. Canadian Journal of Earth Sciences 22:479–483, fig. 1–2.

Rudolph, Frank. 1992. Kopfmuskulatur bei Trilobiten-Rekonstruktion, Funktionsmorphologie und phylogenetisch-systematische Schlussfolgerungen. Diplom-Arbeit aus dem Zoologischen Institut der Christian-Albrechts-Universitat Kiel. F. Rudolph. Wankendorf. p. 1–115, 33 fig., 14 pl., 16 tables.

Ruedemann, R. 1912. The Lower Siluric Shales of the Mohawk Valley. Education Department Bulletin of the University of the State of New York, Museum Bulletin 162:151 p.

Rusconi, C. 1950a. Trilobitas y otros organismos del Cambrico de Canota. Revista del Museo Historia Natural de Mendoza 4:71–84, fig. 1–14.

———. 1950b. Nuevos trilobitas y otros organismos del Cambrico de Canota. Revista del Museo Historia Natural de Mendoza 4(3-4):85–94, fig. 1–11.

———. 1951. Mas trilobitas Cambricos de san Isidro Cerro Pelado y Canota. Revista del Museo Historia Natural de Mendoza 5:3–30.

———. 1952. Varias especies de trilobitas del Cambrico de Canota. Revista del Museo Historia Natural de Mendoza 6(1-4):5–17, 1 pl.

———. 1956. Mares y organismos extinguidos de Mendoza. Revista del Museo de Historia Natural de Mendoza 9(3–4):2–88.

Rushton, A. W. A. 1963. *Paradoxides* from Colombia. Geological Magazine 100:255–257.

———. 1966. The Cambrian Trilobites from the Purley Shales of Warwickshire. Palaeontographical Society, London, Monograph, vol. 120. p. 1–55, fig. 1–18, pl. 1–6.

———. 1978. Fossils from the Middle–Upper Cambrian transition in the Nuneaton district. Palaeontology 21:245–283, fig. 1–3, pl. 24–27.

———. 1979. A review of the Middle Cambrian Agnostida from the Abbey Shales, England. Alcheringa 3:43–61, fig. 1–9.

———. 1983. Trilobites from the Upper Cambrian *Olenus* Zone in central England. Special papers in Palaeontology 30:107–139, pl. 14–19, fig. 1–7.

Rushton, A. W. A., & C. P. Hughes. 1981. The Ordovician trilobite fauna of the Great Paxton Borehole, Cambridgeshire. Geological Magazine 118(6):623–646.

Růžička, R. 1943. Príspevek k ontogenii ceskych Paradoxidu a rodu *Sao* [Contribution on the ontogeny of Bohemian paradoxidids of the genus *Sao*]. Vestnik Královské České Spolecnosti Náuk, Trída Math-prír 1943:1–43.

Pages 1–16, Czech; 17–33, German; 34–43, German and Czech.

Saito, Kazuo. 1934. Older Cambrian Trilobita and Conchostraca from northwestern Korea. Japanese Journal of Geology and Geography, Tokyo 11(3–4):211–237, 7 fig., pl. 25–27.

———. 1936. Older Cambrian Brachiopoda, Gastropoda, etc. from northwestern Korea. Journal Faculty of Science, Imperial University of Tokyo, section II, 4(3):346–367, pl. 1–3.

Appendix: Changes in systematic reference of some trilobites previously described by the writer, p. 363.

Salter, J. W. 1864a. A Monograph of British Trilobites, Part 1. Palaeontographical Society, London, Monograph, vol. for 1862. p. 1–80, pl. 1–6.

———. 1864b. Memoirs of the Geological Survey of the United Kingdom. Figures and descriptions illustrative of British organic remains. Decade XI, Trilobites, pl. 64 p., 9 pl.

———. 1864c. On some new fossils from the *Lingula*-flags of Wales. Quarterly Journal of the Geological Society of London 20:233–241.

———. 1865. A Monograph of British Trilobites, Part 2. Palaeontographical Society, London, Monograph, vol. for 1863. p. 81–128, pl. 7–14.

———. 1866a. A Monograph of British Trilobites, Part 3. Palaeontographical Society, London, Monograph, vol. for 1864. p. 129–176, pl. 15–25.

———. 1866b. On the fossils of North Wales. *In* A. C. Ramsay, The Geology of North Wales. Memoirs of the Geological Survey of Great Britain, no. 3. p. 239–381, 19 fig., pl. 1–26.

Samson, Sara, A. R. Palmer, R. A. Robison, & D. T. Secor, Jr. 1990. Biogeographical significance of Cambrian trilobites from the Carolina slate belt.

Geological Society of America Bulletin 102:1459–1480, 6 fig.

Schevill, W. E. 1936. Habits of trilobites. Report of the Committee on Paleoecology, 1935–1936. Annual Meeting of the Division of Geology and Geography, United States National Research Council, Washington, D.C. p. 29–43.

Schmalfuss, Helmut. 1981. Structure, patterns and function of cuticular terraces in trilobites. Lethaia 14:331–341, fig. 1–7.

Schmidt, F. 1888. Ueber eine neuentdeckte untercambrische Fauna in Estland. Mémoires de l'Académie Impériale des Sciences de St-Petersbourg (7th series) 36(2):1–27.

Schram, F. R. 1982. The fossil record and evolution of Crustacea. *In* L. G. Abele, ed., The Biology of the Crustacea, vol. 1. Academic Press. New York. p. 93–147, 13 fig.

Schrank, Eckart. 1972a. Proetacea, Encrinuridae and Phacopina (Trilobita) aus Silurischen Geschieben. Geologie 21:117 p., 4 fig., 21 pl.

———. 1972b. *Nileus*-Arten (Trilobita) aus Geschieben des Tremadoc bis tieferen Caradoc. Der Deutschen Gesellschaft Geologischen Wissenschaften, A, Geologie-Palaeontologie 17:351–375, 11 fig., 11 pl.

———. 1975. Kambrische Trilobiten der China-Kollektion v. Richthofen, 2. Die Fauna mit *Kaolishania? quadriceps* von Saimaki. Zeitschrift fuer Geologische Wissenschaften 3:591–619, pl. 1–8.

———. 1977. Zur Paläobiogeographie silurischer Trilobiten. Neues Jahrbuch fuer Geologie und Palaontologie, Abhandlungen 155:108–136, 2 fig.

Scotese, C. R., R. K. Bambach, Colleen Barton, Rob Van der Voo, & A. M. Ziegler. 1979. Paleozoic Base maps. Journal of Geology 87:217–277, 43 fig.

Scotese, C. R., & W. S. McKerrow. 1990. Revised world maps and introduction. *In* W. S. McKerrow & C. R. Scotese, eds., Palaeozoic Palaeogeography and Biogeography. Geological Society of London, Memoir 12. p. 1–21.

Sdzuy, Klaus. 1957. Bemerkungen zur Familie Homalonotidae. Senckenbergiana Lethaea 38:275–290, 4 fig., 1 pl.

———. 1958. Fossilien aus dem Tremadoc des Montagne Noire. Senckenbergiana Lethaea 39:255–285, pl. 1–3.

———. 1959. Die unterkambrische Trilobiten-Familie Dolerolenidae. Senckenbergiana Lethaea 44:389–407, 1 fig.

———. 1961. Das Kambrium Spaniens. Teil II: Trilobiten 1. Abschnitt. Akademie der Wissenschaften und der Literatur Mainz, Abhandlungen der Mathematisch-naturwissenschaftlichen Klasse (Wiesbaden) 7:499–594 (217–312), fig. 1–23, pl. 1–15.

———. 1962a. Neue Kambrische fossilien aus Bohrungen im Gebiet von Doberlug. Geologie (Jahrgang 11) 9:1087–1101, 1 pl.

———. 1962b. Trilobiten aus dem Unter-Kambrium der Sierra Morena (S-Spanien). Senckenbergiana Lethaea 43(3):181-229, fig. 1–4, pl. 18–23.

———. 1968. Trilobites del Cambrico medio de Asturias. Trabajos de Geologia, Faculte de Ciencias, Universidad de Oviedo 1:77–133, 1 fig., 10 pl.

———. 1971a. Acera de la correlación del Cámbrico medio en España. 1 Congreso Hispano-Luso-Americano de Geología Económica. Geologia 2:753–766.

———. 1971b. La subdivisión bioestratigráfica y la correlatión del Cámbrico medio en España. 1 Congreso Hispano-Luso-Americano de Geología Económica. Geologia 2:769–782.

———. 1972. Das Kambrium der acadobaltischen Faunenprovinz. Zentralblatt fuer Geologie und Palaeontologie 2(1–2):1–91.

———. 1978. The Precambrian-Cambrian boundary beds in Morocco (preliminary report). Geological Magazine 115:83–94, fig. 1–6, pl. 1.

———. 1979. Two rare trilobites from the Tremadoc Leimitz Shales, Germany. Alcheringa 3:63–72, 5 fig.

———. 1981. Der Beginn des Phanerozoikums—Paläobiologische und stratigraphische Probleme. Natur und Museum 111:390–398, fig. 1–20.

Sedgwick, Adam, & R. I. Murchison. 1840. On the physical structure of Devonshire, and on the subdivisions and geological relations of its older stratified deposits, etc. Transactions of the Geological Society of London (second series) 5:633–703, pl. 50–58.

Seilacher, Adolf. 1955. Spuren und Lebenweise der Trilobiten. *In* O. H. Schindewolf & Adolf Seilacher, eds., Beitrage zur Kenntnis des Kambriums in der Salt Range (Pakistan). Akademie der Wissenschaften und der Literatur., Abhandlungen der Mathematisch-naturwissenschaftlichen Klasse, Mainz 10:342–372, 5 fig., pl. 16–21.

———. 1959. Vom Leben der Trilobiten. Die Naturwissenschaften 12:389–393, 5 fig.

———. 1962. Form und Funktion des Trilobiten-Daktylus. Palaontologische Zeitschrift (H. Schmidt-Festband). p. 218–227, 2 fig., pl. 24–25.

Not bound with Band 36 (1962).

———. 1970. Cruziana stratigraphy of "non-fossiliferous" Palaeozoic sandstones. *In* T. P. Crimes & J. C. Harper, eds., Trace Fossils. Geological Journal, Special Issue 3. p. 447–476, 11 fig.

———. 1985. Trilobite palaeobiology and substrate relationships. Transactions of the Royal Society of Edinburgh, Earth Sciences 76:231–237, fig. 1–4.

Sekiguchi, K., S. Seshimo, & H. Sugita. 1988. Postembryonic development. *In* K. Sekiguchi, ed., Biology of Horseshoe Crabs. Science House Co. Tokyo. p. 181–195.

Shaler, N. S., & A. F. Foerste. 1888. Preliminary description of North Attleborough fossils. Bulletin of the Museum of Comparative Zoology at Harvard College (series 2) 16:27–41, pl. 1–2.

Shaw, A. B. 1950. A revision of several Early Cambrian trilobites from eastern Massachusetts. Journal of Paleontology 24:577–590, fig. 1–3, pl. 79.

———. 1951. The paleontology of northwestern Vermont. I. New Late Cambrian trilobites. Journal of Paleontology 25:97–114, pl. 21–24.

———. 1956. Quantitative trilobite studies I. The statistical description of trilobites. Journal of Paleon-

tology 30:1209–1224, fig. 1–2.

———. 1957. Quantitative trilobite studies II. Measurement of the dorsal shell of non-agnostidean trilobites. Journal of Paleontology 31:193–207, fig. 1–13.

———. 1959. Quantitative trilobite studies III. *Proliostracus strenuelliformis* Poulsen, 1932. Journal of Paleontology 33:474–487, fig. 1–15.

Shaw, F. C. 1968. Early Middle Ordovician Chazy trilobites of New York. New York State Museum and Science Service Memoir 17:163 p.

———. 1974. Simpson Group (Middle Ordovician) trilobites of Oklahoma. Paleontological Society Memoir 6, Journal of Paleontology 48 (supplement to no. 5):1–54, fig. 1–6, pl. 1–12.

———. 1991. Viola Group (Ordovician, Oklahoma) cryptolithinid trilobites, biogeography and taxonomy. Journal of Paleontology 65:919–935, 9 fig.

Shaw, F. C., & R. A. Fortey. 1977. Middle Ordovician facies and trilobite faunas. Geological Magazine 114:409–443, fig. 1–8.

Shaw, F. C., & P. J. Lespérance. 1994. North American biogeography and taxonomy of *Cryptolithus* (Trilobita, Ordovician). Journal of Paleontology 68:808–823, 7 fig.

Sheldon, P. R. 1987. Parallel gradualistic evolution of Ordovician trilobites. Nature 330:561–563, fig. 1–4.

———. 1988. Trilobite size-frequency distributions, recognition of instars, and phyletic size changes. Lethaia 21:293–306, fig. 1–11.

Shergold, J. H. 1969. Oryctocephalidae (Trilobita: Middle Cambrian) of Australia. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 104:1–66, 18 fig., 12 pl.

———. 1972. Late Upper Cambrian trilobites from the Gola Beds, western Queensland. Bureau of Mineral Resources of Australia, Bulletin 112:127 p., 19 pl.

———. 1975. Late Cambrian and Early Ordovician trilobites from the Burke River structural belt, western Queensland, Australia. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Bulletin 153:1–251, 72 fig. (vol. 1); 58 pl. (vol. 2).

———. 1977. Classification of the trilobite *Pseudagnostus.* Palaeontology 20:69–100, pl. 15–16.

———. 1980. Late Cambrian trilobites from the Chatsworth Limestone, western Queensland. Commonwealth of Australia, Bureau of Mineral Resources, Bulletin 186:111 p., 35 pl.

———. 1981. Towards a global Late Cambrian agnostid biochronology. *In* M. E. Taylor, ed., Short Papers for the Second International Symposium on the Cambrian System, 1981. United States Geological Survey, Open-file Report 81-743:208–214.

———. 1982. Idamean (Late Cambrian) trilobites, Burke River Structural Belt, western Queensland. Bureau of Mineral Resources of Australia, Bulletin 187:69 p., 17 pl.

———. 1988. Review of trilobite biofacies distributions at the Cambrian-Ordovician boundary. Geological Magazine 125(4):363–380.

———. 1989. Australian Phanerozoic Timescales, 1. Cambrian biostratigraphic chart and explanatory notes. Commonwealth of Australia, Bureau of Mineral Resources, Record 1989/31:25 p.

———. 1991. Protaspid and early meraspid growth stages of the eodiscoid trilobite *Pagetia ocellata* Jell, and their implications for classification. Alcheringa 15:65–86, fig. 1–8.

———. 1993. The Iverian, a proposed Late Cambrian Stage, and its subdivision in the Burke River Structural Belt, western Queensland. BMR Journal of Australian Geology & Geophysics 13(4):345–358.

Shergold, J. H., & M. D. Brasier. 1986. Biochronology of Proterozoic and Cambrian phosphorites. *In* P. J. Cook & J. H. Shergold, eds., Phosphate Deposits of the World. Volume 1: Proterozoic and Cambrian Phosphorites. Cambridge University Press. Cambridge. p. 295–326.

Shergold, J. H., & J. R. Laurie. 1991. *Ptychagnostus* Jaekel, 1909 and *Glyptagnostus* Whitehouse, 1936 (Trilobita): Proposed conservation of accepted usage. Bulletin of Zoological Nomenclature 48(3):200–202.

Shergold, J. H., J. R. Laurie, & Xiaowen Sun. 1990. Classification and review of the trilobite order Agnostida Salter, 1864: An Australian perspective. Commonwealth of Australia, Bureau of Mineral Resources, Geology and Geophysics, Report 296:iv + 1–92, fig. 1–19.

Shergold, J. H., & R. S. Nicoll. 1992. Revised Cambrian-Ordovician boundary biostratigraphy, Black Mountain, western Queensland. *In* B. D. Webby & J. R. Laurie, eds., Global Perspectives on Ordovician Geology. Balkema. Rotterdam. p. 81–92.

Shimer, H. W., & R. R. Shrock. 1944. Index Fossils of North America. Technology Press, Massachusetts Institute of Technology. Cambridge. 837 p.

Shone, R. W. 1979. Giant *Cruziana* from the Beaufort Group. Transactions of the Geological Society of South Africa 81:327–329, 6 fig.

Shu, Degan, Gerd Geyer, Ling Chen, & Xingliang Zhang. 1995. Redlichiacean trilobites with preserved soft parts from the Lower Cambrian Chengjiang fauna (South China). Beringia (special issue) 2:203–241, 21 fig., pl. 1.

Shuster, C., Jr. 1982. A pictorial review of the natural history and ecology of the horseshoe crab *Limulus polyphemus,* with reference to other Limulidae. *In* J. Bonaventura, C. Bonaventura, & S. Tesh, eds., Physiology and Biology of Horseshoe Crabs. Alan R. Liss, Inc. New York. p. 1–59.

Siegfried, Paul. 1936. Über das Pandersche Organ bei den Asaphiden des Ostbaltischen Ordoviciums. Publications of the Geological Institution of the University of Tartu, no. 69, *in* Acta ad Res Naturae Estonicae Perscrutandus (series 1) 9(fasc. 2):1–42, 12 fig., 10 pl.

———. 1939. Von der Lebensweise der trilobiten der Gattung *Illaenus* Dalm. Beiträgen zur Kunde Estlands, Naturwissenschaftliche Reihe 1:43–48, pl. 1–2.

Siveter, D. J. 1980. Evolution of the Silurian trilobite *Tapinocalymene* from the Wenlock of the Welsh Borderlands. Palaeontology 23:783–802, 3 fig., pl. 97–101.

———. 1983. *Calymene lawsoni* and allied species from the Silurian of Britain and their stratigraphic significance. Special Papers in Palaeontology 30:69–88.

Sjögren, A. 1872. Om några försteningar i Ölands kambriska lager. Geologiska Foereningens i Stockholm Forhandlingar 1:67–80, pl. 5.

Skinner, D. M. 1985. Molting and Regeneration. *In* D. E. Bliss & L. H. Mantel, eds., The Biology of Crustacea. Vol. 9: Integument, Pigments and Hormonal Processes. Academic Press. San Diego. p. 43–146.

Smeenk, Z. 1983. Devonian trilobites of the southern Cantabrian mountains (Northern Spain), with a systematic description of the Asteropyginae. Leidse Geologische Mededelingen 52(2):383–511, 26 fig., 35 pl.

Smith, A. G., J. C. Briden, & G. E. Drewry. 1973. Phanerozoic world maps. *In* N. F. Hughes, ed., Organisms and Continents through Time, Special Papers in Palaeontology, no. 12. p. 1–42, fig. 1–21.

Smith, A. G., A. M. Hurley, & J. C. Briden. 1981. Phanerozoic Paleocontinental World Maps. Cambridge University Press. Cambridge. 102 p., 88 maps.

Šnajdr, Milan. 1950. *Aculeodiscus* nov. gen. ze středočeského středního kambria (Trilobitae) [*Aculeodiscus* gen. nov. from the Middle Cambrian of central Bohemia (Trilobita)]. Sborníku Statního Geologického Ústavu Československé Republiky, Paleontologicky, Praha 17:201–212, fig. 1, pl. 15–17.

———. 1957. O nových trilobitech z českého Kambria [On new trilobites of the Cambrian of Bohemia]. Věstník Ústředního Ústavu Geologického 32:235–244, 1 fig., 2 pl.

———. 1958. Trilobiti českého středního Kambria [The trilobites of the Middle Cambrian of Bohemia]. Rozpravy Ústředního Ústavu Geologického 24:1–280, 46 fig., 46 pl.

Czech text, English summary p. 237–280.

———. 1960. Studie o Celedi Scutelluidae (Trilobitae). Rozpravy Ústředního Ústavu Geologického 26:1–264, 61 fig., 36 pl.

Czech text, English summary.

———. 1975. On the ontogeny of Bohemian representatives of the genus *Parabarrandia* Prantl et Přibyl (Trilobita). Věstník Ústředního Ústavu Geologického 50:241–244, 2 pl.

———. 1977. Nový nález trilobita *Luhops expectans* (Barrande, 1852) ve skryjském kambriu. Casopis Narodniho Muzea 145:47–48.

———. 1978. Anomalous carapaces of Bohemian paradoxidid trilobites. Sborník Geologických Věd Paleontologie 20:7–31, 5 fig., 8 pl.

———. 1980. Bohemian Silurian and Devonian Proetidae (Trilobita). Rozpravy Ústředního Ústavu Geologického 45:1–324, 80 fig., 64 pl.

In English, Czech summary.

———. 1981a. Ontogeny of some representatives of the trilobite genus *Scharyia*. Sborník Geologických

Věd Paleontologie (Journal of Geological Sciences Paleontology) 24:7–32.

———. 1981b. Bohemian Proetidae with malformed exoskeletons (Trilobita). Sborník Geologických Věd Paleontologie 24:37–61, 11 fig., 8 pl.

———. 1985. Anomalous exoskeletons of Bohemian encrinurine trilobites. Věstník Ústředního Ústavu Geologického 60:303–306, 2 pl.

———. 1986. Two new paradoxid trilobites from the Jince Formation (Middle Cambrian, Czechoslovakia). Věstník Ústředního Ústavu Geologického 61:169–174.

———. 1990. Bohemian Trilobites. Geological Survey. Prague. 265 p., 8 fig., 112 pl.

———. 1991. On the digestive system of *Deanaspis goldfussi* (Barrande). Casopis Národního Muzea 156:8–16, fig. 1–3, pl. 1–4.

In Czech, English summary.

Soloviev, I. A. 1964. Nekotorye novye trilobity iz amginskogo iarusa v Olenekskom raione iakutii [Some new trilobites from the Amga Stage in the Olenek region of Yakutia]. Uchenya Zapiski Nauchno-Issledovatel'skikh, Instituta Geologiska Arktika, Paleontologia i Biostratigrafia 4:33–55, fig. 1–3, pl. 1.

———. 1969. Novye vidy *Paradoxides* (Triloboty) iz goriuchikh slantsev amginskogo iarusa severnoi Iakutii [New species of *Paradoxides* (Trilobite) from the oil shales in the Amgan Stage of northern Yakutia]. Uchenya Zapiski Nauchno-Issledovatel'skikh, Instituta Geologiska Arktika, Paleontologia i Biostratigrafia 25:9–20.

Southgate, P. N., & J. H. Shergold. 1991. Application of sequence stratigraphic concepts to Middle Cambrian phosphogenesis, Georgina Basin, Australia. BMR Journal of Australian Geology & Geophysics 12(2):119–144.

Speyer, S. E. 1985. Moulting in phacopid trilobites. Transactions of the Royal Society of Edinburgh, Earth Sciences 76:239–253, fig. 1–10.

———. 1987. Comparative taphonomy and palaeoecology of trilobite lagerstatten. Alcheringa 11:205–232, 13 fig.

———. 1988. Biostratinomy and functional morphology of enrollment in two Middle Devonian trilobites. Lethaia 21:121–138, fig. 1–12.

———. 1991. Trilobite taphonomy: a basis for comparative studies of arthropod preservation, functional anatomy and behaviour. *In* S. K. Donovan, ed., The Processes of Fossilization. Belhaven Press. London. p. 194–219, fig. 1–4.

Speyer, S. E., & C. E. Brett. 1985. Clustered trilobite assemblages in the Middle Devonian Hamilton Group. Lethaia 18:85–103, fig. 1–8.

———. 1986. Trilobite taphonomy and Middle Devonian taphofacies. Palaios 1:312–327, fig. 1–5.

Speyer, S. E., & B. D. E. Chatterton. 1989. Trilobite larvae and larval ecology. Historical Biology 3:27–60, 15 fig.

———. 1990. Trilobite larvae, larval ecology and developmental paleobiology. Short Courses in Palaeon-

tology Number 3. Arthropod Paleobiology. Paleontological Society. Knoxville, Tennessee. p. 137–156.

Speyer, S. E., & G. D. Edgecombe. 1989. The evolution of early development in Ordovician and Silurian phacopid trilobites. Geological Society of America, Abstracts with Programs 21(6):115.

Spizharski, T. N., G. Kh. Ergaliev, I. T. Zhuravleva, L. N. Repina, A. Yu. Rozanov, & N. E. Chernysheva. 1983. Yarusnaya shkala kembriyskoy Sistemy [Yarus scale for the Cambrian System]. Sovetskaya Geologiya 1983(8):57–72.

In Russian.

Spizharski, T. N., I. T. Zhuravleva, L. N. Repina, A. Yu Rozanov, N. Ye. Tchernysheva, & G. H. Ergaliev. 1986. The stage scale of the Cambrian System. Geological Magazine 123(4):387–392.

Stabile, G. 1864. Mollusques terrestres vivants du Piémont. Atti della Societa Italiana di Scienze Naturali 7:3–141.

Stitt, J. H. 1975. Adaptive radiation, trilobite paleoecology and extinction, *Ptychaspid* biomere, late Cambrian of Oklahoma. Fossils and Strata 4:381–390.

———. 1976. Functional morphology and life habits of the Late Cambrian trilobite *Stenopilus pronus* Raymond. Journal of Paleontology 50:561–576, fig. 1–7, pl. 1–2.

———. 1983. Enrolled Late Cambrian trilobites from the Davis Formation, southeast Missouri. Journal of Paleontology 57:93–105, fig. 1–3.

Stitt, J. H., & R. L. Clark. 1984. A complete specimen of *Peachella brevispina* Palmer: An unusual olenellid trilobite (Arthropoda: Olenellida) from the Lower Cambrian of California. Transactions of the San Diego Society of Natural History 20(9):145–150, 3 fig.

Stockton, W. L., & Richard Cowen. 1976. Stereoscopic vision in one eye: Palaeophysiology of the schizochroal eye of trilobites. Paleobiology 2:304–315, fig. 1–10.

Størmer, Leif. 1930. Scandinavian Trinucleidae: With special references to Norwegian species and varieties. Skrifter Utgitt av Der Norske Videnskaps-Akademi i Oslo, I, Matematisk-naturvidenskapelig Klasse 1930, no. 4:1–111, fig. 1–47, pl. 1–14.

———. 1933. Are trilobites related to arachnids? American Journal of Science (series 5) 26:147–157, fig. 1–2.

———. 1939. Studies on trilobite morphology. Part 1: The thoracic appendages and their phylogenetic significance. Norsk Geologisk Tidsskrift 19:143–274, 35 fig., 12 pl.

———. 1942. Studies on trilobite morphology. Part II: The larval development, the segmentation and the sutures, and their bearing on trilobite classification. Norsk Geologisk Tidsskrift 21:49–164, 19 fig., 2 pl.

———. 1951. Studies on trilobite morphology. Part III: The ventral cephalic structures with remarks on the zoological position of the trilobites. Norsk Geologisk Tidsskrift 29:108–158, 14 fig., 4 pl.

———. 1980. Sculpture and microstructure of the exoskeleton in chasmopinid and phacopid trilobites.

Palaeontology 23:237–271, fig. 1–8, pl. 25–34.

Strand, T. 1927. The ontogeny of *Olenus gibbosus.* Norsk Geologisk Tidsskrift 9:320–329.

Strusz, D. L. 1980. The Encrinuridae and related trilobite families, with a description of Silurian species from southeastern Australia. Palaeontographica (Abt. A) 168:1–68, fig. 1–16, pl. 1–6.

Stubblefield, C. J. 1926. Notes on the development of a trilobite, *Shumardia pusilla* (Sars). Linnean Society Journal of Zoology 36:345–372.

———. 1936. Cephalic sutures and their bearing on current classifications of trilobites. Biological Reviews 11:407–440, 9 fig.

———. 1959. Evolution in trilobites. Quarterly Journal of the Geological Society of London 115:145–162, fig. 1–2.

Stürmer, Wilhelm. 1970. Soft parts of cephalopods and trilobites: Some surprising results of X-ray examination of Devonian slates. Science 170:1300–1302, fig. 1–5.

Stürmer, Wilhelm, & Jan Bergström. 1973. New discoveries on trilobites by X-rays. Palaeontologische Zeitschrift 47:104–141, fig. 1–6, pl. 16–24.

Suarez-Soruco, R. 1975. Nuevos trilobites del Tremadociano inferior (Ordovicico) del sur de Bolivia. Revista Tecnica de Yacimientos Petroliferos Fiscales Bolivianos 4(3):129–146, pl. 1–2.

Šuf, Jiri. 1926. O Ceskych Paradoxidech se zvlástním zretelem k jejich vyvoji. Sborník Statniho Geologického Ústavu Ceskoslovenske Republiky 6:31–67, 1 fig., pl. 1–4.

In Czech and French.

Sun, Xiaowen. 1989. Cambrian agnostids from the North China Platform. Palaeontologia Cathayana 4:53–129, pl. 1–15.

Sun, Yunzhu. 1924. Contributions to the Cambrian faunas of North China. Palaeontologia Sinica (series B) 1(4):1–109, pl. 1–5.

Suvorova, N. P. 1958. Novye triloby nezhnego Kembriya Yakutii [New Lower Cambrian trilobites from Yakuti]. Doklady Akademii Nauk SSSR 122(5):917–920.

———. 1959. Novye triloby Nadsemejstv Corynexochoidea i Redlichioidea Lenskogo Yarusa Nizhnego Kembriya Yakutii [New trilobites of the superfamilies Corynexochoidea and Redlichioidea from the Lower Cambrian Lena Stage of Yakuti]. Paleontologicheskij Zhurnal 3:66–77, pl. 6.

———. 1960. Triloby kembriia vostoka Sibirskoi Platformy. Vypusk 2: Olenellidy—Granuliariidy [Cambrian trilobites from the eastern part of the Siberian platform. Part 2: Olenellida—Granulariida]. Paleontological Institute Academy of Sciences USSR Trudy 84:1–230.

Swinnerton, H. H. 1915. Suggestions for a revised classification of trilobites. Geological Magazine (new series) 6(2):487–496, 538–545.

Taylor, M. E. 1976. Indigenous and redeposited trilobites from Late Cambrian basinal environments of Central Nevada. Journal of Paleontology 50:668–700, fig. 1–9, pl. 1–3.

———. 1977. Late Cambrian of western North America: Trilobite biofacies, environmental significance, and biostratigraphic implications. *In* E. G. Kauffman & J. E. Hazel, eds., Concepts and Methods of Biostratigraphy. Dowden, Hutchinson and Ross. Stroudsburg, Pennsylvania. p. 397–425, 14 fig.

Taylor, M. E., & R. M. Forester. 1979. Distributional model for marine isopod crustaceans and its bearing on early Paleozoic paleozoogeography and continental drift. Geological Society of America, Bulletin 90:405–413, 5 fig.

Tchernysheva, N. E., ed. 1960. Chlenistonogie: Trilobitoobraznye i rakoobraznye [Arthropoda: Trilobitomorpha and Crustacea]. Osnovy Paleontologii [Fundamentals of Paleontology]. Akademiia Nauk SSSR, Ministerstvo Geologii i Okhrany Nedr SSSR. Moscow. 515 p.

———, ed. 1971. Amginskii iarus Altae-Saianskoi oblasti [The Amga Stage in the Altay-Sayan region]. Trudy Sibiriskogo Nauchno-Issledovatel'skogo Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya 111:1–267, fig. 1–10, pl. 1–25.

———. 1972. Novye rannekembriyskie triloby Pamira [New early Cambrian trilobites from Pamira]. *In* Novye vidy drevnikh rastenij i bespozvonochnykh SSSR [New Species of Prehistoric Plants and Vertebrates of the USSR]. Akademii Nauk SSSR. Moscow. p. 211–214, fig. 6–9, pl. 53.

———. 1977. Novye rody trilobitov iz srednego Kembriya Tuvy i Sibirskoj Platformy [New trilobite genera from the Middle Cambrian of Tuva and Siberian Platform]. *In* G. A. Stukalina, ed., Novye vidy drevnikh rastenij i bespozvonochnykh SSSR [New Species of Prehistoric Plants and Invertebrates of the USSR], vol. 4. Akademiya Nauk SSSR. Moscow. p. 61–65.

Tchernysheva, N. E., L. I. Egorova, L. V. Ogienko, O. K. Poletaeva, & L. N. Repina. 1956. Novye rody trilobitov [New genera of Trilobita]. Trudy Vsesoyuznogo Nauchnogo-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI) (new series) 12:145–182, pl. 28–33.

Teichert, Curt. 1944. Permian trilobites from western Australia. Journal of Paleontology 18:455–463, 1 fig., pl. 77.

Teigler, D. J., & K. M. Towe. 1975. Microstructure and composition of the trilobite exoskeleton. Fossils and Strata 4:137–149, pl. 1–9.

Temple, J. T. 1952. The ontogeny of the trilobite *Dalmanitina olini.* Geological Magazine 89:251–262.

———. 1975. Standardisation of trilobite orientation and measurement. Fossils and Strata 4:461–467, fig. 1.

———. 1980. A numerical taxonomic study of species of Trinucleidae (Trilobita) from the British Isles. Transactions of the Royal Society of Edinburgh, Earth Sciences 71:213–233, fig. 1–11.

Temple, J. T., & R. P. Tripp. 1979. An investigation of the Encrinurinae (Trilobita) by numerical taxonomic methods. Transactions of the Royal Society of Edinburgh 70:223–250, fig. 1–7.

Temple, J. T., & Hongji Wu. 1990. Numerical taxonomy of Encrinurinae (Trilobita): Additional species from China and elsewhere. Transactions of the Royal Society of Edinburgh, Earth Sciences 81:209–219, fig. 1–2.

Theokritoff, George. 1985. Early Cambrian biogeography in the North Atlantic region. Lethaia 18:282–293, 3 fig.

Thomas, A. T. 1977. Classification and phylogeny of homalonotid trilobites. Palaeontology 20:159–178, fig. 1, pl. 23–24.

———. 1978. British Wenlock Trilobites, Part 1. Palaeontographical Society, London, Monograph, vol. 132. p. 1–56, 7 fig., pl. 1–14.

———. 1979. Trilobite associations in the British Wenlock. *In* A. L. Harris, C. H. Holland, & B. E. Leake, eds., The Caledonides of the British Isles—reviewed. Special Publications of the Geological Society of London 8. p. 447–451, 3 fig., 1 pl.

———. 1981. British Wenlock trilobites, Part 2. Palaeontographical Society, London, Monograph, vol. 134. p. ix–xii, 57–99, fig. 8–10, pl. 15–25.

Thomas, A. T., & D. J. Holloway. 1988. Classification and phylogeny of the trilobite order Lichida. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 321:179–262, fig. 1–365.

Thomas, A. T., & P. D. Lane. 1984. Autecology of Silurian trilobites. *In* M. G. Bassett & J. D. Lawson, eds., Autecology of Silurian Organisms, Special Papers in Palaeontology, no. 32. p. 55–69, fig. 1–2.

Thomas, A. T., & G. M. Narbonne. 1979. Silurian trilobites from arctic Canada. Geological Magazine 116:1–19, fig. 1–2, pl. 1–5.

Thomas, A. T., & R. M. Owens. 1978. A review of the trilobite family Aulacopleuridae. Palaeontology 21:65–81, fig. 1, pl. 7.

Thorson, G. 1936. The larval development, growth, and metabolism of Arctic marine bottom invertebrates. Meddelelser om Grønland 100:155 p., 32 fig.

Tillman, C. G. 1960. *Spathacalymene,* an unusual new Silurian trilobite genus. Journal of Paleontology 34:891–895, pl. 116.

Toll, E. von. 1899. Beiträge zur Kenntniss des Sibirischen Cambrium. Imp. Akad. Nauk, Leningrad, Zap. (series 8) 8(10):1–57, fig. 1–9, pl. 1–8.

Towe, K. M. 1973. Trilobite eyes: Calcified lenses in vivo. Science 179:1007–1009, fig. 1.

———. 1978. Do trilobites have a typical arthropod cuticle? Palaeontology 21:459–461.

Travis, D. 1954. The molting cycle of the spiny lobster, *Panuliris argus* Latreille. I. Molting and growth in laboratory-maintained individuals. Biological Bulletin 107:433–450.

Tripp, R. P. 1957. The trilobite *Encrinurus multisegmentatus* (Portlock) and allied Middle and Upper Ordovician species. Palaeontology 1:60–72, fig. 1, pl. 11–12.

———. 1962. The Silurian trilobite *Encrinurus punctatus* (Wahlenberg) and allied species. Palaeontology 5:460–477, fig. 1–2, pl. 65–68.

Tripp, R. P., & W. R. Evitt. 1981. Silicified Lichidae (Trilobita) from the Middle Ordovician of Virginia. Geological Magazine 118:665–677, fig. 1–4, pl. 1–2.

———. 1983. Silicified trilobites of the genus

Dimeropyge from the Middle Ordovician of Virginia. Special Papers in Palaeontology 30:229–240.

———. 1986. Silicified trilobites of the family Asaphidae from the Middle Ordovician of Virginia. Palaeontology 29:705–724, fig. 1–7, pl. 54–57.

Tripp, R. P., J. T. Temple, & K. C. Gass. 1977. The Silurian trilobite *Encrinurus variolaris* and allied species, with notes on *Frammia.* Palaeontology 20:847–867, fig. 1–4, pl. 113–115.

Troedsson, G. T. 1937. On the Cambro-Ordovician faunas of the western Quruq Tagh, eastern Tien-Shan. Palaeontologica Sinica (new series B, no. 2) 106:74 p., 10 pl.

Tullberg, S. A. 1880. Om Agnostus-arterna i de kambriska aflagringarna vid Andrarum. Sveriges Geologiska Undersökning (series C) 42:1–38, pl. 1–2.

Vermeij, G. J. 1978. Biogeography and adaptation. Patterns of marine life. Harvard University Press. Cambridge, Massachusetts. 332 p.

Vogdes, A. W. 1917. Palaeozoic crustacea: The publications and notes on the genera and species during the past twenty years, 1895–1917. Transactions of the San Diego Society of Natural History 3(1):1–141, pl. 1–5.

———. 1925. A list of the genera and subgenera of the Trilobita. Transactions of the San Diego Society of Natural History 4:89–115.

Wahlenberg, G. 1818. Petrificata Telluris Svecanae. Nova Acta Regiae Societatis Scientiarum Upsaliensis 8:1–116, pl. 1–4.

Walch, J. E. I. 1771. Die Naturgeschichte der versteinerungen zur erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur. Nürnberg.

Volume 3 of G. W. Knorr and J. E. I. Walch, 1768–1774.

Walcott, C. D. 1879. The Utica Slate and related formations of the same geological horizon. Transactions of the Albany Institute 10:38 p.

Author's extras were printed in 1879; the rest were printed in 1883.

———. 1881. The trilobite: New and old evidence relating to its organization. Bulletin of the Museum of Comparative Zoology at Harvard College 8(10):191–224, pl. 1–6.

———. 1884a. On the Cambrian faunas of North America. United States Geological Survey, Bulletin 10:285–354, pl. 1–10.

———. 1884b. Paleontology of the Eureka district. United States Geological Survey, Monograph 8:1–298, 7 fig., pl. 1–24.

———. 1885. Paleozoic notes: New genus of Cambrian trilobites, *Mesonacis.* American Journal of Science (series 3) 29:328–330, fig. 1–2.

———. 1886. Second contribution to the studies on the Cambrian faunas of North America. Unites States Geological Survey Bulletin 30:369 p.

———. 1890a. Descriptive notes of new genera and species from the Lower Cambrian or *Olenellus* Zone of North America. United States National Museum, Proceedings 12:33–46.

———. 1890b. The fauna of the Lower Cambrian or *Olenellus* zone. *In* 10th Annual Report of the Director, 1888–1889, United States Geological Survey. p. 509–774, fig. 44–69, pl. 43–98.

———. 1905. Cambrian fauna of China. Proceedings of the United States National Museum 29:1–106.

———. 1906. Cambrian fauna of China. Proceedings of the United States National Museum 30:563–595.

———. 1910. Cambrian geology and paleontology, no. 6: *Olenellus* and other genera of the Mesonacidae. Smithsonian Miscellaneous Collections 53(6):231–422, 17 fig., pl. 23–44.

———. 1912a. Cambrian geology and paleontology II, no. 9: New York Potsdam-Hoyt fauna. Smithsonian Miscellaneous Collections 57(9):251–304, pl. 37–49.

———. 1912b. Cambrian geology and paleontology II, no. 10: Group terms for the Lower and Upper Series of formations. Smithsonian Miscellaneous Collections 57(10):305–307.

———. 1912c. Cambrian Brachiopoda. United States Geological Survey, Monograph 51:1–872 (vol. 1); 1–363, pl. 1–104 (vol. 2).

———. 1912d. The Sardinian Cambrian genus *Olenopsis* in America. Smithsonian Miscellaneous Collections 57(8):239–249, pl. 36.

———. 1913a. The Cambrian faunas of China. *In* Research in China, vol. 3. Carnegie Institute Publication 54:3–276, pl. 1–24.

———. 1913b. Cambrian geology and paleontology, no. 11: New Lower Cambrian subfauna. Smithsonian Miscellaneous Collections 57(11):309–326, pl. 50–54.

———. 1916a. Cambrian geology and paleontology III, no. 3: Cambrian trilobites. Smithsonian Miscellaneous Collections 64(3):157–258, pl. 24–38.

———. 1916b. Cambrian geology and paleontology III, no. 5: Cambrian trilobites. Smithsonian Miscellaneous Collections 64:303–457, pl. 45–67.

———. 1918. Cambrian geology and paleontology IV: The appendages of trilobites. Smithsonian Miscellaneous Collections 67:115–216.

Wallerius, I. D. 1895. Undersökningar öfver zonen med Agnostus laevigatus i Vestergötland. Gleerupska Universitets-Bokhandeln. Lund. 72 p.

Wandås, B. T. G. 1984. The Middle Ordovician of the Oslo region, Norway, 33. Trilobites from the lowermost part of the Ogygiocaris Series. Norske Geologisk Tidsskrift 63(1983):211–267, fig. 1–8, pl. 1–13.

Wang Yu, ed. 1964. Handbook of Index Fossils of China, Huanan Region. Geology Press. Beijing. 173 p., 92 pl.

Wanner, A. 1901. A new species of *Olenellus* from the Lower Cambrian of York County, Pennsylvania. Washington Academy of Sciences Proceedings 3:267–272.

Warburg, Elsa. 1925. The Trilobites of the Leptaena Limestone in Dalarne, with a discussion of the zoological position and the classification of the Trilobita. Bulletin of the Geological Institute of the University of Uppsala 17:vi + 1–446, fig. 1–23, pl. 1–11.

———. 1939. The Swedish Ordovician and Lower

Silurian Lichidae. Kungliga Svenska Vetenskapsakademiens Handlingar (series 3) 17(4):1–162, 1 fig., 14 pl.

Webby, B. D. & R. S. Nicoll, compilers. 1989. Australian Phanerozoic timescales 2: Ordovician biostratigraphic chart and explanatory notes. Bureau of Mineral Resources of Australia, Record 1989/32: 42 p.

Weller, J. M. 1935. Adolescent development of *Ditomopyge.* Journal of Paleontology 9:503-513, fig. 1–31.

———. 1969. The Course of Evolution. McGraw-Hill Series in Population Biology. McGraw-Hill. New York. 696 p.

Wells, J. W. 1942. Supposed color-markings in Ordovician trilobites from Ohio. American Journal of Science 240:710–713, 1 fig., 1 pl.

Wenndorf, Klaus-Werner. 1990. Homalonotinae (Trilobita) aus dem Rheinischen Unter-Devon. Palaeontographica (Abt. A) 211:1–184, fig. 1–57, pl. 1–15.

Westergård, A. H. 1922. Sveriges Olenidskiffer. Sveriges Geologiska Undersökning, Series Ca, no. 18:205 p., 39 fig, 16 pl.

In Swedish and English.

———. 1936. *Paradoxides oelandicus* beds of Oland: With the account of a diamond boring through the Cambrian at Mossberga. Sveriges Geologiska Undersökning, Series C, no. 394, Årsbok 30, no. 1:1–66, 12 fig., 12 pl.

———. 1946. Agnostidae of the Middle Cambrian of Sweden. Sveriges Geologiska Undersökning, Series C, no. 477, Årsbok 40, no. 1: 1–140, fig. 1–2, pl. 1–16.

———. 1947. Supplementary notes on the Upper Cambrian trilobites of Sweden. Sveriges Geologiska Undersökning, Series C, no. 489, Årsbok 41, no. 8:1–34, 3 pl.

———. 1948. Non-agnostidean trilobites of the Middle Cambrian of Sweden. Sveriges Geologiska Undersökning, Series C, no. 498, Årsbok 42, no. 7:1–32, 1 fig., 4 pl.

———. 1950a. Non-agnostidean trilobites of the Middle Cambrian of Sweden (II). Sveriges Geologiska Undersökning, Series C, no. 511, Årsbok 43, no. 9: 56 p., pl. 1–8.

———. 1950b. *Opsidiscus,* a new name replacing *Aulacodiscus* Westergård, 1946. Geologiska Foereningens i Stockholm Forhandlingar 71:606.

———. 1953. Non-agnostidean trilobites of the Middle Cambrian of Sweden. Sveriges Geologiska Undersökning, Series C, no. 526, Årsbok 46, no. 2: 58 p., pl. 1–8.

Westrop, S. R. 1983. The life habits of the Ordovician illaenine trilobite *Bumastoides.* Lethaia 16:15–24, fig. 1–4.

———. 1986a. Taphonomic versus ecologic controls on taxonomic relative abundance patterns in tempestites. Lethaia 19:123–132, fig. 1–11.

———. 1986b. Trilobites of Upper Cambrian Sunwaptan Stage, southern Canadian Rocky Moun-

tains, Alberta. Palaeontographica Canadiana 3:1–179, 39 fig., pl. 1–41.

Westrop, S. R., & Rolf Ludvigsen. 1987. Biogeographic control of trilobite mass extinction at an Upper Cambrian "biomere" boundary. Paleobiology 13:84–99, fig. 1–11.

Whitehouse, F. W. 1927. Notes accompanying an exhibit of fossils. Proceedings of the Royal Society of Queensland 39:vii–viii.

———. 1930. The geology of Queensland. Australasian Association for the Advancement of Science, Handbook for Queensland. Brisbane. p. 23–39.

———. 1931. Report of the Palaeontologists. Annual Report of the Queensland Department of Mines for 1930. Brisbane. p. 141.

———. 1936. The Cambrian faunas of north-Eastern Australia. Part 1: Stratigraphical outline; Part 2: Trilobita (Miomera). Memoirs of the Queensland Museum 11(1):59–112, fig. 1–4, pl. 8–10.

———. 1939. The Cambrian faunas of north-Eastern Australia. Part 3: The polymerid trilobites (with supplement no. 1). Memoirs of the Queensland Museum 11(3):179–282, unnumbered figures, pl. 19–25.

Whittard, W. F. 1940. The Ordovician trilobite fauna of the Shelve-Corndon district, west Shropshire. Part I: Agnostidae, Raphiophoridae, Cheiruridae. Annals and Magazine of Natural History (series 2) 5:153–172, pl. 5–6.

———. 1955. The Ordovician Trilobites of the Shelve Inlier, Shropshire, Part 1. Palaeontographical Society, London, Monograph, vol. 109. p. 1–40, pl. 1–4.

———. 1960. The Ordovician trilobites of the Shelve Inlier, West Shropshire, Part IV. Palaeontographical Society, London, Monograph, vol. 113. p. 117–162, pl. 16–21.

Whittington, H. B. 1941. Silicified Trenton trilobites. Journal of Paleontology 15:492–522, fig. 1–13, pl. 72–75.

———. 1949. *Dolichoharpes* and the origin of the harpid fringe. American Journal of Science 247:276–285, pl. 1–2.

———. 1950. Sixteen Ordovician genotype trilobites. Journal of Paleontology 24:531–565, fig. 1–9, pl. 68–75.

———. 1952a. The trilobite family Dionididae. Journal of Paleontology 26:1–11, fig. 1, pl. 1–2.

———. 1952b. A unique remopleuridid trilobite. Breviora, Museum of Comparative Zoology, no. 4:1–9, 1 fig., 1 pl.

———. 1953. North American Bathyuridae and Leiostegiidae (Trilobita). Journal of Paleontology 27:647–678, fig. 1–5, pl. 65–69.

———. 1954a. Two silicified Carboniferous trilobites from West Texas. Smithsonian Miscellaneous Collections 122(10):16, 1 fig., pl. 1–3.

———. 1954b. Ordovician trilobites from Silliman's Fossil Mount. *In* A. K. Miller, Walter Youngquist, & Charles Collinson, Ordovician cephalopod fauna of Baffin Island. Geological Society of America Memoir 62. p. 119–149, pl. 59–63.

———. 1954c. Trilobita. *In* B. Kummel, ed., Status

of invertebrate paleontology, 1953. Bulletin of the Museum of Comparative Zoology at Harvard College 112:193–200.

———. 1956a. Beecher's supposed odontopleurid protaspis is a phacopid. Journal of Paleontology 30:104–109, fig. 1–2.

———. 1956b. Type and other species of Odontopleuridae (Trilobita). Journal of Paleontology 30:504–520, fig. 1–4, pl. 57–60.

———. 1956c. Beecher's lichid protaspis and *Acanthopyge consanguinea* (Trilobita). Journal of Paleontology 30:1200–1204, fig. 1, pl. 131.

———. 1956d. Silicified Middle Ordovician trilobites: The Odontopleuridae. Bulletin of the Museum of Comparative Zoology at Harvard College 114(5):155–288, 25 fig., 24 pl.

———. 1957a. Ontogeny of *Elliptocephala, Paradoxides, Sao, Blainia,* and *Triarthrus* (Trilobita). Journal of Paleontology 31:934–946, pl. 115–116.

———. 1957b. The ontogeny of trilobites. Biological Reviews 32:421–469, 29 fig.

———. 1958. Ontogeny of the trilobite *Peltura scarabaeoides* from Upper Cambrian, Denmark. Palaeontology 1:200–206, pl. 38.

———. 1959a. Silcified Middle Ordovician trilobites: Remopleurididae, Trinucleidae, Raphiophoridae, Endymioniidae. Bulletin of the Museum of Comparative Zoology at Harvard College 121(8):371–496, 8 fig., 36 pl.

———. 1959b. Ontogeny of Trilobita. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology, Part O. Geological Society of America & The University of Kansas Press. New York & Lawrence, Kansas. p. 127–144, fig. 86–106.

———. 1960a. *Cordania* and other trilobites from the Lower and Middle Devonian. Journal of Paleontology 34:405–420, fig. 1, pl. 51–54.

———. 1960b. Trilobita. *In* McGraw-Hill Encyclopedia of Science and Technology. McGraw-Hill Book Company. New York. p. 102–106, fig. 1–4.

———. 1961a. Silurian *Hemiarges* (Trilobita) from Cornwallis Island and New York State. Journal of Paleontology 35:433–444, pl. 55–57.

———. 1961b. Middle Ordovician Pliomeridae (Trilobita) from Nevada, New York, Quebec, Newfoundland. Journal of Paleontology 35:911–922, fig. 1–5, pl. 99–102.

———. 1963. Middle Ordovician trilobites from Lower Head, western Newfoundland. Bulletin of the Museum of Comparative Zoology 129(1):1–118, 6 fig., 36 pl.

———. 1964. Taxonomic basis of paleoecology. *In* John Imbrie & N. D. Newell, eds., Approaches to Paleoecology. John Wiley & Sons. New York, London, & Sydney. p. 19–27

———. 1965. Trilobites of the Ordovician Table Head Formation, western Newfoundland. Bulletin of the Museum of Comparative Zoology 132(4):275–442, 7 fig., 68 pl.

———. 1966. Phylogeny and distribution of Ordovician trilobites. Journal of Paleontology 40:696–737, fig. 1–16.

———. 1971. A new calymenid trilobite from the Maquoketa Shale, Iowa. *In* J. Thomas Dutro, Jr., ed., Paleozoic Perspectives: A Paleontological Tribute to G. Arthur Cooper. Smithsonian Contributions to Paleobiology, no. 3. Smithsonian Institution Press. Washington, D.C. p. 129–136, 1 fig., 2 pl.

———. 1975. Trilobites with appendages from the Middle Cambrian, Burgess Shale, British Columbia. Fossils and Strata 4:97–136, fig. 1–31, pl. 1–25.

———. 1977. The Middle Cambrian trilobite *Naraoia,* Burgess Shale, British Columbia. Philosophical Transactions of the Royal Society of London (series B) 280:409–443, fig. 1–99.

———. 1980a. Exoskeleton, moult stage, appendage morphology, and habits of the Middle Cambrian trilobite *Olenoides serratus.* Palaeontology 23:171–204, fig. 1–16, pl. 17–22.

———. 1980b. The significance of the fauna of the Burgess Shale, Middle Cambrian, British Columbia. Proceedings of the Geologists Association, London 91:127–148, 12 fig., 4 pl.

———. 1981. Paedomorphosis and cryptogenesis in trilobites. Geological Magazine 118:591–602, fig. 1, pl. 1–2.

———. 1985. *Tegopelte gigas,* a second soft-bodied trilobite from the Burgess Shale, Middle Cambrian, British Columbia. Journal of Paleontology 59:1251–1274, fig. 1–17.

———. 1988a. Hypostomes and ventral cephalic sutures in Cambrian trilobites. Palaeontology 31:577–609, fig. 1–20, pl. 52–55.

———. 1988b. Hypostomes of post-Cambrian trilobites. New Mexico Bureau of Mines and Mineral Resources, Memoir 44:321–339, 26 fig.

———. 1989. Olenelloid trilobites: Type species, functional morphology and higher classification. Philosophical Transactions of the Royal Society of London (series B) 324:111–147, fig. 1–54.

———. 1990. Articulation and exuviation in Cambrian trilobites. Philosphical Transactions of the Royal Society of London (Series B, Biological Sciences) 329:27–46, 31 fig.

———. 1993a. Anatomy of the ordovician trilobite *Placoparia.* Philosophical Transactions of the Royal Society of London (Series B, Biological Sciences) 339:109–118, 9 fig.

———. 1993b. Morphology, anatomy and habits of the Silurian homalonotid trilobite *Trimerus.* Memoirs of the Association of Australasian Palaeontologists 15:69–83, 10 fig.

———. 1994. Burlingiids, small proparian Cambrian trilobites of enigmatic origin. Palaeontology 37:1–16, 1 fig., pl. 1–4.

———. 1997. Illaenidae (Trilobita): Morphology of thorax, classification, and mode of life. Journal of Paleontology 71:878–896.

Whittington, H. B., & J. E. Almond. 1987. Appendages and habits of the Upper Ordovician trilobite *Triarthrus eatoni.* Philosophical Transactions of the Royal Society of London (series B) 317:1–46, fig. 1–43.

Whittington, H. B., & D. E. G. Briggs. 1985. The

largest Cambrian animal, *Anomalocaris,* Burgess Shale, British Columbia. Philosophical Transactions of the Royal Society of London (series B) 309:569–609, fig. 1–108.

Whittington, H. B., & K. S. W. Campbell. 1967. Silicified Silurian trilobites from Maine. Bulletin of the Museum of Comparative Zoology 135(9):447–483, 10 fig., 19 pl.

Whittington, H. B., & W. R. Evitt. 1954. Silicified Middle Ordovician trilobites. Geological Society of America, Memoir 59:1–137, fig. 1–27, pl. 1–33.

Whittington, H. B., & C. P. Hughes. 1972. Ordovician geography and faunal provinces deduced from trilobite distribution. Philosophical Transactions of the Royal Society of London (series B) 263:235–278, 12 fig.

———. 1973. Ordovician trilobite distribution and geography. *In* N. F. Hughes, ed., Organisms and Continents Through Time. Special Papers in Palaeontology, no. 12:235–240, fig. 1–2.

———. 1974. Geography and faunal provinces in the Tremadoc Epoch. *In* Charles A. Ross, ed., Paleogeographic Provinces and Provinciality. Society of Economic Paleontologists and Mineralogists, Special Publication 21:203–218, 5 fig.

Whitworth, P. H. 1970. Ontogeny of the Upper Cambrian trilobite *Leptoplastus crassicornis* (Westergaard) from Sweden. Palaeontology 13:100–111, fig. 1–2, pl. 22–24.

Wilde, P. 1991. Oceanography in the Ordovician. *In* C. R. Barnes & S. H. Williams, eds., Advances in Ordovician Geology, Geological Survey of Canada, Paper 90-9:283–298, fig. 1–6.

Williams, J. S. 1930. A color pattern on a new Mississippian trilobite. American Journal of Science (series 5) 20:61–64, 1 fig.

Wilmot, N. V. 1990a. Cuticular structure of the agnostine trilobite *Homagnostus obesus.* Lethaia 23:87–92, fig. 1–2.

———. 1990b. Primary and diagenetic microstructures in trilobite exoskeletons. Historical Biology 4:51–65, 6 fig.

———. 1990c. Biomechanics of trilobite exoskeletons. Palaeontology 33:749–768, fig. 1–11.

———. 1991. Sensory field maps of proetide trilobites. Transactions of the Royal Society of Edinburgh, Earth Sciences 82:183–193, fig. 1–9.

Wilmot, N. V., & A. E. Fallick. 1989. Original Mineralogy of trilobite exoskeletons. Palaeontology 32:297–304, fig. 1–2.

Wilson, J. L. 1957. Geography of olenid trilobite distribution and its influence on Cambro-Ordovician correlation. American Journal of Science 255:321–340, fig. 1–3.

Wilson, J. T. 1966. Did the Atlantic close and then reopen? Nature 211:676–681, fig. 1–5.

Winchell, N. H. 1873. Potsdam Sandstone. Minnesota Geological and Natural History Survey, First Annual Report (1872). p. 68–80.

———. 1886. Revision of the stratigraphy of the Cambrian in Minnesota. Minnesota Geological and Natural History Survey, Fourteenth Annual Report (1885). p. 325–337.

Wolfart, Reinhard. 1968. Die trilobiten aus dem Devon Boliviens und ihre Bedeutung fur Stratigraphie und Tiergeographie. *In* Reinhard Wolfart & Adolf Voges, Beitrage zur Kenntnis des Devons von Bolivien. Beihefte zum Geologischen Jahrbuch 74:5–201, 8 fig., 29 pl.

———. 1974. Die fauna (Brachiopoda, Mollusca, Trilobita) des älteren Ober-Kambriums (Ober-Kushanian) von Dorah Shah Dad, Südost-Iran, und Surkh Bum, Zentral-Afghanistan. Geologischen Jahrbuch B8:71–184, fig. 9–16, pl. 10–27, table 2.

Woodward, H. 1884. Note on the remains of trilobites from South Australia. Geological Magazine (new series, decade 3) 1:372–374.

Xiang, Liwen. 1991. On the Middle/Upper Cambrian boundary of China. *In* Zunyi Yang, ed., Stratigraphy and Palaeontology of China 1. Geological Publishing House. Beijing. p. 199–210.

Xiang, Liwen, Shanji Li, Runshan Nan, Zhenming Guo, Jialu Yang, Guoqiang Zhou, Taixiang An, Kexing Yuan, & Yi Qian. 1979. The Cambrian System of China. *In* Chinese Academy of Geological Sciences, Second All-China Stratigraphic Congress, 1979, Stratigraphy of China (Abstract). p. 6–9.

Xiang, Liwen & others. 1981. Stratigraphy of China, 4. The Cambrian System of China. Geological Publishing House. Beijing. 198 p., 12 pl.

In Chinese.

Xiang, Liwen, & Tairong Zhang. 1985. Stratigraphy and trilobite faunas of the Cambrian in the western part of northern Tianshan, Xinjiang. Ministry of Geology and Mineral Resources, Geological Memoirs (series 2) 4:1–243, fig. 1–30, pl. 1–52, table 1–6.

In Chinese with an English summary.

Yang, Guisen. 1981. Notes on a Lower Cambrian Trilobite. Journal of Geological College of Xian, China 1:78–81, pl. 21.

Yang, Jialu. 1978. Middle and Upper Cambrian trilobites of western Hunan and eastern Guizhou. Chinese Academy of Geological Sciences, Professional Papers of Stratigraphy and Palaeontology 4:1–83, pl. 1–13.

In Chinese.

Yin, Gongzheng, & Sanji Li. 1978. Trilobita. *In* Paleontological Atlas of Southwest China. Part 1: Guizhou volume. Geological Publishing House. Beijing. p. 385–594, pl. 143–192.

In Chinese.

Young, G. C. 1995. Cladistics—Application or non-application in paleontology. Memoirs of the Association of Australasian Palaeontologists 18:1–20, 8 fig.

Yuan, Jinliang. 1988. Proetiden aus dem jüngeren Oberdevon von Süd-China. Palaeontographica (Abt. A) 201:1–102, fig. 1–46, pl. 1–15.

Zapasnik, H. T., & P. A. Johnston. 1984. Replication in plastic of three-dimensional fossils preserved in indurated clastic sedimentary rocks. Science 224:1425–1427, fig. 1–2.

Zhang, Jinlin. 1985. New materials of the early

Gushanian trilobites in Zhouzishan district, Nei Monggol Zizhiqu (Autonomous region). Tianjin Institute of Geology and Mineral Resources, Bulletin 13:111–120, pl. 1.

Zhang, Jinlin, & Shaoxin Wang. 1985. Trilobita. *In* Tianjin Institute of Geology & Mineral Resources, ed., Palaeontological Atlas of North China 1: Paleozoic Volume. Geological Publishing House. Beijing. p. 327–488, pl. 103–147.

In Chinese.

———. 1986. Some Late Cambrian Kushanian trilobites from Pinglu, Shanxi. Acta Palaeontologica Sinica 25(6):663–671, pl. 1–3.

Zhang, Wentang [see also Chang, Wentang]. 1953. Some Lower Cambrian trilobites from western Hupei. Acta Palaeontologica Sinica 1:121–149, pl. 1–4.

———, ed. 1964. Atlas of Palaeozoic fossils of northern Guizhou. Nanjing Institute of Geology and Palaeontology, Academia Sinica. p. 1–41, pl. 1–20.

———. 1980. On the Miomera and Polymera (Trilobita). Scientia Sinica 23(2):223–234, pl. 1.

———. 1987. Early Cambrian Chengjiang fauna and its trilobites. Acta Palaeontologica Sinica 26:223–235, pl. 1–2.

———. 1989. World Cambrian biogeography. Developments in Geoscience, Chinese Academy of Sciences, Contribution to 28th International Geological Congress, 1989, Washington, D.C. Science Press. Beijing. p. 209–220, 4 fig.

Zhang, Wentang [see also Chang, Wentang], & Xianguang Hou. 1985. Preliminary notes of the occurrence of the unusual trilobite *Naraoia* in Asia. Acta Palaeontologica Sinica 24:591–595, fig. 1, pl. 1–4.

In Chinese, with English summary.

Zhang, Wentang [see also Chang, Wentang], & P. A. Jell. 1987. Cambrian trilobites of North China: Chinese Cambrian trilobites housed in the Smithsonian Institution. Science Press. Beijing. xvi + 459 p., 23 fig., 125 pl.

Zhang, Wentang [see also Chang, Wentang], Huanling Lin, Hongji Wu, & Jinliang Yuan. 1980. Cambrian stratigraphy and trilobite fauna from the Zhongtiao Mountains, southern Shanxi. Nanjing Institute of Geology and Palaeontology, Memoir 16:39–110, pl. 1–11.

In Chinese, with English summary.

Zhang, Wentang [see also Chang, Wentang], Yanhao Lu, Zaoling Zhu, Yiyuan Qian, Huanling Lin, Zhiyi Zhou, Sengui Zhang, & Jinliang Yuan. 1980. Cambrian trilobite faunas of southwestern China. Palaeontologia Sinica 159 (new series B, no. 16):1–497, 105 fig., 134 pl.

In Chinese, with English summary.

Zhang, Wentang [see also Chang, Wentang], & Jinliang

Yuan. 1981. Trilobites from the Hsuchuang Formation (lower Middle Cambrian) in western marginal parts of the North China platform. Geological Society of America, Special Paper 187:161–175, pl. 1–3.

Zhang, Xiguang. 1987. Moult stages and dimorphism of Early Cambrian bradoriids from Xichuan, Henan, China. Alcheringa 11:1–19.

———. 1989. Ontogeny of an Early Cambrian eodiscoid trilobite from Henan, China. Lethaia 22:13–29, fig. 1–12.

Zhang, Xiguang, & E. N. K. Clarkson. 1990. The eyes of Lower Cambrian eodiscid trilobites. Palaeontology 33:911–932, fig. 1–9, pl. 1–4.

———. 1993. Ontogeny of the eodiscid trilobite *Shizhudiscus longquanensis* from the Lower Cambrian of China. Palaeontology 36:785–806, 8 fig., pl. 1–2.

Zhao, Yuanlong, Jianquan Mao, Youzhuang Huang, & Jianwei Liu. 1984. Trilobites of the Lower Cambrian Huanglianba Formation from Zhongxin of Kaiyang, Guizhou. Acta Palaeontologica Sinica 23(6):755–763, pl. 1–2.

In Chinese, with English abstract.

Zhou, Zhiqiang, & K. S. W. Campbell. 1990. Devonian phacopacean trilobites from the Zhusilenghaierhan region, Ejin Qi, western Inner Mongolia, China. Palaeontographica (Abt. A) 214:57–77, fig. 1–8, pl. 1–6.

Zhou, Zhiqiang, Jinseng Li, & Xinguo Qu. 1982. Trilobita. *In* Paleontological Atlas of northwest China, Shaanxi-Gansu-Ningxia Volume. Part 1: Precambrian and Early Paleozoic. Geological Publishing House. Beijing. p. 215–294, pl. 57–72.

In Chinese.

Zhou, Zhiyi. 1987. Notes on the Chinese Ordovician agnostids. Acta Palaeontologica Sinica 26(6):639–661.

In Chinese, with English summary.

Zhou, Zhiyi, & W. T. Dean. 1989. Trilobite evidence for Gondwanaland in east Asia during the Ordovician. Journal of Southeast Asian Earth Sciences 3:131–140.

Zhu, Zhaoling [see also Chu, Chaoling], & Huanling Lin. 1983. Some early Cambrian trilobites from the Xidashan Formation of Kuruktag, Xinjiang. Acta Palaeontologica Sinica 22(1):21–30, pl. 1–2.

In Chinese, with English summary.

Zhuravleva, I. T., & others. 1979. Biostratigrafyia i paleontologiya nizhnego Kembriya Sibiri [Lower Cambrian biostratigraphy and palaeontology of Siberia]. Trudy Instituta Geologii i Geofizikii Akademiia Nauk SSSR, Sibirskoe Otdelenie 406:1–160, pl. 1–16.

Ziegler, A. M., C. R. Scotese, W. S. McKerrow, M. E. Johnson, & R. K. Bambach. 1979. Paleozoic palaeogeography. Annual Review of Earth and Planetary Sciences 7:473–502, 8 fig.

INDEX