PART O
ARTHROPODA 1

ARTHROPODA—GENERAL FEATURES
PROTARTHROPODA
EUARTHROPODA—GENERAL FEATURES
TRILOBITOMORPHA

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INTRODUCTION
By Raymond C. Moore

This volume of the *Treatise,* primarily concerned with the trilobites, is the product of collaboration of 18 specialists who represent 7 different nations, as follows: 6 from the United States of America, 5 from West Germany, 2 each from England and Norway, and one each from Argentina, Denmark, and Sweden. Harmonious joint effort of such an international group is unusual, especially when account is taken of voluminous correspondence exchanged, not only by individual contributors and the Editor but by authors writing to each other. In this way many problems have been settled more or less definitely and satisfactorily, but it is natural that divergent viewpoints on some items of morphological terminology, interpretation of evolutionary trends, and especially taxonomic arrangement of trilobite genera should persist. Authors have been allowed greatest possible freedom to make determinations of the diagnostic characters of genera allocated to them and to define familial groupings.

A great deal of work in organizing the assignments to authors and in dealing with problems of several kinds, especially during initial phases of effort, was done by C. J. STUBBLEFIELD, who at the beginning of the program and for some time thereafter was Chief Palaeontologist of the Geological Survey of Great Britain; his official duties then prevented him from accepting responsibility for an important share of writing on such themes as the nature and significance of morphological characters of trilobites or classification of these fossils, but he aided in preparing a first draft of definitions of morphological terms. Later, when Dr. STUBBLEFIELD was made Assistant Director of the Survey, he continued to help by giving counsel orally and through correspondence and by contributing editorial criticisms of typescripts referred to him. These services entitle him to special recognition and the expression of sincere thanks that I record here on behalf of each individual author and of users of the volume. Although Dr. STUBBLEFIELD's name as a contributing author appears only in connection with the "Glossary of Morphological Terms" applicable to trilobites, actually he has shared in one way or another in shaping the content of various other sections.

In my capacity as general director of the organization of *Treatise* volumes, it is appropriate to acknowledge the co-operative attitude, patience, and especially the very great amount of painstaking labor that the numerous authors have provided. Without these things and teamwork of unusually high order, it would be impossible to accomplish our goal, particularly in view of the fact that no monetary compensation goes to anyone. Acknowledgment consists simply in publication of the names of authors. For some units, such as general descriptions and discussions prepared by H. J. HARRINGTON, LEIF STØRMER, and H. B. WHITTINGTON, no difficulty is encountered in specifying authorship, but the situation is otherwise in recording the authors of systematic descriptions. Because the allocations of taxonomic units to individual authors deviate widely from arrangement of these units in zoological order, the segregation of descriptions and illustrations by authorship would be a most effective way to destroy utility, and the adoption of a zoological order requires a highly interspersed listing of authorship of taxonomic segments having diverse rank. Complications have been introduced by revisions of classification during the progress of work, transferring genera from one family assignment to another and revising familial classification; commonly, such changes have served to blur the distinctness of authorship boundaries. Accordingly, as the most practicable means of specifying the authors of intermingled taxonomic descriptions, record is given in connection with the tabular outline of classificatory divisions of the trilobites (p. O160). Reference should be made to this list in order to determine the author or authors of any given taxonomic description.

Some contributors to the volume on Trilobitomorpha were active in undertaking work on their assignments virtually from the time they were accepted in 1949 and 1950. In this group, along with C. J. STUBBLEFIELD, belong CHRISTINA LOCHMAN-BALK, CHRISTIAN POULSEN, FRANCO RASETTI, J. M. WELLER, and H. B. WHITTINGTON. When their work on systematic descriptions was finished, most of these paleontologists accepted an additional load and thus have aided importantly in completing the whole task. Meanwhile, death intervened to prevent ELSA WARBURG from doing much *Treatise* work and later (1956) both EMMA RICHTER and RUDOLF RICHTER died before more than a fraction of their important assignment on Phacopacea had been sent to the Editor. These were unhappy losses. Special acknowledgment and thanks are due to persons who have filled in the ranks, at relatively late dates accepting responsibility for organizing descriptions and illustrations of taxa in unfinished groups; these contributors are GUNNAR HENNINGSMOEN, VALDAR JAANUSSON, HERTA SCHMIDT, WOLFGANG STRUVE, KLAUS SDZUY, and RONALD TRIPP. In much the same way but for other reasons, important segments of the trilobitomorph volume still were lacking in 1956, which made the date of readiness for publication very doubtful; these segments included general description of the nature of Arthropoda, treatment of the Trilobitoidea, and discussion of the mor-

phology and classification of the Trilobita. LEIF STØRMER accepted the assignment to contribute materials on the first two mentioned segments, and H. J. HARRINGTON expressed willingness to grapple with the appreciably larger task of preparing introductory sections on the trilobites. It is almost superfluous for me to express thanks for this help. Also, I should not omit statement of appreciation to B. F. HOWELL for the efforts given by him to completion of a rather formidable assignment of systematic descriptions in time to permit organization of the typescript when other sections were ready.

It is appropriate here to record the valuable support furnished by Professor PER THORSLUND of the Paleontological Institution of Uppsala in authorizing work done by VALDAR JAANUSSON for this volume and in furnishing highly competent services of an illustrator. Likewise, the Carlsberg Foundation financed illustrations needed by CHR. POULSEN. Thanks for this aid are expressed.

Special acknowledgments are made to CAROLE F. BAILEY, Editorial Assistant, for careful attention to innumerable tasks related to preparation of this volume, especially in dealing with complexities of rearrangements among various authors of work on systematic descriptions and in supervising parts of the organization of figures. Finally, the Editor has been aided greatly by GUNNAR HENNINGSMOEN in completion of the text on systematic descriptions and in dealing with some unsettled questions of trilobite classification. This was made possible by his visit at the University of Kansas in January and February, 1958.

ARTHROPODA—GENERAL FEATURES

By LEIF STØRMER

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The joint-legged invertebrates grouped together in the phylum Arthropoda (Gr. *arthros,* joint; *podos,* foot) are an extremely numerous and varied assemblage that is represented by fossils of extreme antiquity. They include several kinds of complexly organized trilobites found in lowermost fossil-bearing Paleozoic strata, and thus the origin of arthropods surely belongs to some part of Precambrian time. The nature of earliest ancestors classifiable as belonging to the Arthropoda, probably characterized by close resemblance to annelids, is conjectural. Despite reasoning that supports conclusions as to great evolutionary development of arthropod stocks before the Paleozoic Era, none of the supposed Precambrian arthropods, such as *Beltina* (from Belt strata of Montana), *Xenusion* (?onychophoran from ?Precambrian quartzite erratic in Sweden), and *Protadelaidea* (from Precambrian rocks of Australia), are accepted as fossil representatives of the phylum demonstrating Precambrian age. Classification as arthropods is doubtful or age of the fossil-bearing rock is doubtful.

Phylum ARTHROPODA Siebold & Stannius, 1845

Aquatic, terrestrial, and aerial invertebrates with heteronomous segmentation and jointed legs; body covered with chitinous cuticula, each segment movably connected to adjoining ones by an articulating membrane. Segments ordinarily provided with one pair of jointed appendages. Growth takes place through molts. Nervous system with well-developed brain and ventral cord with ganglia in each segment; ocelli or compound eyes. Respiration by gills, tracheae, or body surface. Circulatory system lacunar. Coelome reduced in adults. Eggs with much yolk, cleavage superficial. *L.Cam.-Rec.*

Because the arthropod body is inclosed in a more or less solid exoskeleton, a great number of fossil forms have been found and described from all geological systems younger than Precambrian. Fossil arthropod remains—trilobites from early Paleozoic deposits, and eurypterids, crustaceans, and insects from later rocks—early attracted the attention of students in natural science.

The arthropods play a very dominant role in the Recent faunas. The number of living arthropods constitutes 75 to 80 per cent of the one million or more Recent animals described, among which the 700,000 species of insects form the greatly predominant part. Members of the arthropod phylum occupy the sea, land, and air, and occur from tropic to arctic regions. They have disclosed a most extraordinary ability to accommodate themselves to very different modes of life, for arthropods live both in cold and hot, light and dark environments. Very pronounced morphological changes are noticed in connection with transition into a parasitic mode of life.

In Recent times certain groups occur in a great number of species, as for example some 350,000 species of the order Coleoptera among the insects, whereas others, such as the subclass Xiphosura, include only a few species. The groups with many species seem to be in a state of rapid evolution or radiation, and the same was true in earlier times. The rapid increase of trilobite species in the Middle and Late Cambrian and the sudden development of pterygote insects in the Late Carboniferous may be mentioned.

In segmentation of the body the arthropods demonstrate their relation to the annelids, and on this basis the two phyla were placed by Cuvier in a common major group called Articulata. The main difference between the Annelida and Arthropoda is found in the development of the appendages. The annelid parapodia, which consist of unjointed lateral outgrowths of the body wall are fundamentally different from the jointed arthropod appendages, which are structures only possible in a body with a solid exoskeleton.

The typical Arthropoda (Euarthropoda) comprise the following groups: Trilobitomorpha (Trilobita, Trilobitoidea), Chelicerata (Merostomata, Arachnida), Pycnogonida, Crustacea, Myriapoda, and Hexapoda (including Insecta). The Onychophora and the aberrant Tardigrada and Pentastomida have several characteristics common to both the Annelida and Arthropoda. The onychophoran legs have claws but no distinct articulation. The mentioned arthropod-like groups are generally regarded as arthropods different from the typical ones and in the *Treatise* are designated as Protarthropoda (Lankester, 1904); they have been classed together as Pararthropoda by Vandel (1949).

MORPHOLOGY

BODY WALL

The arthropod body is incased in a more or less solid **exoskeleton,** which serves the purposes of forming an armor against enemies, a protection against desiccation, and a framework for support of the softer parts and for attachment of the muscles (Fig. 1). The body wall may be sclerotized so as to form a rigid exoskeleton, with softer membranes occurring between the sclerotized parts (called sclerites), or remain flexible.

The outer integument (cuticula) is secreted from the cellular epidermis (Fig. 2). In the stratified cuticula an endo- and exocuticula may be distinguished, the latter more dense and pigmented. The cuticula chiefly consists of chitin, a very characteristic substance that occurs in various invertebrate groups. It is a polyacetyl-glucosamin re-

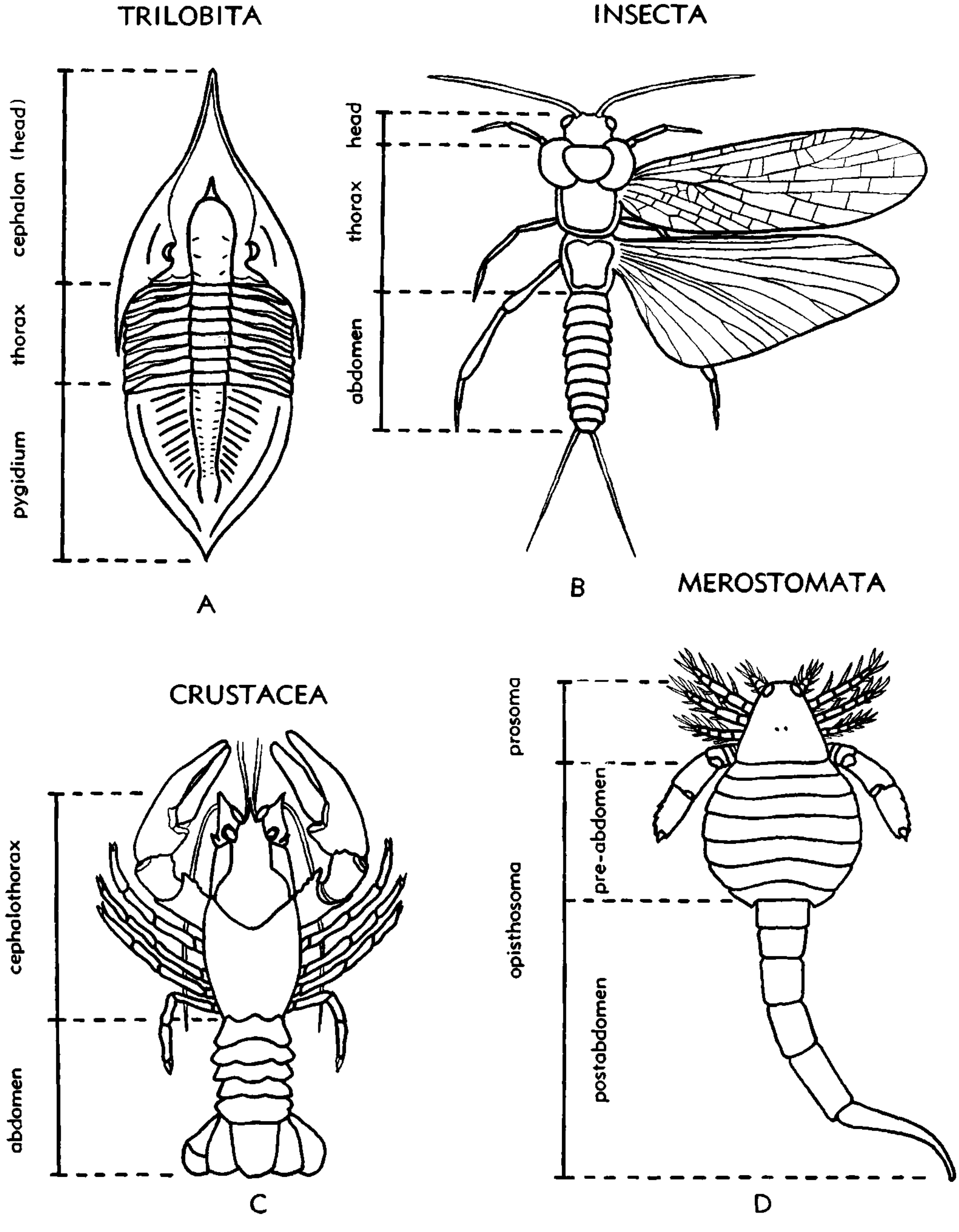

Fig. 1. Division of the arthropod body in representative types.

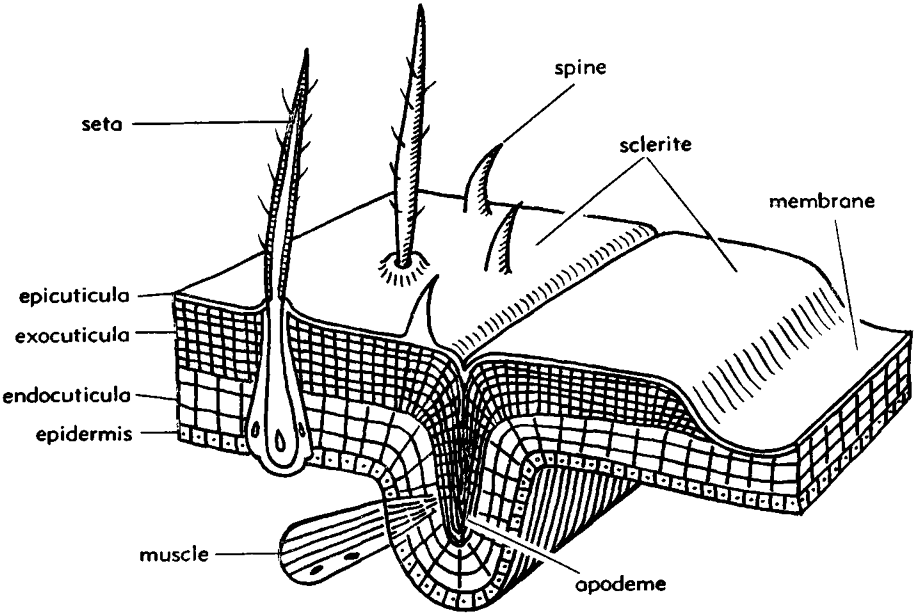

FIG. 2. Morphological features of the arthropod integument (diagrammatic).

lated in molecule structure to cellulose. The long molecular chains form the fibrillous micellae. Chitin is very resistant to chemical agencies, being insoluble in water, most acids, alcohol, and alkalies. The flexible chitin may be strengthened (sclerotized) by an impregnation of calcium carbonate and phosphate, but in most arthropods only the outer part of the cuticula (exocuticula) is sclerotized. The hard sclerotized parts contain much less chitin than the cuticula of soft membranes. The body wall is covered by a thin epicuticula, which is not chitinous but contains a waxy substance that prevents water and acids from penetrating the cuticula.

The cuticula may be provided with spines or movable setae (hairs), with tubulae leading from the cells in the epidermis below. Invaginations of the sclerotized cuticula, called apodemes, serve as attachments for muscles (Figs. 2, 3).

Sclerotization of the body wall creates problems with regard to the growth and

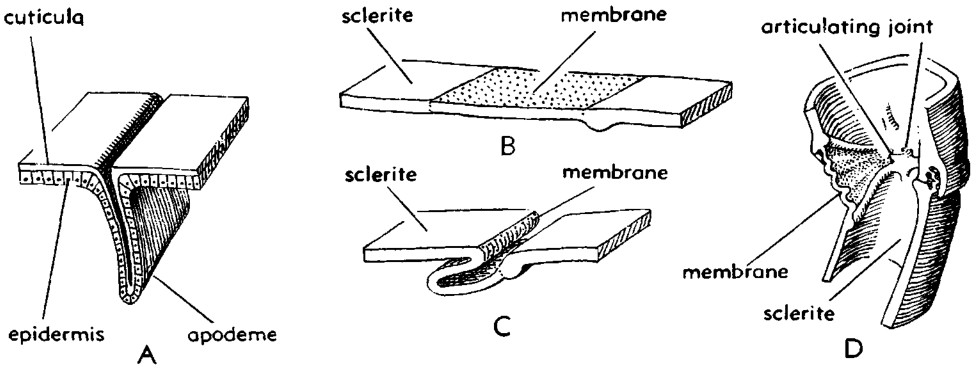

FIG. 3. Morphological features of the arthropod exoskeleton.——*A*. Formation of apodeme.——*B*. Flexible membrane between sclerites, membrane not infolded.——*C*. Same as *B* but showing infolded membrane. *D*. Articulation between segments of appendage. *(All after Snodgrass and Weber.)*

mobility of arthropods. Growth leads to increase of body volume that can be accommodated only by molting (ecdysis) of the hardened exoskeleton. Fluids dissolve the endocuticula so that the exocuticula peels off and splits along ecdysal nonsclerotized sutures. The ecdysal sutures have considerable taxonomic importance in certain groups. A solid exoskeleton impedes mobility of the body and appendages. Accordingly, the armor has to be divided into a number of sclerites separated by flexible membranes that permit bending or telescoping of the various parts (Figs. 3, 4). An articulation between adjoining sclerites (ball-and-socket joints) also may be provided.

BODY SEGMENTS

The body of annelids and arthropods is divided into a number of segments (**somites** or **metameres**) primarily alike. In the generalized annelid the cylindrical body has transverse grooves marking the border of segments (Fig. 4*a*). Movements of the body are controlled by transverse and longitudinal muscles. Among arthropods the cylindrical body segments may be more or less sclerotized. A dorsal sclerite is called a **tergite,** and the ventral a **sternite.** The intermediate lateral parts, mostly membranous, are termed **pleurites.** The articulation between succeeding segments may not necessarily follow the primarily segmental borders, for each tergite commonly has a part of the frontal one incorporated in it (Fig. 4*b*).

APPENDAGES

In its typical development each body segment is provided with a pair of locomotor appendages. As expressed in the name of the group, jointed appendages are characteristic of the Arthropoda, each segment ordinarily bearing one pair of appendages. Throughout the phylum, as well as within

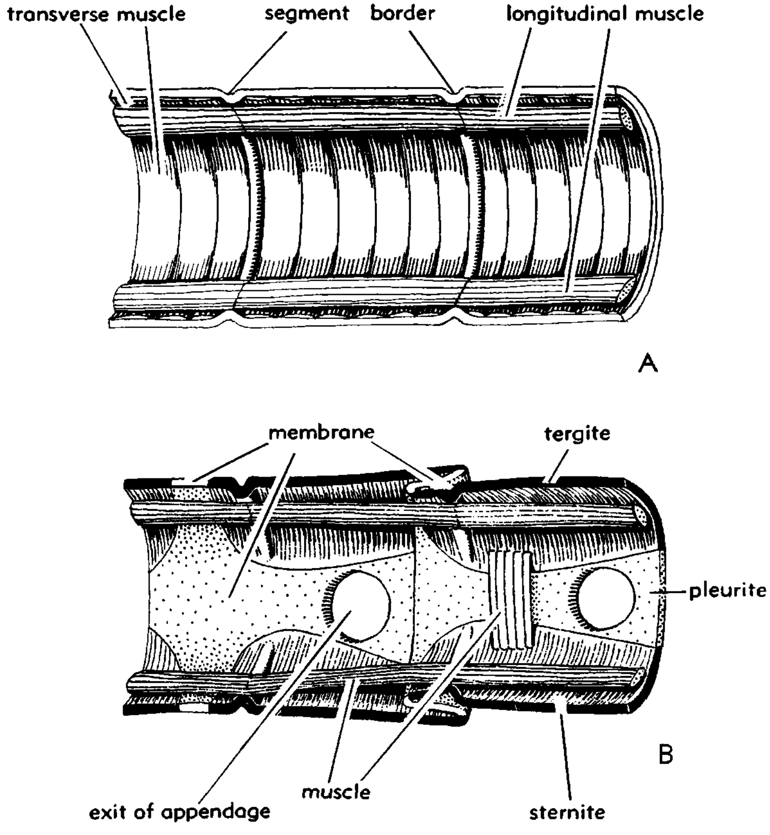

FIG. 4. Internal views of body segments of an annelid *(A)* and an arthropod *(B)*, diagrammatic. *(Mod. from Weber.)*

a single individual, the appendages show a diversity in form that is unique in the animal kingdom. The limbs are adapted to the most different functions, some forming highly specialized tools needing a highly developed nervous system. The appendages are situated in the lateral (or ventrolateral) pleural part of the segment, between the tergite and sternite (Fig. 4*b*). The limbs form hollow outgrowths of the body wall, connected with the body by various muscles, chiefly promotor and remotor types. Each limb has several sclerotized cylindrical joints mutually connected by membranes or articulations (Fig. 3*d*), these joints being regarded as true joints only when they have separate muscles inserted at their bases. A secondary division into numerous separate rings does not mean appearance of new joints.

Much work and discussion have been devoted to the problem of homology of the arthropod appendages. Effort to homologize different joints of the limbs must take into account possible tendency of a limb to develop a more or less common type. Functionally, the simple cylindrical, locomotory limb is divided into coxal, femoral, tibial, and tarsal portions, according to position of the joints and their axis of articulation. The limbs of trilobites, eurypterids, and primitive arachnids (Fig. 5*c*) possess 8 or 9 joints: precoxa (doubtfully distinguished as a true separate joint), coxa, 1st trochanter, 2nd trochanter (prefemur), femur, patella, tibia, tarsus, and pretarsus. The patella (knee) occurs in Chelicerata, Pycnogonida, and probably Trilobita; since the musculature of trilobite legs is unknown, the joint here considered may represent the proximal half of a divided tibia, but this is rather improbable. In Crustacea, joints of the limb mostly have other names: precoxa (presence uncertain), coxopod (or coxopodite), basipod, ischiopod, meropod, cercopod, propod, and dactylopod. No joint corresponding to the patella is known in the Crustacea, Myriapoda, and Insecta.

The arthropod limb may have lateral lobes, either fixed or movable. The outer (lateral) ones are called **exites** and the inner (median) ones are **endites** (Fig. 5*c,g,i*). Exites of the precoxa, coxopod (coxa), and basis (1st trochanter) are called **pre-epipodite, epipodite,** and **exopodite.** The pre-epipodites and epipodites are generally developed as a respiratory organ in the Crustacea (Fig. 5*d,g,i*). The exopodite forming the lateral branch of the biramous crustacean limb has mostly a natatory function. In Crustacea the basal uniramous part of the biramous appendage, the so-called **sympod,** may have 3 joints (precoxa, coxopod, and basipod or basis), 2 joints (coxopod and basipod), or a single joint (protopod consisting of an undivided coxopod and basipod). Although some authors (HANSEN, LANG) assume that the 3-jointed sympod is most primitive, others (CALMAN, HEEGAARD, VANDEL) regard the single-jointed (protopod) limb as the ancestral type. A correct assumption is important for interpretation of the trilobite limb, which has a characteristic structure that is found in various trilobites of different age and likewise in crustacean- and merostome-like arthropods of the Middle Cambrian. In biramous trilobite appendages (Fig. 5*c*) the lateral gill branch is attached to the very base of the limb, although uncertainty exists as to whether the attachment is to a short precoxa or the basal part of a large basal joint. According to the different interpretations mentioned, the lateral branch of the trilobite limb may be explained as a pre-epipodite or epipodite (SNODGRASS, STØRMER) or an exopodite (HEEGAARD, VANDEL). If the first view is correct, the trilobitan and crustacean legs are fundamentally different, leaving little support for assumptions of a close relationship between these major groups, whereas if the second interpretation is true, the Trilobita and Crustacea are shown by this character to be closely related.

RELATIONS OF BODY SEGMENTS AND APPENDAGES

The number of arthropod somites varies considerably in primitive groups such as the trilobites but becomes fixed in advanced forms. During ontogeny the 1st segmentation, producing a small number of somites, seems to take place approximately simultaneously. To these segments (classed as primary by IVANOV) new secondary ones are added by teloblastic growth in a subterminal generative zone. A definite number (4) of postoral primary somites is indicated in the Trilobita and Xiphosura, but in the Crustacea the number (?2) is uncertain; in the Myriapoda and Insecta it is unknown. Some Lower Cambrian trilobites exhibit characters suggesting the presence of more than 4 postoral segments in the head of their ancestors.

Unlike the body of annelids, which has a series of more or less uniform segments behind the head, that of arthropods reveals more complicated and specialized structures. The body generally is divided into groups of segments **(tagmata)**, in which each segment and its appendages are somewhat closely alike. A tagma may comprise a number of fused segments forming a continuous shield, such as the **cephalon** (head) and **pygidium** of a trilobite (Fig. 1), or it may consist of several mutually similar movable segments, such as the **thorax** of a trilobite or **abdomen** of an insect. In the arthropod head fusion of segments may be so complete that the borders of original segments have become quite obsolete. The naming of tagmata differs among the major groups of Arthropoda (Fig. 1) to such extent that the same names do not necessarily embrace corresponding segments (for example, cephalothorax in the Crustacea).

The homology of segments in the arthropod head presents a difficult problem, for interpretation of the segments must be based primarily on studies of early embryonic growth stages, and especially on the nerves leading from cephalic appendages to the brain or ventral nerve cord. The annelids have a mass of nerve tissue or brain (archicerebrum) in front and above the stomodaeum (fore-gut). Behind and below it comes a double ventral nerve cord with segmented ganglia and paired connectives.

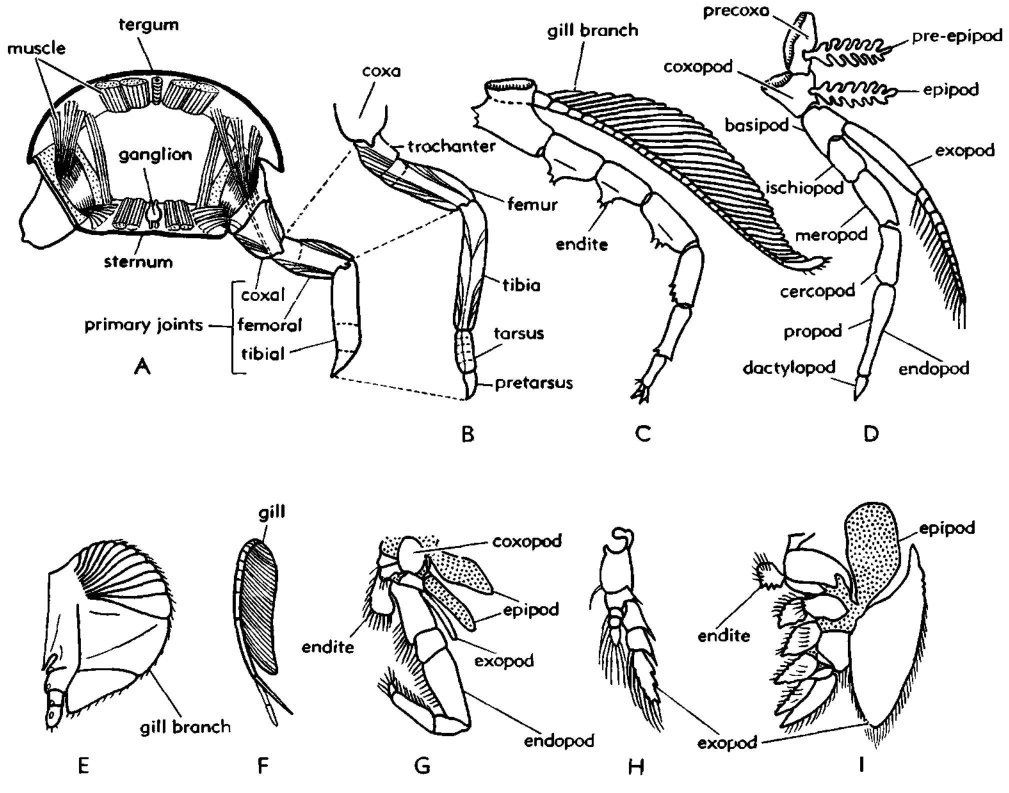

Fig. 5. Appendages of arthropods.——*A*. Transverse section of arthropod body segment and attached limb with primary joints (diagrammatic, hypothetical).——*B*. Limb of type belonging to insects and arachnids. ——*C*. Biramous trilobite limb showing gill branch and walking leg.——*D*. Biramous limb of crustacean (Decapoda), diagrammatic.——*E,F*. Abdominal appendages of xiphosurans.——*G*. Crustacean maxilliped (Anaspidacea).——*H*. Crustacean thoracic appendage (Copepoda).——*I*. Crustacean thoracic leg (Branchiopoda). *(A-B, after Weber; G-I, after Hansen.)*

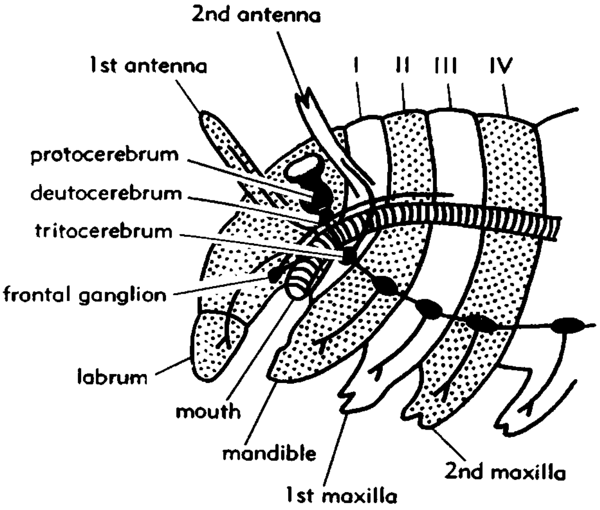

FIG. 6. Nervous system and segmentation of arthropod head (diagrammatic), showing undivided preoral portion (acron+antennal and preantennal segments). *(After Weber.)*

In the Arthropoda, the brain is normally divided into a protocerebrum, deutocerebrum, and tritocerebrum (Fig. 6).

The protocerebrum contains the optic centers and the centers of nerves leading to possible **preantennae,** which are appendages identified in the embryos of certain terrestrial forms (Chilopoda, Insecta). Vestigial coelomic sacs also suggest the presence of frontal segments.

The deutocerebrum contains the ganglia of the **1st antennae (antennules).** These antennae are unique among arthropod appendages in usually having numerous articulations (although few are true joints) and in being uniramous (although branched in Pauropoda). The antennae of primitive trilobites differ markedly from the other appendages (except cerci in *Olenoides*). The deutocerebrum is strongly reduced in the Chelicerata, which is connected with complete reduction of the 1st antennae in members of this group. Traces of antenna-glomeruli, however, have been found, supporting the assumption of a secondary reduction of the appendages.

The **2nd antennae** of crustaceans, belonging to the tritocerebral segment, have the structure of biramous "normal" appendages. The tritocerebral lobes are united by a commissure running below the esophagus (stomodaeum), thus indicating that the corresponding ganglia actually belong to the ventral nerve cord, being secondarily incorporated in the brain complex. The tritocerebral somite has accordingly been called the 1st postoral segment (I).

The preoral portion of the brain was regarded as a primarily unsegmented acron by SNODGRASS and others (Fig. 6), the unique structure of the 1st antennae possibly serving to support this view. The occurrence of coelomic sacs and vestiges of preantennae in certain forms, however, rather favors the assumption that at least 2 more segments (deuto- and protocerebral) are to be incorporated. This means also that these 2 once were primarily postoral (Fig. 7). In the concept of TIEGS & WEBER the acron, corresponding to the prostomium of annelids, is restricted to the portion in front of these segments (Fig. 7). The possible occurrence of even more incorporated segments and a corresponding restriction of the acron, is suggested in the structure of certain lower Lower Cambrian trilobites (HUPÉ) (Fig. 7*d*). A secondary backward movement of the mouth (or corresponding forward movement of postoral segments) is characteristic of the Arthropoda. In the Chelicerata the chelicerae secondarily attain a pronounced preoral position. The probable homology of the segments and appendages in the anterior part of the arthropod body is indicated in the following tabulation.

Suggested Homology of Segments and Appendages in Anterior Part of Arthropod Body

Preoral region and postoral segments (I-VI)	Appendages			
	TRILOBITA	CHELICERATA	CRUSTACEA	MYRIAPODA INSECTA
acron	....	....	....	....
preantennal	....	....	....	....
antennal	antennae	....	1st antennae	antennae
I	legs	chelicerae	2nd antennae	....
II	legs	pedipalpi	mandibles	mandibles
III	legs	legs	1st maxillae	maxillae
IV	legs	legs	2nd maxillae	labia
V	....	legs	maxillipeds	....
VI	....	legs	....	....

A distinct head, evidently comprising 4 (or primarily 6) postoral segments, is present in the Trilobita, Myriapoda, and Insecta (Fig. 1) (although Pauropoda have only 3 segments). In the Chelicerata the prosoma contains 6 postoral segments, a reduced 7th being incorporated in the Xiphosura. Among the Crustacea cephalization is less distinct. The "head" may include 1, 3, or 4 postoral segments.

As mentioned above, the deutocerebral appendages are developed as antennae (1st antennae or antennules). The tritocerebral appendages are lacking in Myriapoda and Insecta, but they form the biramous 2nd antennae in Crustacea, the characteristic chelicerae in the Chelicerata, and the undifferentiated limbs of Trilobita. The 2nd postoral appendages form the mandibles or jaws of Crustacea, Myriapoda, and Insecta, the pedi-

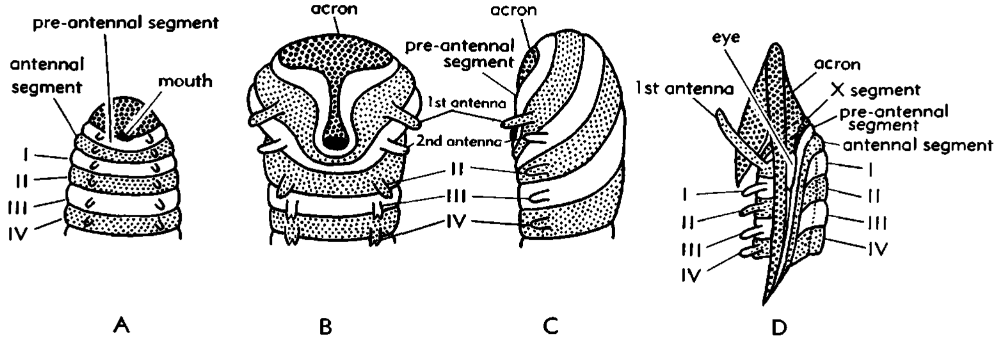

FIG. 7. Cephalic segmentation in an annelid-like arthropod prototype *(A)*, generalized typical arthropod *(B,C)*, and a trilobite *(D)*. Ventral views in *A,B;* lateral views in *C,D*. The backward migration of the mouth is indicated in *B,C*. Traces of an "x segment" in trilobites *(D)* suggest that at least one segment is incorporated in the acron. *(Mod. from Weber and Hupé.)*

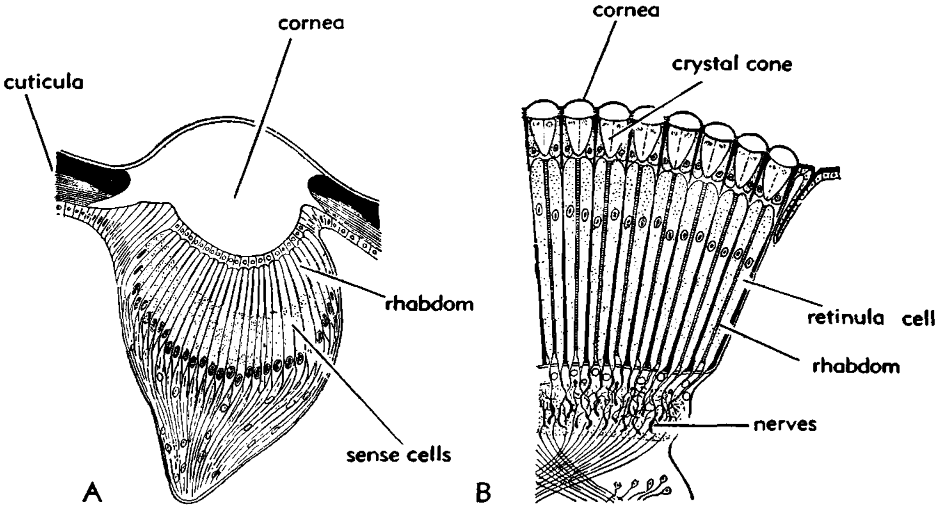

FIG. 8. Simple eye and part of compound eye of arthropods in section.——*A*. Median ocellus of an insect (*Formica*).——*B*. Diagrammatic section of compound eye normal to surface. (*Both after Snodgrass.*)

palpi of Arachnida, and the simple 2nd legs of Trilobita. The mandibles are limbs in which only the coxa has escaped reduction. Also the next-following appendages (maxillae borne by segments III and IV) take part in the masticatory functions. The 3 segments numbered II, III, and IV form a gnathocephalon. Jaws are lacking in trilobites and arachnids, but in the Merostomata the coxae of the well-developed prosomal legs serve to a certain extent as masticatory organs.

SENSE ORGANS

In connection with the nervous system mentioned above, the arthropods possess well-developed sense organs. Most characteristic are the sensory hairs (or setae) and eyes. Each of the movable setae (Fig. 2) has the extension of a nerve cell leading through a pore in the shell to the base of the body wall below. Fixed spines are only outgrowths of the outer cuticula.

The **eyes**, which are organs receptive to light, comprise the dorsal ocelli, lateral ocelli (or stemmata), and compound eyes. They are all connected with the optic centers in the frontal (protocerebral) part of the brain. Two main types of eyes are distinguished: simple eyes (or ocelli) and compound eyes (Fig. 8). Both have a similar ectodermal origin and are not fundamentally different. The simple eye consists of a transparent cornea, that commonly is developed as a lens; a vitreous crystal body beneath the cornea, which takes over the function of the cornea when it is not lenticular; and a retina composed of elongate optic nerve cells. Adjacent retina cells unite so as to form a rodlike structure called rhabdom. Groups of simple eyes may replace the lateral compound eyes.

In typical development the compound eyes are composed of a large number of individual elements, termed **ommatidia**, each having a group of elongate retinal cells enclosing a long rhabdom with a crystal body and corneal lens above (Fig. 8*b*). Compound eyes occur in the earliest trilobites and are characteristic also of crustaceans, insects, and possibly extinct types of myriapods. In merostomes (xiphosurids and probably eurypterids) the primitive compound eyes have a common cornea with groups of rhabdom-forming sense cells below. The compound eyes, so very similar in crustaceans and insects, have evidently developed independently in several major arthropod groups.

FEEDING AND DIGESTIVE ORGANS

The crustaceans, insects, and myriapods, together comprising the so-called Mandibulata, have well-developed jaws that permit chewing of prey before digestion. The prosomal coxae of the merostomes partly serve as jaws, but other chelicerates and trilobites have no masticatory organs. Arachnids suck out the liquids of the prey. The intestine has an ectodermal frontal part, the stomodaeum, which may be associated with a gizzard (in crustaceans and merostomes). An ectodermal hind part of the intestine is called the proctodaeum. The middle, mesodermal one, the mesentron, has numerous diverticular sacs in the Chelicerata, certain Crustacea, and evidently in the Trilobita. Excretion also takes place through special glands (coxal glands opening at the base of the 2nd antennae in crustaceans).

RESPIRATORY AND CIRCULATORY SYSTEMS

Very small arthropods, including both aquatic (Copepoda) and terrestrial (Pauropoda) types, have cutaneous respiration. The gills or branchiae are the characteristic respiratory organs in aquatic forms. These generally form lateral lobes extending from the basal portion of the appendages (Figs. 5*c,d,f*). Terrestrial arthropods (Myriapoda, Insecta, Arachnida, Onychophora, and certain Crustacea) have **tracheae,** consisting of invaginated parts of the integument that form either branched tubuli or so-called **book lungs** (Fig. 9).

In contrast to conditions in annelids, the circulatory system is incomplete, the blood running from the dorsal heart into lacunae or sinuses.

ONTOGENY

The arthropod egg, which is rich in yolk, exhibits a discoidal cleavage. The 1st larva may be more or less developed when it is hatched. In several crustacean groups a small larva, called the **nauplius,** is very characteristic. It has a convex elliptical body with only 3 pairs of appendages (1st and 2nd antennae and maxillae). The corresponding 3 body segments, 2 of which are postoral, have been regarded as primary somites, suggesting development from an annelid with the same number of primary segments (IVANOV, 1933). This interpretation, however, is uncertain (VANDEL, 1949). In trilobites the small larva, called **protaspis** (pl., protaspides), has a circular outline with a segmented convex dorsal surface. The early trilobite larva seems to have had 4 postoral segments, a number also indicated in the embryo of the Xiphosura.

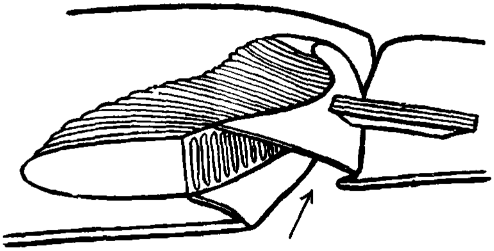

FIG. 9. Lung books of an arachnid (Phrynichida). (*After Kästner.*)

GEOLOGICAL OCCURRENCE

No arthropod remains are known certainly from Precambrian rocks. The so-called *Protadelaidea* of Australia (DAVID & TILLYARD, 1936) and *Beltina* (WALCOTT, 1911) are evidently inorganic formations (HUPÉ, 1952). The onychophoran-like fossil *Xenusion* (POMPECKJ, 1927) has been referred to the Precambrian but it may be younger.

The trilobites appeared near the beginning of Cambrian time. Although several groups of trilobites are represented in the Lower Cambrian, one need not expect a very long existence of typical trilobites (with solid exoskeleton) before the dawn of the Paleozoic. The trilobites had a very strong development and radiation through the Middle and Late Cambrian. Subsequently, they declined and became extinct in the Permian (Fig. 10).

The Crustacea probably existed in the Early Cambrian (identification being uncertain because appendages are unknown).

Primitive Merostomata (Aglaspida) also occur in the Lower Cambrian. The Eurypterida became extinct in the Permian but the Xiphosura still exist, the Recent representatives forming excellent examples of very long-enduring forms.

The Arachnida were well established in the Silurian and the first Myriapoda appear near the beginning of the Devonian.

The first insects (Apterygota) occur in the Middle Devonian. A sudden strong development of the Pterygota took place from Early to Late Carboniferous.

The Pycnogonida are represented in the Lower Devonian.

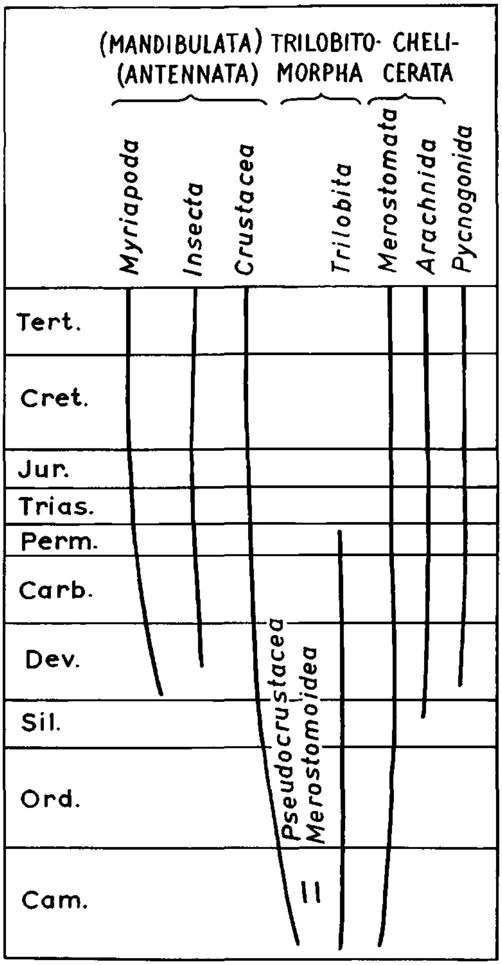

FIG. 10. Geological distribution of major arthropod groups. (For "Pseudocrustacea," read "Pseudonotostraca.")

PHYLOGENY

Among fossil arthropods, conclusions as to affinities have to be based on structure of the solid parts, the exoskeleton. Since the skeleton to a large extent serves functional purposes, phylogenetic conclusions may be misled by homeomorphy.

Primitive arthropod features are expressed by uniformity of the appendages of trilobites (only the antennae and in some forms a pair of cerci, differing from the common type). Another primitive feature is expressed in variation of the number of body segments. On the other hand, the development of compound eyes, known even in Lower Cambrian forms, indicates advanced evolution at least as concerns the eyes.

The Xiphosura and Eurypterida of the Merostomata have many common characteristics, and the presence of an apparently more or less ancestral form *(Paleomerus)* in the Lower Cambrian suggests that division of the Merostomata into 2 separate branches took place at about that time.

The Arachnida probably branched off earlier. The Xiphosura, both earliest and Recent representatives, have features suggesting a relationship with trilobites.

The Pycnogonida commonly have been placed among the Chelicerata because of their chelicera-like appendages, but the presence of many particular and unique structures supported classification in a separate subphylum (HEDGPETH).

The Crustacea form a heterogeneous but still fairly well-defined group. They have been regarded as relatives (close or remote) of the Trilobita, because of the presence in both of antennae and biramous legs, although homology of the legs may be doubted.

With few exceptions, the Myriapoda and Insecta are terrestrial forms, their morphology showing many adaptations to this mode of life. The 2 groups are definitely related. The insects form a well-established, compact group (comparable to the trilobites), whereas the myriapods (Pauropoda, Diplopoda, Chilopoda, Symphyla) demonstrate a wide field of variation. The origin of the Myriapoda and Insecta is still unknown, their postulated derivation from trilobite- or crustacean-like forms being supported by little evidence. Affinities with the Onychophora have recently been pointed out by TIEGS (1947). Generally, however, the Onychophora have been regarded as having a more isolated position, being a kind of "arthropodan annelid," little related to the other arthropod groups.

In phylogenetic discussions of arthropods, certain Middle Cambrian fossils described by WALCOTT (1911, 1912, 1931) have played an important role. The specimens, though flattened to films in shale, show fine details of the exoskeleton, including minute setae. They vary considerably in general appearance. Some (Pseudonotostraca, including *Burgessia, Yohoia, Opabinia, Waptia*) are very crustacean-like, whereas others (Marrellomorpha, containing *Marrella*) are trilobite-like or resemble merostomes (Merostomoidea, including *Emeraldella, Naraoia, Leanchoilia, Sidneyia*). In development of the appendages, however, all these different arthropods seem to be linked together by their apparently common trilobitan appendages (or modifications of these structures). This points to existence of a mutual relationship of the forms mentioned and at the same time suggests definite affinities to trilobites. The Middle Cambrian arthropods discussed are mostly regarded as representatives of a primitive, more or less ancestral group called Trilobitomorpha by Størmer (1944) and Proarthropoda by Vandel (1949); it is from this group that the 2 stems, Crustacea and Chelicerata, are generally presumed to have been developed (Raymond, 1920, 1935). On the other hand, the crustacean-like features may be interpreted as indicating homeomorphy, the whole group including the trilobites (Trilobita) belonging to the trilobite-chelicerate stem (Størmer, 1944). The problem is not settled. A monophyletic origin of the Arthropoda has been advocated among others by Heymonds, Lankester, Carpenter, Snodgrass, Waterlot, and Heegaard. In recent years the idea of a polyphyletic origin has become more common (Packard, Kingsley, Plate, Fedotov, Ivanov, Størmer, Vandel, Tiegs, Weber).

CLASSIFICATION

A detailed clasification of arthropod assemblages is given in the individual treatments of the various groups. Here only the major groups are considered.

The Pentastomida, Tardigrada, and Onychophora differ from the rest and have often been placed in a separate group (Protarthropoda Lankester, 1904; Pararthropoda Vandel, 1949; Oncopoda Weber, 1954).

The typical arthropoda (Euarthropoda Lankester, 1904) comprise 5 major groups. (1) The Trilobitomorpha (=Proarthropoda, Vandel, 1949) comprehend the host of trilobites that together form the class Trilobita and the chiefly Middle Cambrian forms known as Marrellomorpha, Merostomoidea, and Pseudonotostraca. These latter are here ranked as subclasses of nontrilobite Trilobitomorpha collectively designated as the class Trilobitoidea. (2) The Chelicerata is a well-defined group that includes xiphosurans and arachnids (*Treatise,* Part P). (3) The Pycnogonida (sea spiders), which in some respects seem comparable to the chelicerates and by many authors have been classified with them, are regarded as a distinct subphylum (*Treatise*, Part P). (4) The Crustacea are a very distinct assemblage consisting of the branchiopods, ostracodes, copepods, cirripeds, and malacostracans. (5) The myriapod-insect group comprises the Pauropoda, Diplopoda, Chilopoda, Symphyla, and Hexopoda (Collembola, Protura, Insecta).

The Crustacea with Myriapoda and Insecta have often been placed together in an assemblage called Mandibulata (or Antennata), a group that may be artificial in not being based on true relationships.

The main divisions of the Arthropoda may be given in tabular form as follows; in this outline the category "supersubphylum" is introduced so that divisions treated elsewhere (see *Treatise,* Part P) as subphyla may retain this assignment of rank.

Main Divisions of Arthropoda[1]

- Protarthropoda *(supersubphylum). ?Precam., Cam.-Rec.*
  - Pentastomida *(subphylum). Rec.*
  - Tardigrada. *Rec.*
  - Onychophora. *?Precam., Cam.-Rec.*
- Euarthropoda *(supersubphylum). Cam.-Rec.*
  - Trilobitomorpha *(subphylum). Cam.-Perm.*
    - Trilobitoidea *(class). Cam.-Dev.*
      - Merostomoidea *(subclass). Cam.-Dev.*
      - Pseudonotostraca. *Cam.*
      - Marrellomorpha. *Cam.*
    - Trilobita *(class). Cam.-Perm.*
  - Chelicerata *(subphylum). Cam.-Rec.*
    - Merostomata *(class). Cam.-Rec.*
      - Xiphosura *(subclass). Cam.-Rec.*
      - Eurypterida. *Ord.-Perm.*
    - Arachnida *(class). Sil.-Rec.*
      - Latigastra *(subclass). Sil.-Rec.*
      - Stethostomata. *Carb.(Penn.)*
      - Soluta. *Dev.-Carb.(Penn.)*
      - Caulogastra. *?Dev., Carb.(Penn.)-Rec.*
- Pycnogonida *(subphylum). Dev.-Rec.*
  - Mandibulata. *Cam.-Rec.*

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[1] The outline of classification given here conforms to views of the author of this section in recognizing the Protarthropoda (with their subdivisions) and Euarthropoda; also, the arrangement and taxonomic rank of the Trilobitomorpha (with their subdivisions) are adopted from Størmer. The Editor is responsible for the portion of the table that follows Trilobitomorpha; this is based partly on consultation with other contributors to volumes of the *Treatise* allotted to arthropods.—R.C.M.

Crustacea *(class). Cam.-Rec.*
  Branchiopoda *(subclass). Cam.-Rec.*
  Cephalocarida. *Rec.*
  Ostracoda. *Ord.-Rec.*
  Copepoda. *Rec.*
  Cirripedia. *Ord.-Rec.*
  Malacostraca. *Perm.-Rec.*
Myriapoda *(class). Penn.-Rec.*
  Chilopoda *(subclass). Penn.-Rec.*
  Diplopoda. *Penn.-Rec.*
  Symphyla. *Rec.*
  Pauropoda. *Rec.*
Hexapoda *(class). Dev.-Rec.*
  Collembola *(subclass). Dev.-Rec.*
  Protura. *Rec.*
  Insecta. *Penn.-Rec.*

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PROTARTHROPODA

By Raymond C. Moore

INTRODUCTION

The Protarthropoda (6) include invertebrates having subcylindrical, wormlike form and morphological characters intermediate between those of annelids and typical arthropods. No members of the group, however, are entitled to serious consideration as possible ancestors of the Arthropoda, for they possess obvious marks of evolutionary divergence that distinguish them as more or less aberrant stocks. Three assemblages, each classified as a subphylum, are recognized: Onychophora, Tardigrada, and Pentastomida. The onychophores are surely a very ancient group that exhibits hardly any perceptible change in external form during approximately 500 million years of their existence from Cambrian, or possibly Precambrian, time down to the present, although they have changed from originally marine habitats to a present exclusively terrestrial mode of life. The tardigrades (so-called "water bears") are very minute animals found on land, in fresh waters, and in the sea; they are unknown as fossils. The pentastomids are exclusively parasitic protarthropods that also have no fossil record.

ONYCHOPHORA

Living Onychophora (*onychus,* claw; *phora,* bearing) are represented by 70 described species, distributed in a dozen genera (1). Except for reported occurrence in the West Indies, Mexico, Central America, northern South America, and southeastern Asia, they are restricted to widely scattered parts of the Southern Hemisphere. They are found most commonly in moist dark places, such as beneath leaves and stones, in rock crevices, and concealed by the loosened bark of rotting logs. Generally, they are adapted to lowland forests in warm temperate to tropical areas, but some species exist in mountains to an elevation of about 6,000 feet above sea level where a snow cover may persist 4 or 5 months, and at least one form has been observed in arid parts of central Australia. During unfavorable periods of cold and dryness, onychophores are relatively or entirely immobile.

The Onychophora are elongate cylindrical animals of wormlike appearance ranging

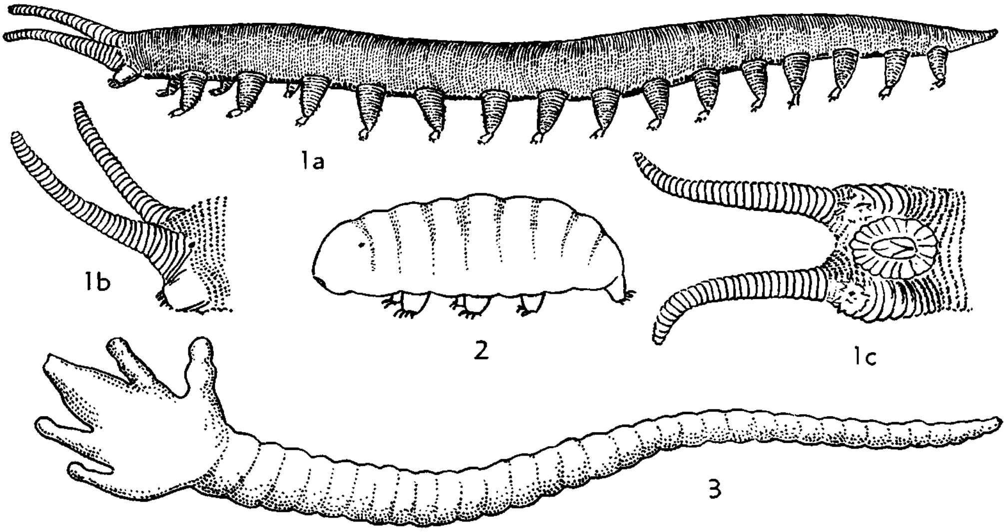


FIG. 11. Types of living Pararthropoda.——*1.* Onychophora; *1a, Peripatus,* from South Africa, side view of whole animal, ×2; *1b,c,* side and ventral views of same, ×2.5 *(Mod. from Snodgrass).*——*2.* Tardigrada; *Macrobiotus* from side, a cosmopolitan genus, ×60 *(Mod. from Cuenot).*——*3.* Pentastomida; *Cephalobaena,* parasite in lungs of snakes, ×4 *(Mod. from Heymons).*

in length from less than 1 inch (25 mm.) to a maximum of about 8 inches (200 mm.) (1). The body lacks evident marks of segmentation, but on its underside are regularly spaced pairs of thick and rather short stumpy legs, in different species (fossil and Recent) ranging in number from 10 to 43 pairs (Fig. 11,*1*). The anterior extremity bears 2 short antennae and a pair of small eyes, but there is no distinct head. The mouth, located between and just below the antennae, is bordered by a fleshy lip and provided with a pair of small horny jaws or mandibles laterally opposed to one another. On each side of the mouth is a blunt oral papilla that projects obliquely forward. The integument of the body is a flexible thin chitinous covering that bears numerous closely spaced transverse rings of fine papillae, each with a short hairlike spine. The fat rounded legs also carry transverse rings and lack division into joints such as characterize the limbs of typical arthropods; they are tapered toward their distal extremity, which is provided with a pair of claws (or in some extinct forms with 6 claws on each foot). The bluntly conical rear end of the body contains the anus and just ahead of it on the underside, a single genital opening (7).

Layers of longitudinal and transverse muscles immediately underlie the chitinous integument and in tubular manner inclose the undivided body cavity, digestive tract, excretory organs, and other soft parts. Special muscles control movement of the legs. The nervous system consists of a pair of ill-defined ganglia above the mouth, various nerves in the anterior part of the body, and a pair of ventral nerve cords (with many transverse connections) running the length of the body. Reproductive organs are paired and the sexes are separate. Most onychophores are viviparous. A large female may produce as many as 40 young in a year, each resembling the adult except in size and color.

Fossil onychophores are known only from Middle Cambrian rocks of British Columbia *(Aysheaia)* and possibly from Precambrian quartzite in Scandinavia *(Xenusion)* (4,5). They resemble modern species in external form but differ in some morphological characters and in being found (at least as regards *Aysheaia*) to occur in a marine habitat. The ancient onychophores are distinguished by their small number of body segments (10 in *Aysheaia* bearing limbs, as compared with 15 to 43 in living forms), fewer and more widely spaced transverse rings of papillae, branched antennae instead of simple undivided antennae, presence of 6 terminal claws on the walking legs, and frontal rather than ventral position of the mouth. *Xenusion* is known only from a rather poorly preserved single specimen, which, however, clearly shows a pair of moderately large tubercles on the ventral side of each segment, their significance being quite unknown.

OTHER GROUPS

Protarthropoda unrepresented by fossils are included in the subphyla named Tardigrada and Pentastomida (2,3). For the purpose of completeness in survey of divisions of the Arthropoda, it is desirable to notice these even though discovery of them in the paleontological record is unlikely. Both have a cylindrical wormlike form, with a body that lacks distinct segmentation inclosed by a thin chitinous integument, and such locomotor appendages as are developed (4 pairs in tardigrades and a single pair in pentastomids) consist of rather stumpy unjointed limbs. The legs of Tardigrada, like those of Onychophora, are armed with terminal claws. The Pentastomida include only somewhat aberrantly specialized parasites that infest various mammals, snakes, and birds.

SYSTEMATIC DESCRIPTIONS

Supersubphylum PROTARTHROPODA Lankester, 1904

[=Pararthropoda, VANDEL, 1949; Oncopoda WEBER, 1954]
[Type—*Peripatus* GUILDING, 1825]

Wormlike invertebrates having some characteristics of arthropods, which may include occurrence of molts, but lacking rigid or semirigid chitinous body covering and possession of jointed appendages; mouth with pair of modified appendages serving as mandibles. Includes some aberrant specialized forms, in part parasitic (6). *?Precam., Cam.-Rec.*

It is true that LANKESTER (1904, p. 565) assigned only the Onychophora to the "grade" Protarthropoda, but the lack of mention by him of the Tardigrada and Pentastomida (or Linguatulida) is not construed to be a significant omission, (1) because at the time of his writing these groups had received little attention from the standpoint of general taxonomy, being unrecognized as entitled to rank correlative with the Onychophora, and (2) because modification of the assigned limits of the assemblage named Protarthropoda does not require rejection of the taxon itself since the essential concepts relating to it and its content of the Onychophora remain. Accordingly, designations proposed a half century after publication of Lankester's classification are here treated as synonyms; they are Pararthropoda (VANDEL, 1949) and Oncopoda (WEBER, 1954).

Subphylum ONYCHOPHORA Grube, 1853

Relatively slender, subcylindrical, wormlike body with anterior extremity not differentiated as a distinct head but bearing a pair of short antennae, small eyes, blunt oral papillae, and mouth opening with 2 laterally placed mandibles on underside; body unsegmented, marked by numerous transverse rings of small papillae and bearing 10 to 43 pairs of short, stout, unjointed walking legs that terminate in claws; body and legs covered by thin chitinous integument; anus at conical posterior extremity behind slitlike genital opening. *?Precam., Cam.-Rec.*

Order PROTONYCHOPHORA Hutchinson, 1930

Extinct marine Onychophora with terminal mouth, frontal papillae, and branched antennae, pairs of short walking legs provided with 6 terminal claws (5). *?Precam., Cam.*

Family AYSHEAIIDAE Walcott, 1911

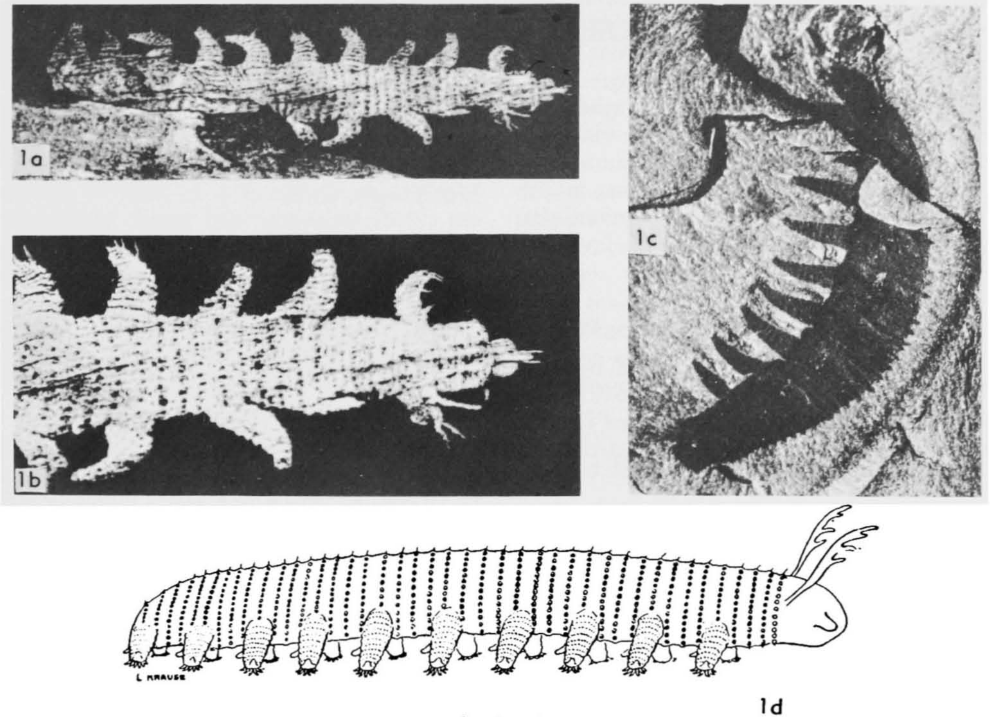
[*nom. correct.* MOORE, herein (*pro Aysheaidae* WALCOTT, 1911)]

Characters of the order. *M.Cam.*

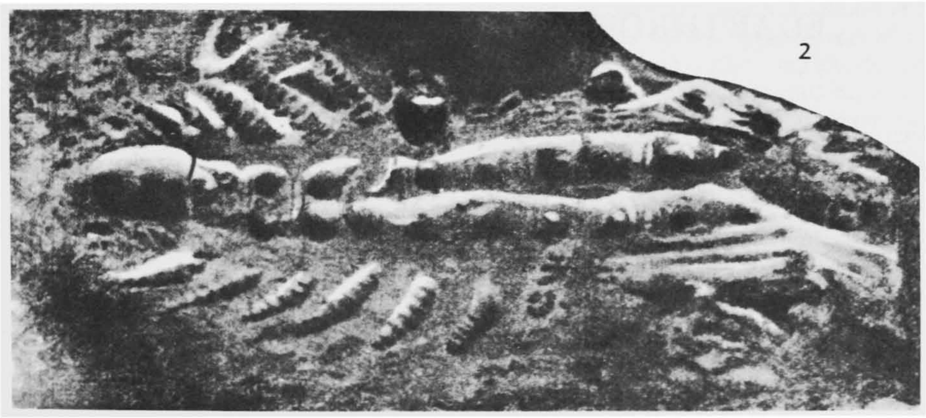
Aysheaia WALCOTT, 1911 [**A. pedunculata*]. Small (length 15-50 mm.), body unsegmented, but on basis of paired appendages divisible into 11 parts, each with 4 transverse rings of minute papillae; anterior pair of appendages antenniform, with 4 laterally diverging branchlets, attached above midline of sides and directed obliquely forward; other appendages consisting of short, blunt, tapered walking legs that are transversely annulated and provided with 6 terminal claws; unbranched alimentary canal extending length of body; obscure ventral or internal organs, possibly respiratory in function, located near extremities of legs (4,5,9). Burgess Shale, W.Can.(B.C.).——FIG. 12,*1*. **A. pedunculata; 1a,b,* type specimen, ×2, ×4 (6); *1c,* another specimen, ×1.5 (5); *1d,* reconstr., ×2.5 (5). [Species known from 9 specimens.]

Family UNCERTAIN

Xenusion POMPECKJ, 1927 [**X. auerswaldae*]. Body subcylindrical, moderately large (length more than 100 mm.), weakly segmented, with pair of rounded prominences on ventral side of each segment except at ?posterior extremity (opposite end



Aysheaia



Xenusion

FIG. 12. Fossil Onychophora.——*1. Aysheaia pedunculata* WALCOTT, M.Cam., W.Can.(B.C.); *1a,b,* type specimen, ×2, ×4 (6); *1c,* another specimen, ×1.5 (5); *1d,* reconstr., ×2.5 (5).——*2. Xenusion auerswaldae* POMPECKJ, ?Precam., Swed.; ventral side, ×1 (4).

unknown); legs thick, rounded and annulated, tapering distally, without observed claws; antenniform appendages unknown (4). *?Precam.* (erratic in glacial drift), Swed.——Fig. 12.2. **X. auerswaldae*; cast made from type (only known specimen), which is a mold, ventral side, ×1 (4).

Order EUONYCHOPHORA Hutchinson, 1930

Terrestrial Onychophora with tracheal respiratory system; anterior end with unbranched, moderately short antennae and blunt, laterally directed oral papillae; mouth anteroventral, with pair of horny mandibles; walking legs with terminal pair of claws (5). *Rec.*

Family PERIPATIDAE Evans, 1901

Reddish brown pigment altered by light and soluble in alcohol; with 22 to 43 pairs of legs; species tending to large size (length to 200 mm.). *Rec.,* distribution circumtropical.

Family PERIPATOPSIDAE Bouvier, 1907

Blue to green pigment not altered by light or soluble in alcohol; with 14 to 25 pairs of legs; species tending to medium or small size. *Rec.,* distribution south of equator (Chile, C.Afr., S.Afr., Austral., Tasm., N.Z.).

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EUARTHROPODA—GENERAL FEATURES

By Raymond C. Moore

Determination of the classificatory limits of the phylum Arthropoda and the definition of first-rank divisions within the phylum are matters involving a large amount of subjective judgment. For example, the groups designated as Onychophora, Tardigrada, and Pentastomida are almost universally considered to stand sufficiently apart from one another and from other invertebrates to warrant treatment of them as subphyla, but if this is accepted, to what phylum do they belong? Obviously they possess characters denoting affinity with typical arthropods, yet lack jointed legs and well-chitinized exoskeleton such as basically distinguish the Arthropoda. Recognition of the Protarthropoda as an independent phylum intermediate between Annelida and Arthropoda seems to be less satisfactory than stretching limits of the later enough to admit the Protarthropoda. This course is adopted in the *Treatise.*

Lankester (1904) introduced the "grade" Euarthropoda to contain all typical arthropods, including particularly the classes Diplopoda, Arachnida, Crustacea, Chilopoda, and Hexapoda (insects), as enumerated by him. Present classification calls for inclusion of the trilobites and related forms (here collectively designated as Trilobitomorpha) as a major division of the Euarthropoda, correlative in rank with Chelicerata, which is composed of the Arachnida and Merostomata; Lankester assigned the Trilobita and merostomes such as *Limulus* to the Arachnida. Also, present judgment of most specialists on the arthropods supports a grouping together of the Crustacea, Myriapoda (Chilopoda, Diplopoda, Symphyla, Pauropoda), and Hexapoda (Insecta, Collembola, Protura) in a subphylum designated Mandibulata. Entomologists commonly recognize the Insecta as including the Collembola and Protura, however.

The Euarthropoda are characterized by their segmented, externally jointed body that is covered by a hardened exoskeleton containing chitin. This covering firmly incloses the internal soft parts, allowing essentially no change of dimensions, expansion in growth being provided for by periodic molts. The body commonly is divided into a head, thorax, and abdomen, but these parts vary in distinctness and in some euarthropods the different regions may be fused together. Appendages consist basically of one pair to each somite and each appendage has few or many hinge joints that are moved by opposed sets of muscles; the appendages may be reduced in number, however, and generally they are differentiated to serve various functions. The digestive tract is a simple or complex tubular structure extending from the mouth, mostly located on the underside of the head, to the anus at the rear of the abdomen; elaborate diverticula may exist. The mouth commonly is provided with lateral jaws adapted for chewing or sucking. Respiration is effected by gills, air ducts (tracheae), so-called book lungs, or by the body surface. A dorsally placed heart forces blood through arteries to the various organs and body tissues, return of blood to the heart being through open body spaces. A well-developed nervous system consists of paired dorsal ganglia connected to ventral nerve cords leading to ganglia in each somite and branches serving the appendages. Eyes generally are present; they include both simple and compound types, although many euarthropods possess only one kind or the other. Tactile and chemoreceptor hairs, antennae, statocysts, and auditory organs are widely occurring sensory equipment of these invertebrates. The sexes usually are separate, with fertilization of eggs inside of the female. After hatching, the young almost invariably pass through a series of larval stages that lead gradually or with abrupt metamorphosis to the adult form (7,8).

Taking account of the enormous number of different kinds of euarthropods, their effective adaptation to almost every conceivable environment, and their extremely long paleontological record, one must judge this group of animals supremely successful. The complex organization of their hard parts, found more or less abundantly and well preserved in rock formations throughout the geologic column, adapts them for purposes of stratigraphic correlation and age determination. As fossils, most of them are intrinsically of great interest to both specialists and laymen.

Supersubphylum EUARTHROPODA Lankester, 1904

Arthropoda distinguished by hardened body covering composed largely of chitin, body usually well segmented and jointed externally and commonly divisible into head, thorax, and abdomen (although with some of these parts fused together in many forms); with jointed appendages composed of few or several segments connected by hinges and moved by opposed sets of internal muscles; with rather highly developed sensory organs, circulatory and nervous systems, and modes of respiration; sexes usually separate; young mostly passing through a number of larval stages before gradual or abrupt attainment of adult form, growth accommodated by molts of exoskeleton (6-8). *?Precam., Cam.-Rec.*

REFERENCES

For references see the preceding section on Protarthropoda.

TRILOBITOMORPHA

By LEIF STØRMER

INTRODUCTION

The name Trilobitomorpha was introduced (STØRMER, 1944)[1] to include the Trilobita and trilobite-like forms, particularly several peculiar Middle Cambrian arthropods found and described by WALCOTT (6-8). These forms, occurring in the Burgess Shale of British Columbia, are excellently preserved. Although flattened into films in the shale, the outlines, even of finest details such as bristles of the appendages, are very well preserved (Fig. 13). In spite of favorable preservation of these fossils, our knowledge of the various species represented is hardly sufficient to warrant definite determination of their taxonomic position. Whereas the trilobites apparently are very conservative as regards their basic structures, the nontrilobite members of the Trilobitomorpha exhibit a considerable variation both in development of the body and of the appendages. This suggests that the trilobites represent a well-established group, in contrast to the others that seem to be in a state of radiation, with ability to develop new and different groups.

The characteristic structure of appendages forms the connecting link between different members of the Trilobitomorpha. On its basic structure the trilobite appendage consists of a jointed, cylindrical walking leg with a lateral gill branch attached to its very base (Fig. 14). As far as can be ascertained from materials available, the nontrilobite forms have trilobitic appendages or derivations of this type. In some genera the walking leg is more or less reduced and in others the gill branch (certain appendages such as those interpreted as 2nd antennae) is too specialized to justify comparison with the trilobite limb.

The common features in development of the appendages seem to justify the establishment of a common group (Trilobitomorpha) for the different forms observed.

Whether the structure of trilobite appendages is sufficiently unique to warrant recognition of trilobitomorphs as a separate subphylum of the Arthropoda, or whether it is so related to the biramous limb of Crustacea as to call for classification with this group remains an open question. The occurrence of the trilobite type of limb in several different trilobites from very different geological ages and its presence in several nontrilobite arthropods, apparently both benthonic and planktonic, are points favoring interpretation as a unique structure. The bifurcate nature of appendages in both trilobitomorphs and crustaceans has been considered to denote relationship. The characteristic gill branch of the trilobite limb, however, might be homologous with the gill-bearing epipodite (or pre-epipodite) of the crustaceans. The name Trilobitomorpha (4) is appropriate for segregation of the trilobites and trilobite-like arthropods as a group distinct from the Crustacea. The name Proarthropoda, suggested for the group by VANDEL (5) in 1949, seems to be less appropriate, especially if forms distinctly more primitive than the trilobitomorphs are found in future.

The Trilobitomorpha are here regarded as a subphylum comprising classes called Trilobitoidea (including the subclasses Merostomoidea, Pseudonotostraca, Marrellomorpha) and Trilobita. A diagnosis of the group follows.

SYSTEMATIC DESCRIPTIONS

Subphylum TRILOBITOMORPHA Størmer, 1944

[=Proarthropoda VANDEL, 1949]

Aquatic Arthropoda with preoral antennae and remaining appendages of typical or modified trilobite type, biramous appendages characterized by presence of a lateral gill branch attached to very base of walking leg. *L.Cam.-M.Perm.*

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[1] Literature cited in this section is included in "References" at the end of the following section on Trilobitoidea.

TRILOBITOIDEA

By LEIF STØRMER

CONTENTS

INTRODUCTION

Practically all forms referred to the Trilobitoidea come from the Middle Cambrian Burgess Shale of British Columbia. The fossils generally appear as thin films in the shale. Only in forms having a relatively solid exoskeleton is a certain relief preserved. Dark imprints of the intestine are seen in a number of specimens, signifying that they represent dead individuals rather than shed molts.

In the light of present knowledge it is difficult to establish a satisfactory taxonomy for the many different forms. WALCOTT (6), RAYMOND (3) and STØRMER (4) have suggested major classifications that contain features now considered unacceptable. The recognition of separate classes and subclasses for these arthropods as here outlined, similarly may be somewhat premature. For the following description of the morphology and relationships of the Trilobitoidea, all non-trilobite forms of the Trilobitomorpha are treated together.

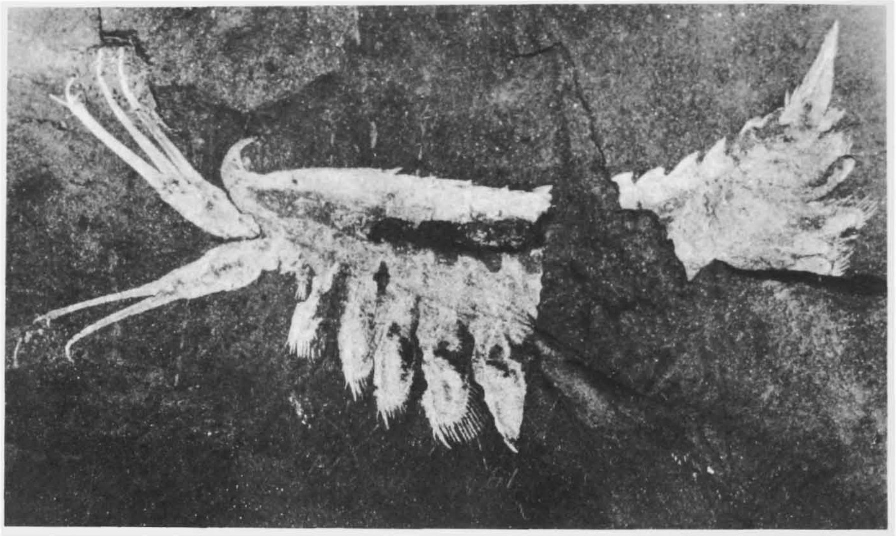

FIG. 13. *Leanchoilia superlata* WALCOTT, M.Cam., W.Can.(B.C.); dorsolaterally compressed specimen (unretouched photo), ×1.5 (3).

MORPHOLOGY

The body length of trilobitoids ranges from 1 to 16 cm., the most common length being 4 to 8 cm. The shape of the body varies from broad and dorsoventrally flattened (Fig. 16) to narrow and laterally compressed (Figs. 21,24). Some have a pronounced merostome-like appearance, whereas others closely resemble crustaceans. Trilobite-like forms *(Marrella)* also occur. The body is divided into parts (tagmata) consisting of severally distinct sorts of more or less closely united segments (somites).

CEPHALIC REGION

A **head shield** is well defined, particularly in merostomoid forms but also in *Opabinia.* It is not possible to decide the number of postoral segments in the head. Only *Mollisonia* and *Yohoia* show traces of a dorsal segmentation of the head shield. In *Leanchoilia, Emeraldella, Burgessia,* and *Marrella,* the appendages suggest about 4 postoral segments (as compared with 4 such segments in trilobites). The Devonian *Cheloniellon* has a short "protocephalon" with only a single postoral segment, but the coxal development of the appendages indicates a functional cephalon having 5 postoral segments. In the trilobite-like *Marrella* the head shield is prolonged into 4 prominent horns that evidently served as a floating organ in this small, probably planktonic, form (Fig. 15). The presence of supposed sutures at the base of the lateral horns suggests interpretation of them as "free cheeks." The posterior horns and their common base are prolonged backward as a sort of carapace. A typical carapace is developed in the most crustacean-like forms *(Burgessia, Waptia)* (Fig. 21). It extends backward so as to cover a small or large part of the trunk.

Eyes have not been distinguished in *Emeraldella* and *Sidneyia,* and they are identified only with doubt in *Leanchoilia* and *Helmetia.* WALCOTT thought that he could recognize small (sessile) eyes in

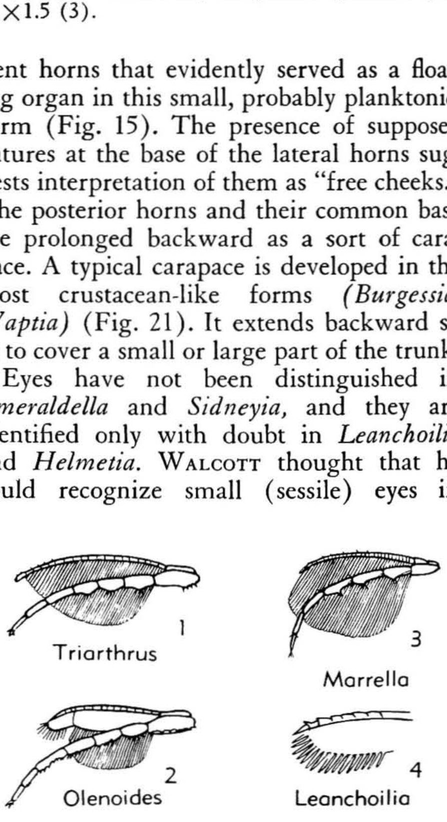

FIG. 14. Trilobite-type appendages of trilobitomorphs.——*1,2.* Trilobites.——*3.* Marrellomorph.——*4.* Merostomoid. (All diagrammatic, not to scale.)

Naraoia and *Burgessia*. Well-developed sessile eyes occur in *Cheloniellon*. Of particular interest is the presence of apparently pedunculate eyes in *Opabinia* and *Waptia*. In other groups of arthropods, pedunculate eyes characterize the Malacostraca. Similar types of eyes, however, seem to develop independently in very different groups of the Arthropoda.

In *Opabinia* a peculiar frontal organ, possibly erectable, with a median canal, has been compared to structures in male Anostraca among the Branchiopoda (Fig. 22).

An upper-lip, resembling the hypostoma of trilobites, has been described in *Burgessia* and *Marrella*. A ventrally located plate in *Cheloniellon* may represent a postoral plate or labium.

POSTCEPHALIC REGION

The **trunk** is generally elongate and divided into a number of movable segments. The number varies from 10 to 12 in the Merostomoidea to more than 12 in the other groups. A tagmatic division occurs. In *Naraoia* all the trunk segments are covered by a continuous abdominal shield (Fig. 18). In *Helmetia* the posterior segments are fused into a "pygidium" (Fig. 25). The last segment of the trunk carries a telson or lateral "fins," comprising either lateral outgrowth of the segments or modified appendages.

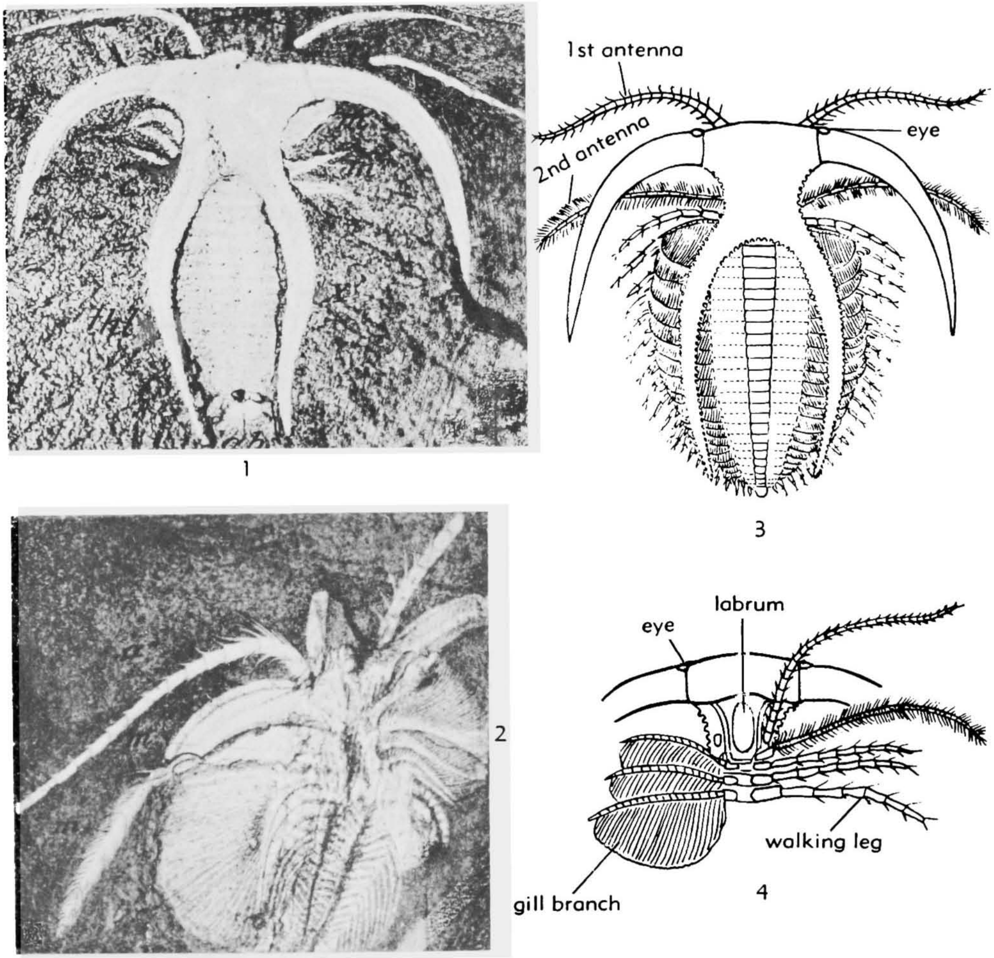

FIG. 15. *Marrella splendens* WALCOTT, M.Cam., W.Can.(B.C.); *1,2,* dorsal and ventral sides, ×3, ×4; *3,* dorsal side (reconstr.), ×3; *4,* frontal appendages in ventral view showing one branch on either side (reconstr.) (4, 7).

The trunk may be fairly broad and flat, its pleural parts then forming a cover to the appendages. A trilobation is characteristic of many forms (*Leanchoilia, Emeraldella, Naraoia, Molaria, Yohoia, Opabinia,* and to some extent in *Cheloniellon*) but is absent in *Sidneyia* and the typical crustacean-like forms in which the pronounced carapaces function as a protecting cover.

In crustacean-like and merostomoid forms (*Waptia, Emeraldella, Sidneyia*) the posterior trunk segments lack appendages, and the tergites and sternites unite to form solid cylindrical segments. A terminal lanceolate telson is characteristic of the Merostomoidea (except *Sidneyia,* in which the terminal segment has a transverse posterior border). The 2 long extensions from the dorsal side of the posterior segment in *Cheloniellon* may have the same origin as the ordinary single telson spines. A secondary jointing of the telson spine seems to have taken place in *Burgessia.*

APPENDAGES

The appendages are well preserved in many trilobitoids, but it is difficult to establish their number in the head and trunk and to decide on their homology. Generally, a pair of anterior uniramous, multijointed antennae are present. They are very characteristic of all 3 major groups. In *Leanchoilia* vestiges of short appendages in front of the "great appendages" are possibly interpreted as 1st antennae. The flexible 1st antennae of all these members of the Trilobitomorpha are probably homologous with the antennae of trilobites and are thus preoral antennae (or antennules) corresponding to those of the Crustacea and Insecta. Whereas in trilobites all postoral appendages are practically alike (except for the antenniform last appendages in *Olenoides*), those of the nontrilobitic forms show considerable variation. Two pairs of antennae occur in *Marrella* (Fig. 15). The 2nd pair may correspond to the 2nd antennae in Crustacea. The "great appendages" of *Leanchoilia* possibly belong to the same segment (Figs. 13, 20). In these appendages endites are prolonged into flexible multijointed tactile organs. The many blade-shaped endites of the powerful cephalic appendage in *Sidneyia* may be homologous structures.

In general, the appendages of the postoral segments of the Trilobitoidea seem to be more or less trilobite-like. Both *Naraoia* and *Marrella* have biramous appendages similar to those found in the trilobites *Triarthrus* and *Cryptolithus* (Fig. 14). The gill branch has a multijointed shaft with a fringe of gills. A similar development seems to be present in the Devonian *Cheloniellon.* In *Burgessia* the gill branch appears to be of the *Olenoides* type, with a broad unjointed shaft. The walking legs have endites like those of *Triarthrus.* In *Opabinia* and the thoracic region of the trunk in *Waptia,* gill branches occur, but the walking legs seem to be much reduced. In *Waptia* the abdominal part of the trunk lacks appendages other than flattened terminal ones (Fig. 21). Walking legs without gill branches possibly occur in the cephalic region of *Burgessia* and *Waptia.* The various nontrilobitic forms seem to bear appendages that are either of trilobite type or derivations of this type. The comparatively strong development of the gills, even in small forms like *Marrella,* may signify a low oxygen content of the sea.

DIGESTIVE TRACT

In some trilobitoid fossils, traces of the **intestine** appear as a dark staining along the median line of the body. In *Naraoia* and *Burgessia* beautifully distinct imprints of the anterior part of the intestine with diverticulae are preserved in many specimens (Figs. 18, 21).

ONTOGENY

Larval stages of described species of Trilobitoidea are unknown but certain fossils, such as those named *Mollisonia* and *Tontoia,* may actually represent larval forms (Fig. 26).

MODE OF LIFE

Among the Trilobitoidea flat forms with a length of more than 10 cm. (*Helmetia, Cheloniellon*) probably were benthonic animals. The tail of *Sidneyia* suggests that this species was a good swimmer. The middle-sized species, with a length of about 4 to 8 cm., probably were able swimmers also. The shrimplike nature of *Waptia* suggests a corresponding mode of life (Fig. 21). It

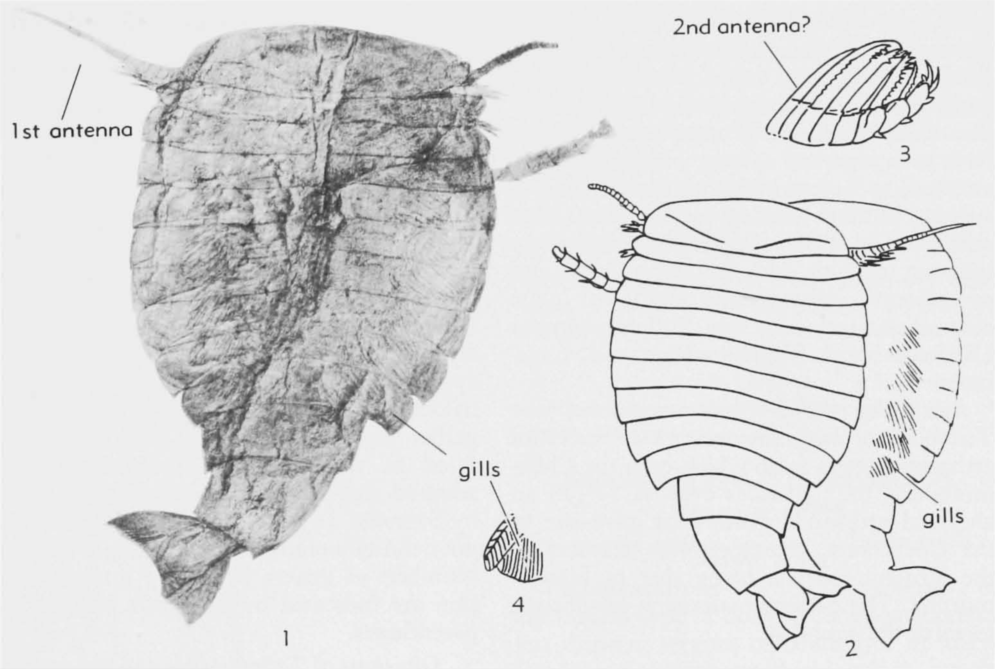

FIG. 16. *Sidneyia inexpectans* WALCOTT, M.Cam., W.Can.(B.C.); *1*, dorsal side with impressions of ventral structures, ×0.7; *2*, dorsal and ventral sides, ×0.5; *3*, ?2nd antenna; *4*, distal parts of trunk appendages (6).

is likely that the small trilobitoids, *Burgessia* and *Marrella* (1 to 1.5 cm. in length), characterized by their broad carapace and horned cephalon, belonged to the plankton (Figs. 15, 21).

RELATIONSHIPS

As pointed out previously, the Trilobitomorpha are linked together by the seemingly common basic structure of their appendages. Since the trilobite limb appears to be a characteristic and conservative structure, its presence in fossil arthropods may be interpreted as evidence of close relationship between the many different forms possessing it.

The Trilobitomorpha possess various morphological features that are characteristic of many members of the Chelicerata. Among these may be mentioned (1) trilobation, including development of broad pleural areas; (2) tendency to develop a styliform telson; (3) lack of true jaws; (4) structure of the appendages; (5) strong development of the intestinal diverticulae; and (6) probably like number of larval segments. The Merostomoidea resemble the Merostomata in shape of the body. The lack of antennae and presence of chelicerae in the Chelicerata do not deny affinities. Indeed, it is probable that the Chelicerata developed from antennate forms.

Some of the characters mentioned above (1, 5), may occur, though less typically, in the Crustacea, but the affinities of Trilobitoidea with crustaceans are suggested especially by some very crustacean-like forms *(Burgessia, Waptia, Opabinia)*. In addition to general appearance, features that suggest crustaceans are presence of a carapace, pedunculate nature of the eyes, and occurrence of a possible "branchiopod" frontal organ *(Opabinia)*. If *Hymenocaris,* from the Burgess Shale, also belongs to the Trilobitoidea, it supports connection of this group with the Crustacea. The typical trilobite limb has not, however, been observed in crustaceans. It is possible, as held by most carcinologists, that this is of minor importance, and not denied is the possibility of deriving crustacean-type limbs from those of the Trilobitomorpha.

The Cambrian crustacean-like forms that here are assigned to the Trilobitoidea have been regarded by Walcott, Calman, Raymond, Henriksen, and others as true crustaceans belonging to an ancestral group from which Recent crustaceans evolved. On the other hand, merostome-like trilobitoids have been regarded as more or less definitely ancestral to Recent merostomes.

A few authors (Størmer, Snodgrass) have advocated a more fundamental difference between trilobitic and crustacean limbs, and consequently they have questioned close connection between the Trilobitomorpha (Trilobita and Trilobitoidea) and Crustacea.

According to divergent opinions, the Trilobitomorpha represent (1) an ancestral arthropod group from which both the Chelicerata and the Crustacea evolved, or (2) an ancestral arthropod group that gave rise to the Chelicerata, crustacean-like features of the Trilobitomorphs being due to homeomorphy. The present material is insufficient to solve the problem.

CLASSIFICATION

Taxonomic divisions may be based either on general morphological characteristics or on some particular element, such as development of the appendages. The latter here is employed for the group (Trilobitomorpha) as a whole. Walcott (6) regarded the Middle Cambrian trilobitoid forms as belonging to the Branchiopoda, Merostomata, and Trilobita *(Naraoia)*. Raymond (2,3) established for them 2 subclasses (Homopoda, Xenopoda), chiefly distinguished by the presence of 2 pairs or a single pair of tactile organs (antennae). The degree of development (specialization) of the frontal appendage was also used by Størmer in his classification, published in 1944. Since the development of the frontal appendages is not well known, taxonomy based on these structures may be uncertain. The general structure of the body has to be taken into account at the same time. Inasmuch as phylogeny of the Trilobitomorpha is uncertain, it is rather undesirable to use group names that express distinct phylogenetic concepts (for example, Palaeanostraca Hutchinson, 1930, and Prochelicerata Størmer, 1944). Raymond's major groups, Homopoda and Xenopoda, are difficult to maintain. The former includes such different forms as *Aglaspis* (now assigned to the Merostomata), *Marrella*, and *Waptia*.

The evolutionary radiation of Middle Cambrian Trilobitoidea occurred at a "low level," that is, it yielded diverse groups of high taxonomic rank, seemingly almost correlative with the class Trilobita. To distinguish the Merostomoidea, Pseudonotostraca, Marrellomorpha, and possibly additional groups as independent classes associated with the class Trilobita seems ill-advised, or at least premature. In the present state of knowledge it is judged more appropriate to recognize assemblages of non-trilobites as subclasses, grouping them together under the name Trilobitoidea, defined as a class. The classification here adopted therefore deviates from that given by Størmer (4) in 1944. Several forms are not definitely placed in named major groups. Numbers of genera belonging to each division are indicated by numerals inclosed by parentheses.

Divisions of Trilobitoidea (16 genera)

- Marrellomorpha *(subclass)* (1). *M.Cam.*
  - Marrellida *(order)* (1). *M.Cam.*
    - Marrellidae (1). *M.Cam.*
- Merostomoidea *(subclass)* (7). *M.Cam.*
  - Limulavida *(order)* (2). *M.Cam.*
    - Sidneyiidae (2). *M.Cam.*
  - Emeraldellida *(order)* (1). *M.Cam.*
    - Emeraldellidae (1). *M.Cam.*
  - Nectaspida *(order)* (3). *M.Cam.*
    - Naraoiidae (3). *M.Cam.*
  - Leanchoiliida *(order)* (1). *M.Cam.*
    - Leanchoiliidae (1). *M.Cam.*
- Pseudonotostraca *(subclass)* (2). *M.Cam.*
  - Burgessiida *(order)* (1). *M.Cam.*
    - Burgessiidae (1). *M.Cam.*
  - Waptiida *(order)* (1). *M.Cam.*
    - Waptiidae (1). *M.Cam.*
- Subclass uncertain (2). *M.Cam.-L.Dev.*
  - Opabiniida *(order)* (1). *M.Cam.*
    - Opabiniidae (1). *M.Cam.*
  - Cheloniellida *(order)* (1). *L.Dev.*
    - Cheloniellidae (1). *L.Dev.*
- Subclass and order uncertain (4). *M.Cam.*
  - Yohoiidae (1). *M.Cam.*
  - Family uncertain (3). *M.Cam.*

SYSTEMATIC DESCRIPTIONS

Class TRILOBITOIDEA
Størmer, nov.

Trilobitomorpha lacking distinctive morphologic characters of Trilobita and, in addition, exhibiting divergent structural pe-

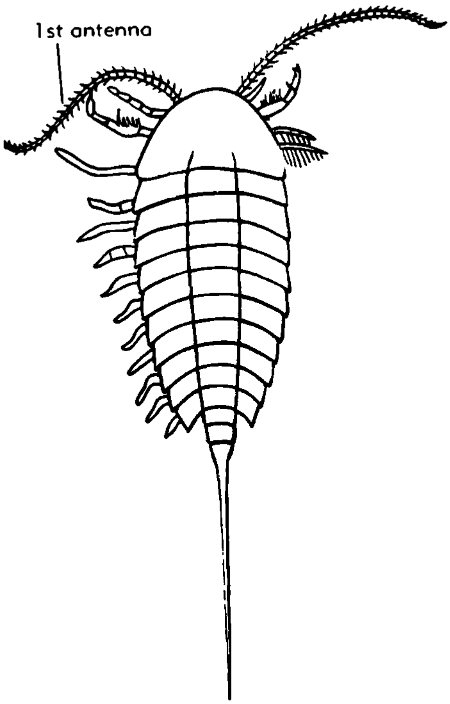

FIG. 17. *Emeraldella brooki* WALCOTT, M.Cam., W. Can.(B.C.); dorsal side, ×1.2 (7).

culiarities of their own, unlike those of trilobites (such as presence of eurypterid-like body, shield covering both cephalic and abdominal regions, laterally compressed carapace, widely divergent flat horns produced from cephalic shield, and others). Postoral appendages less uniform than in Trilobita. *M.Cam.-Dev.*

Subclass MARRELLOMORPHA Beurlen, 1934

Trilobitomorpha with cephalic shield prolonged into flat horns; trunk with numerous free tergites and small telsonic plate; 2 pairs of antennae, other appendages of trilobitic type. *M.Cam.*

Order MARRELLIDA Raymond, 1935

[*nom. correct.* STØRMER, herein (*pro* Marrellina RAYMOND, 1935)]

Characters of subclass (3). *M.Cam.*

Family MARRELLIDAE Walcott, 1912

Small Marrellida characterized by cephalon with 4 flat horns directed backward, bearing facial sutures and sessile eyes; trunk elongate, composed of about 24 segments, probably with pleural areas; telson small, plate-shaped; elongate labrum attached to doublure; 1st pair of antennae uniramous with numerous joints, 2nd antennae with fewer joints, densely covered with setae, other appendages probably of *Triarthrus*-type; fringe of gills broad (7). *M.Cam.*

Marrella WALCOTT, 1912 [**M. splendens*]. Characters of family, order, and subclass. Burgess Sh., W.Can.(B.C.).——FIG. 15. **M. splendens,* Burgess Sh.; 15,*1,2,* dorsal and ventral sides, ×3, ×4; 15,*3,* dorsal side (reconstr.), ×3; frontal appendages, in ventral view showing one branch on either side (reconstr.), ×3 (4, 7).

Subclass MEROSTOMOIDEA Størmer, 1944

[*nom. transl.* STØRMER, herein (*ex* class Merostomoidea STØRMER, 1944)]

Trilobitomorpha with eurypterid or xiphosurid type of body, trilobation more or less distinct; tergites of trunk free or ankylosed into continuous shield, telson mostly styliform; 1st and last pair of trilobitic appendages may be modified and others partly reduced (4). *M.Cam.*

Order LIMULAVIDA Walcott, 1911

[*nom. correct.* STØRMER, herein (*pro* order Limulava WALCOTT, 1912, *nom. transl.* (*ex* suborder Limulava WALCOTT, 1911)] [=Subclass Prochelicerata STØRMER, 1944 *(partim)*]

Merostomoidea with eurypterid-like body, ?2nd pair of appendages provided with numerous flat median spines; trunk appendages of trilobitic type, with walking legs reduced (4, 6). *M.Cam.*

Family SIDNEYIIDAE Walcott, 1911

[*nom. correct.* STØRMER, herein (*pro* Sidneyidae WALCOTT, 1911)]

Limulavida with short cephalon provided with marginal ?eyes and ventral labrum; trunk divided into a preabdomen of 9 segments and postabdomen of 2 or 3 segments, with tail fin formed either by lateral outgrowth of last segment or by modified cerci; ?1st antennae (uniramous, with numerous setiferous joints; ?2nd antennae developed as powerful appendages of 9 to 10 joints provided with numerous long flat spines on their median sides; other cephalic appendages apparently resembling trilobitic walking legs, appendages on preabdomen probably consisting of jointed shafts with broad fringes of gills (6). *M.Cam.*

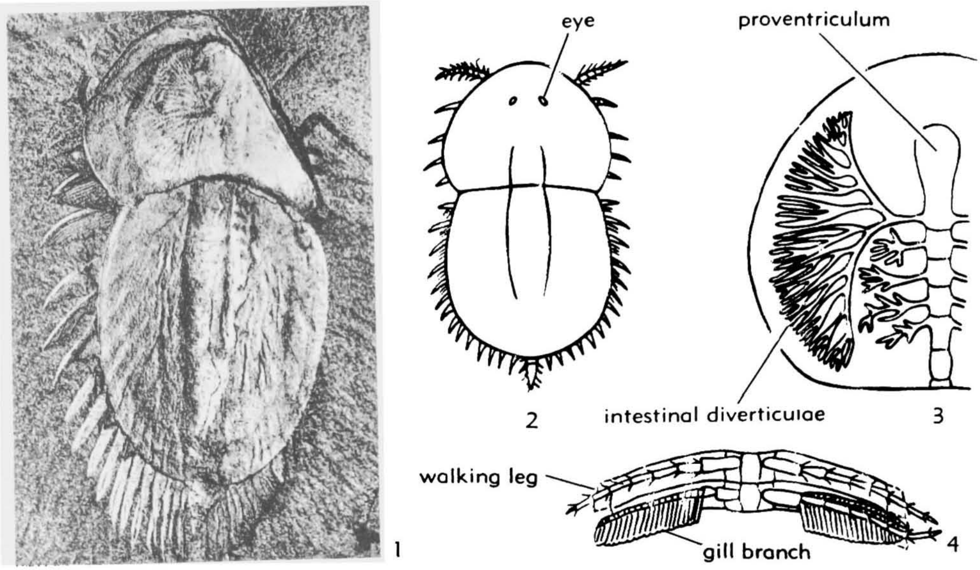

FIG. 18. *Naraoia compacta* WALCOTT, M.Cam., W.Can.(B.C.); *1*, dorsal side, ×2; *2*, reconstr., ×1.5; *3*, intestinal diverticula, ×4.5; *4*, trunk appendages (reconstr.), ×4.5 (4, 7).

Sidneyia WALCOTT, 1911 [**S. inexpectans*] [=*Sidneya* STØRMER, 1944]. Characters of family (4,6). Burgess Sh., W.Can.(B.C.).——FIG. 16. **S. inexpectans*, Burgess Sh.; 16,*1*, dorsal side with impressions of ventral structures, ×0.7; 16,*2*, dorsal and ventral sides, ×0.5; 16,*3*, antenna (?2nd), ×1; 16,*4*, distal parts of trunk appendages, ×1 (all 6).

Amiella WALCOTT, 1911 [**A. ornata*]. Little known, possibly synonym of *Sidneyia*. Burgess Sh., W.Can. (B.C.).

Order EMERALDELLIDA Størmer, 1944

[*nom. transl.* STØRMER, herein (*ex* subclass Emeraldellida STØRMER, 1944)]

Merostomoidea with elongate trilobed body, styliform telson, all appendages of practically unaltered trilobitic type (4). *M. Cam.*

Family EMERALDELLIDAE Raymond, 1935

Body narrow, divided into semicircular cephalon, preabdomen of 10 segments, and narrow, probably 2-segmented postabdomen bearing styliform telson expanded at base, postabdomen without appendages; eyes unknown; labrum elongate; 1st antennae long, uniramous, with many joints, other appendages probably biramous, of trilobitic type (3). *M.Cam.*

Emeraldella WALCOTT, 1912 [**E. brocki*]. Characters of family. Burgess Sh., W.Can.(B.C.)——FIG. 17. **E. brocki*; dorsal side, ×1.2 (7).

Order NECTASPIDA Raymond, 1920

[*nom. correct.* STØRMER, herein (*pro* order Nectaspia RAYMOND, 1920)]

Merostomoidea with body covered by cephalic and abdominal shield, postabdomen short and narrow, with telson; appendages of trilobitic (*Triarthrus*) type; intestinal diverticulae well developed (2,4,7). *M.Cam.*

Family NARAOIIDAE Walcott, 1912

[*nom. correct.* STØRMER, herein (*pro* Naraoidae WALCOTT, 1912)]

Small Nectaspida with subelliptical, trilobate body, cephalon with small sessile eyes, postabdomen short and narrow with ?single segment and short lanceolate telson bearing lateral spines that protrude from below abdominal shield; 1st antennae short, with numerous setiferous joints, other appendages probably of trilobitic (*Triarthrus*) type; intestinal diverticulae with 5 pairs of basal branches (7). *M.Cam.*

Naraoia WALCOTT, 1912 [**N. compacta*]. Characters of family. Burgess Sh., W.Can.(B.C.).——FIG. 18. **N. compacta*; 18,*1*,*2*, dorsal side, photo, ×2, and reconstr., ×1.5; 18,*3*, intestinal diverticulae, ×4.5; 18,*4*, trunk appendages (reconstr.), ×4.5 (4, 7).

?**Molaria** Walcott, 1912 [**M. spinifera*]. Body small, elongate, distinctly trilobate, with lanceolate telson. Cephalon semicircular, with median axis divided into ?3 transverse lobes, traces of intestinal diverticulae. Trunk 9-segmented, elongate last segment possibly representing about 3 fused segments; telson lanceolate; pleurae curved, quite narrow on last segment. Cephalic appendages little known, 1st antennae probably short and delicate; trunk appendages trilobitic, evidently with both branches present; last segment lacking appendages (7). [Genus probably related to *Emeraldella,* but whether it belongs to Emeraldellidae or a separate family is doubtful.] Burgess Sh., W.Can.(B.C.).——Fig. 19,*1,2*. **M. spinifera;* dorsal side and lateral view, ×3 (7).

?**Habelia** Walcott, 1912 [**H. optata*]. Little known; body presumed to be similar to *Molaria* but with long styliform telson; appendages trilobitic (7). [Single known specimen is imperfectly preserved and may belong to another genus (e.g., *Burgessia* with carapace lost).] Burgess Sh., W. Can.(B.C.).——Fig. 19,*3*. **H. optata;* dorsolateral view, ×1.7 (7).

Order LEANCHOILIIDA Størmer, 1944

[*nom. correct.* Størmer, herein (*pro* order Leanchoilida Størmer, 1944)] [=order Pseudanostraca Raymond, 1935 *(partim);* subclass Prochelicerata Størmer, 1944 *(partim)*]

Merostomoidea with elongate trilobate body (aglaspidid type), divided into cephalon and segmented trunk with lanceolate telson; 1st antennae considerably reduced or possibly absent, ?2nd antennae strongly developed and specialized, other appendages filamentous, walking legs (telopodites) missing (4). *M.Cam.*

Family LEANCHOILIIDAE Raymond, 1935

Body narrow, elongate, of medium size; cephalic shield subtriangular, with pointed rostrum, lateral eyes probably missing; trunk distinctly trilobate, with 10 curved tergites; telson short lanceolate, with marginal spines; presence of 1st antennae uncertain, probably reduced to short and delicate appendages, ?2nd appendages developed as powerful tripartite tactile organs; 2 distally jointed ?endites attached to distal portion of 5- or 6-jointed shaft, remaining appendages (2 or 3 pairs belonging to cephalic shield) developed as gill branches of *Olenoides* types, walking legs (telopodites) missing (3). *M.Cam.*

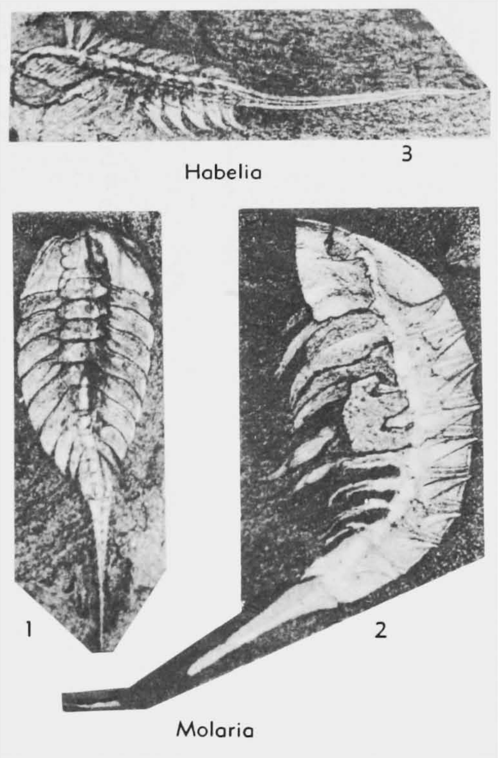

Fig. 19. *Molaria and Habelia,* M.Cam., W.Can. (B.C.); *1,2, M. spinifera* Walcott, dorsal and lateral views, ×3 (7); *3, H. optata* Walcott, dorsolateral view, ×1.7 (7).

Leanchoilia Walcott, 1912 [**L. superlata*]. Characters of family. Burgess Sh., W.Can.(B.C.).——Figs. 13,20. **L. superlata;* 13, dorsolaterally compressed specimen (unretouched photo), ×1.5 (3); 20, dorsal and lateral views (reconstr., convexity probably exaggerated), ×0.7 (4).

Subclass PSEUDONOTOSTRACA Raymond, 1935

[*nom. transl.* Størmer, herein (*ex* order Pseudonotostraca Raymond, 1935] [=Class Pseudocrustacea Størmer, 1944]

Carapace well developed, eyes sessile or pedunculate; pleurae absent in trunk (at least beyond posterior border of carapace); styliform telson or tail fin formed by flat cerci; 1st antennae and other appendages of trilobitic type in postoral appendages with one branch reduced in some; postabdomen without appendages (except cerci) (3,4). *M.Cam.*

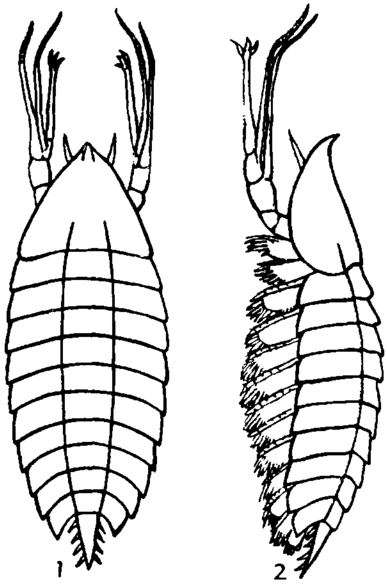

FIG. 20. *Leanchoilia superlata* WALCOTT, M.Cam., W.Can.(B.C.); *1,2,* dorsal and lateral views (reconstr.), convexity probably exaggerated, ×0.7 (4).

Order BURGESSIIDA Størmer, 1944

[*nom. correct.* STØRMER, herein (*pro* order Burgessida STØRMER, 1944)]

Carapace large subcircular, plate-shaped, with small sessile ?eyes and narrow labrum; postabdomen carrying long many-jointed telson; postoral cephalic appendages 3 to 4, of trilobitic type, with gill branch possibly reduced; trunk appendages of trilobitic (*Olenoides*) type; intestinal diverticulae well developed (4). *M.Cam.*

Family BURGESSIIDAE Walcott, 1912

[*nom. correct.* STØRMER, herein (*pro* Burgessidae WALCOTT, 1912)]

Body small, with trunk of 8 segments; walking legs with endites; intestinal diverticulae with single pair of basal branches. *M.Cam.*

Burgessia WALCOTT, 1912 [**B. bella*]. Characters of family and order. Burgess Sh., W.Can.(B.C.).——FIG. 21,*1-5*. **B. bella;* 21,*1,2,* dorsal and ventral sides, with one branch of appendages omitted on either side, ×4.5 (4); 21,*3,* trunk appendages (endites not indicated), ×7.5 (4); 21,*4,* intestinal diverticulae, ×4.5 (4); 21,*5,* dorsal side with intestinal diverticulae visible below carapace, ×3 (7).

Order WAPTIIDA Størmer, 1944

[*nom. correct.* STØRMER, herein (*pro* order Waptida STØRMER, 1944)]

Carapace laterally compressed, covering head, thorax, and part of ?preabdomen, with rostrum and pedunculate eyes; trunk lacking pleurae, postabdomen with 6 cylindrical segments; 1st antennae with comparatively long joints, cephalothoracic appendages little known, apparently trilobitic walking legs, preabdominal appendages filamentous, with jointed shaft (*Triarthrus* type); postabdomen with flat jointed cerci on distal segment (4). *M.Cam.*

Family WAPTIIDAE Walcott, 1912

[*nom. correct.* STØRMER, herein (*pro* Waptidae WALCOTT, 1912)]

Medium size, with thorax of 5 to 7 short segments, ?preabdomen with 5 to 7 segments. *M.Cam.*

Waptia WALCOTT, 1912 [**W. fieldensis*]. Characters of family and order. Burgess Sh., W.Can.(B.C.).——FIG. 21,*6-8*. **W. fieldensis;* 21,*6,* dorsal side (reconstr.), ×1.5 (4); 21,*7,8,* dorsal and lateral views, ×1.5 (7,8).

Subclass UNCERTAIN

Order OPABINIIDA Størmer, 1944

[*nom. correct.* STØRMER, herein (*pro* order Opabinida STØRMER, 1944)] [=Suborder Palaeanostraca HUTCHINSON, 1930; order Pseudanostraca RAYMOND, 1935 *(partim)*]

Body elongate, with small head bearing erectable frontal organ and pedunculate eyes; segmented trunk trilobate, with pleurae covering gill appendages of trilobitic type; postabdominal segment with telsonic plate (4). *M.Cam.*

Family OPABINIIDAE Walcott, 1912

[*nom. correct.* STØRMER, herein (*pro* Opabinidae WALCOTT, 1912)]

Body fairly large, narrowly elongate, with distinct trilobation; cephalon short and narrow, frontal organ long, with median canal and distal paired portion with spines; trilobitic cephalic limbs unknown; trunk with ?15 segments; postabdomen spatulate; trunk appendages trilobitic, consisting of gill branches of *Olenoides* type (7). *M.Cam.*

Opabinia WALCOTT, 1912 [**O. regalis*]. Characters of family and order. Burgess Sh., W.Can.(B.C.). [*Opabinia* generally has been regarded as belonging to the Branchiopoda division of the Anostraca (WALCOTT, 1912; FEDOTOV, 1924; HUTCHINSON,

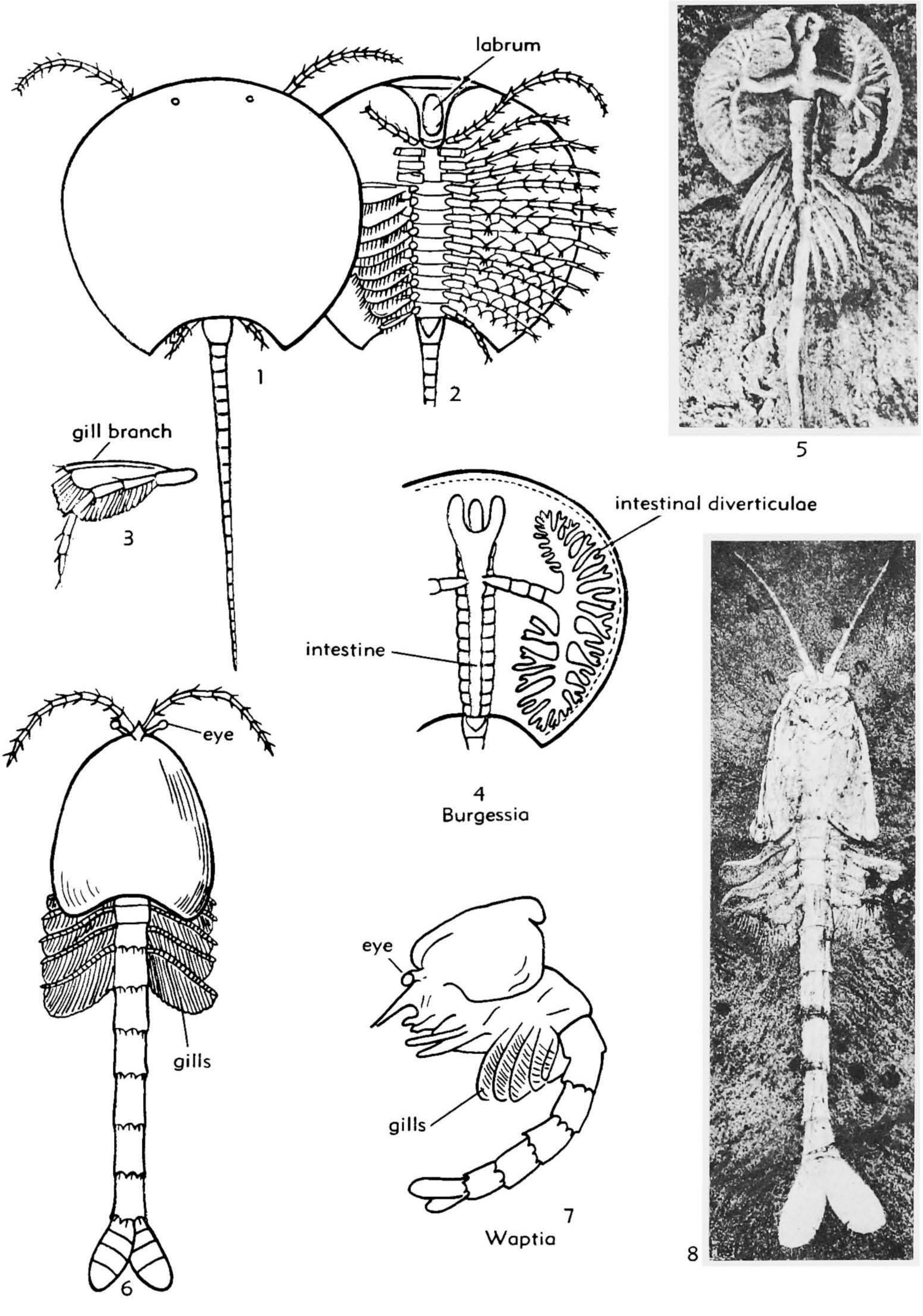

FIG. 21. *Burgessia* and *Waptia,* M.Cam., W.Can.(B.C.).——*1-5, B. bella* WALCOTT; *1,2,* dorsal and ventral sides, with one branch of appendages omitted on either side, ×4.5 (4); *3,* trunk appendages, with endites not shown, ×7.5 (4); *4,* intestinal diverticula, ×4.5 (4); *5,* dorsal side with intestinal diverticula visible below carapace, ×3 (7).——*6-8, W. fieldensis* WALCOTT; *6,* dorsal side (reconstr.), ×1.5 (4); *7,8,* lateral and dorsal views, ×1.5 (7, 8).

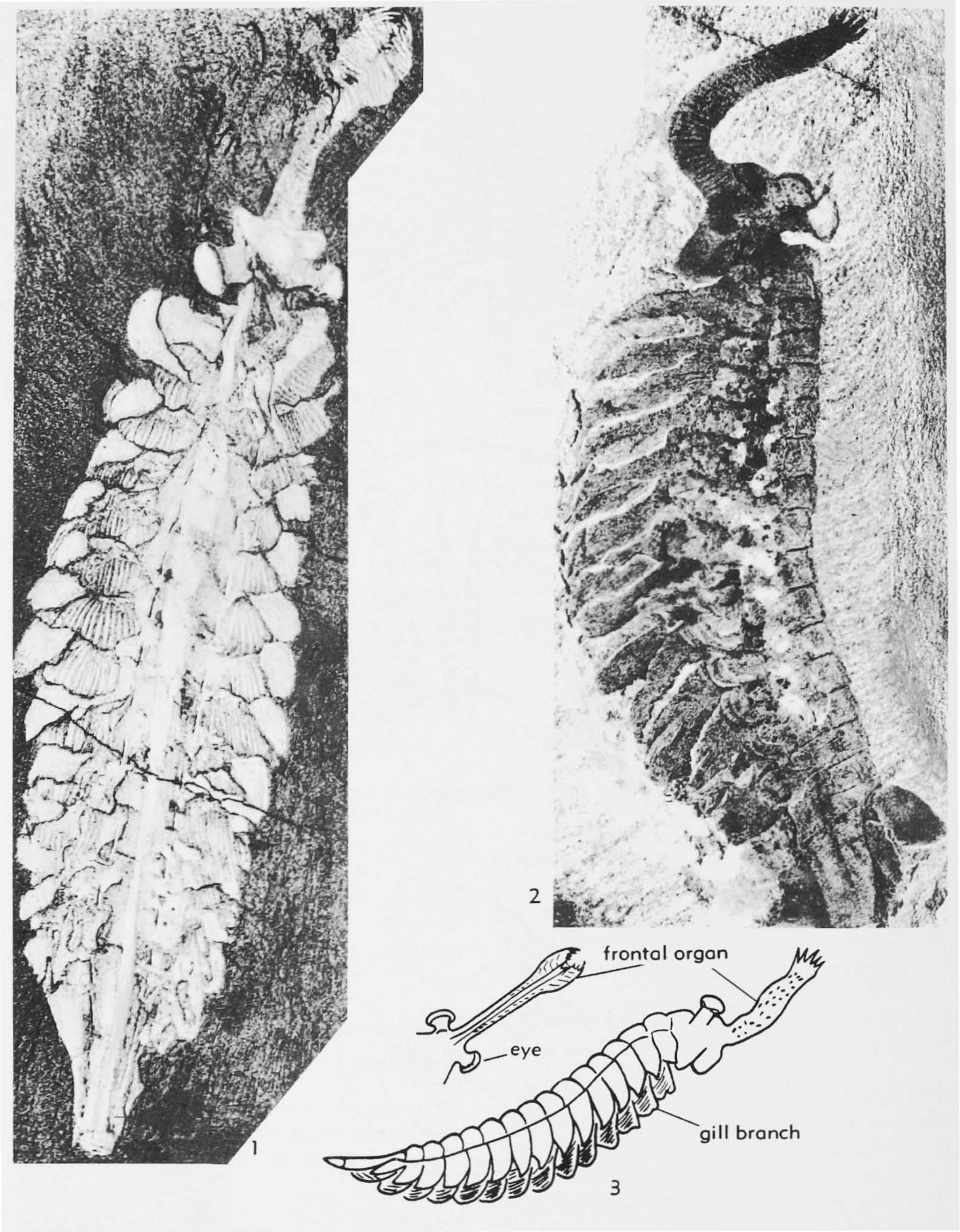

FIG. 22. *Opabinia regalis* WALCOTT, M.Cam., W.Can.(B.C.); *1,* dorsal side wtih exoskeleton of trunk removed, ×2.5 (7); *3,* dorsolateral and lateral views showing frontal organ (reconstr.), ×1 (7).

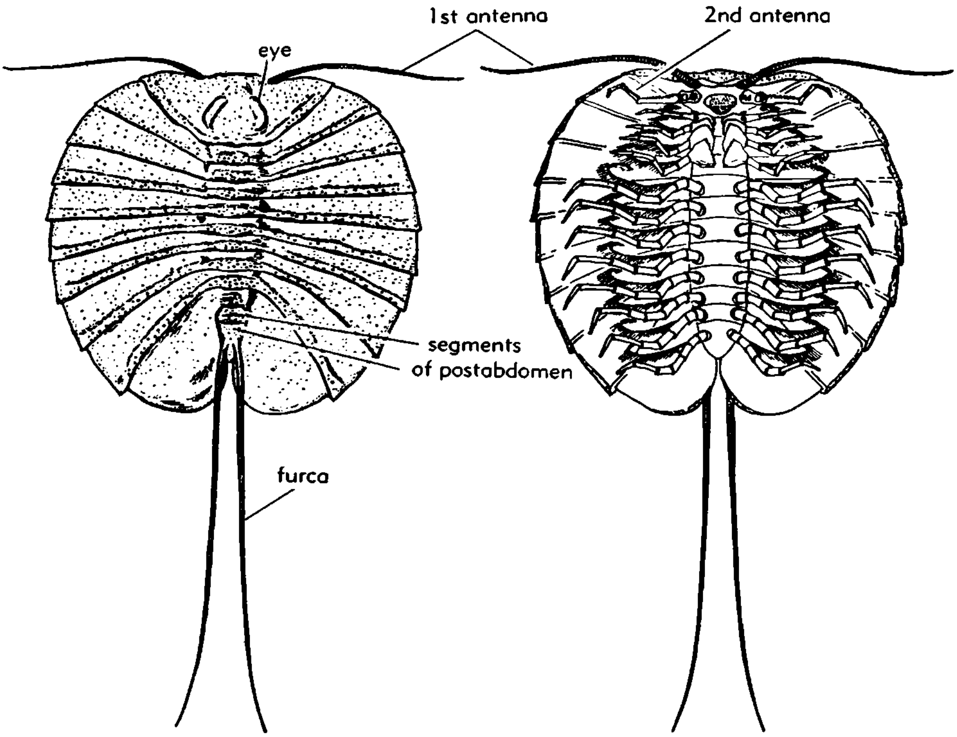

Fig. 23. *Cheloniellon calmani* Broili, L.Dev., Ger.; dorsal and ventral views (reconstr.), ×0.4 (7).

1930). Raymond (1935), however, placed it in a separate order (Pseudanostraca), interpreted as probably leading to the Anostraca. Since homology of the frontal organ with the fused and modified 2nd antennae in Anostraca is problematical and since trunk appendages are fundamentally different in the 2 forms, the taxonomic position of this genus remains an open question.]——Fig. 22. **O. regalis;* 22,*1*, dorsal side, exoskeleton of trunk removed, ×2.5; 22,*2*, dorsolateral view, axis less distinct, ×2.5; 22,*3*, lateral and dorsal views of frontal organ (reconstr.), ×1 (7).

Order CHELONIELLIDA Broili, 1933

[*nom. transl.* Størmer, herein (*ex* subclass Cheloniellida Broili, 1933)]

Body broad trilobate with short cephalon; trunk segmented, 1st segment double; narrow and short postabdomen with long furca; head short with lateral eyes and 2 pairs of antennae, trunk with trilobitic appendages, coxae of 4 first pairs enlarged. *L.Dev.*

Family CHELONIELLIDAE Broili, 1933

Body large, flat, subcircular, with narrow axis; head with centrally situated lateral eyes, ventral labrum or labium; 1st antennae uniramous, many-jointed, 2nd antennae uniramous, with 4 or 5 joints, basal one with pit suggesting aperture of ?gland; trunk with 9 radiating segments, of which 1st is double; postabdomen narrow, 2-segmented, with furca inserted between pleurae of last pre-abdominal segments; trunk appendages trilobitic, with walking legs and delicate gill branches, anterior 4 pairs of coxae enlarged, probably forming gnathites. *L.Dev.*

Cheloniellon Broili, 1932 [**C. calmani*]. Characters of family and order. Ger.——Fig. 23. **C. calmani;* dorsal and ventral sides (reconstr.), ×0.4 (7).

Subclass and Order UNCERTAIN

Family YOHOIIDAE Henriksen, 1928

[=Order Pseudanostraca Raymond, 1935 *(partim)*]

Body small, narrowly elongate; head subtriangular, with 4 transverse lobes on axis, possibly with pedunculate eyes and small rostrum; trunk with 12 segments, 8 anterior ones with short pleurae, 4 posterior ones cylindrical without pleurae; telson spatulate (cerci described by Walcott not demon-

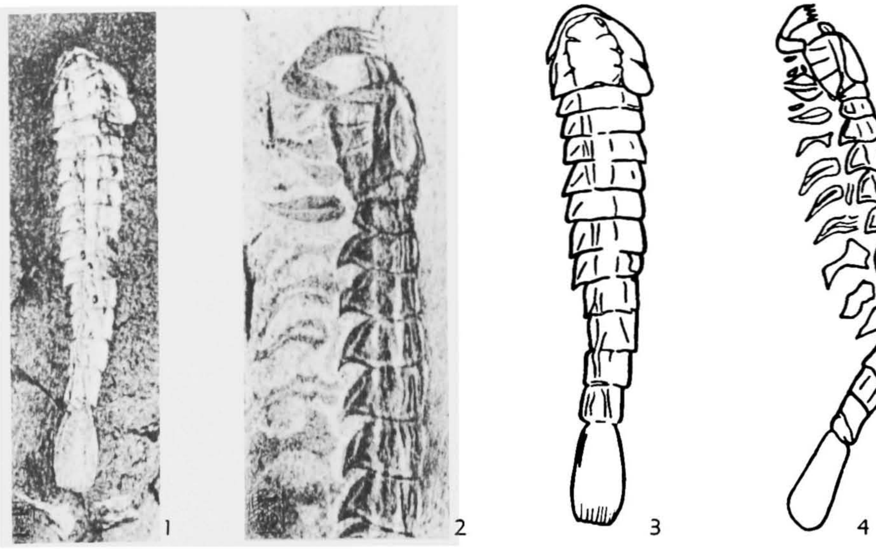

FIG. 24. *Yohoia tenuis* WALCOTT, M.Cam., W.Can.(B.C.); *1,3,* dorsal side, ×3, ×3.5 (7); *2,4,* lateral views, ×6, ×4 (7).

strated in illustrations of type species); appendages little known, indications of powerful cephalic limb with distal spines possibly representing 2nd antennae (or frontal organ similar to that of *Opabinia*), trunk appendages probably similar to gill branch of trilobitic appendages. *M.Cam.*

Yohoia WALCOTT, 1912 [**Y. tenuis*]. Characters of family (7). Burgess Sh., W.Can.(B.C.). [WALCOTT described *Y. plena* with bilobed telson or pair of flat cerci. This species may represent another genus, possibly little related to *Yohoia*. The small size of *Yohoia* suggests that it may represent a larval stage of *Opabinia* or a related form. Taxonomically, *Yohoia* may belong in intermediate position between Merostomoidea and the Pseudonotostraca.]——FIG. 24. **Y. tenuis;* dorsal side, ×3, ×3.5 (7); 24,*2,4,* lateral views, ×6, ×4 (7).

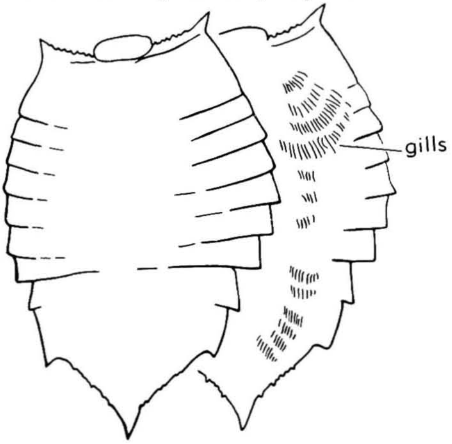

FIG. 25. *Helmetia expansa* WALCOTT, M.Cam., W. Can.(B.C.); dorsal side, with impressions of ventral gills at right, ×0.2 (8).

Family UNCERTAIN

Helmetia WALCOTT, 1917 [**H. expansa*]. Body large, flat, divided into cephalic shield, thorax, and pygidium, trilobation faintly suggested; cephalic

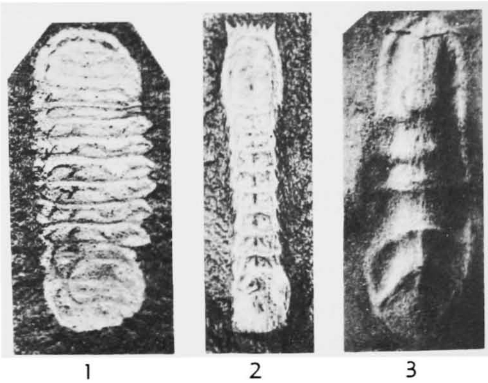

FIG. 26. Yohoiidae *(Mollisonia* and *Tontoia),* M. Cam.——*1, M. symmetrica* WALCOTT, W.Can. (B.C.), dorsal side, ×0.7 (7).——*2, M. gracilis* WALCOTT, W.Can.(B.C.), dorsal side, ×1.8 (7). ——*T. kwaguntensis* WALCOTT, Tonto Ss., SW. USA(Ariz.), dorsal side, ×0.7 (7).

shield trapezoid, with pointed anterolateral corners (median anterior lobe possibly representing displaced labrum); thorax with 6 segments; pygidium subtriangular, with 2 lateral and 1 median point; filamentous appendages probably of trilobitic type present in cephalic shield, thorax, and pygidium; antennae and walking legs unknown. *M.Cam.* (Burgess Sh.), W.Can.(B.C.).——FIG. 25. **H. expansa,* dorsal side with impressions of ventral gills at right, ×0.2 (8).

Mollisonia WALCOTT, 1912 [**M. symmetrica*]. Body small to medium in size, elongate, more or less narrow, divided into cephalic shield, thorax, and pygidium of equal width, trilobation faintly indicated; cephalic shield semicircular to elongate subovate, with 5 transverse lobes and marginal rim; thorax with narrow pleurae; pygidium subcircular, about equal to cephalic shield in size; appendages unknown (7). *M.Cam.* (Burgess Sh.), W.Can.(B.C.).——FIG. 26,*1*. **M. symmetrica;* dorsal side, ×0.7 (7).——FIG. 26,*2*. *M. gracilis* WALCOTT, dorsal side, ×1.8 (7).

Tontoia WALCOTT, 1912 [**T. kwaguntensis*]. Body small, elongate, with convex somewhat indistinct axis, divided into cephalic shield, thorax, and pygidium; cephalic shield elongate subovate, with marginal rim; thorax 4-segmented, with concave-posterior margin; pygidium smaller than cephalic shield, with rounded posterior margin; appendages unknown. [Since appendages are unknown in *Mollisonia* and *Tontoia,* the subclass and order to which they belong cannot be decided with certainty. The development of a cephalic shield, thorax, and pygidium indicates, however, that they belong to the Trilobitomorpha.] *M.Cam.,* SW. USA(N. Ariz.).——FIG. 26,*3*. **T. kwaguntensis,* Tonto Ss.; dorsal side, ×0.7 (7).

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TRILOBITA

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GENERAL DESCRIPTION OF TRILOBITA

By H. J. Harrington

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[1] Deceased 15 November 1956. [2] Deceased 5 January 1957.

INTRODUCTION

DEFINITION OF CLASS

The Trilobita are extinct Arthropoda distinguished by an exoskeleton that is trilobed longitudinally into axial and side regions and differentiated transversely into anterior, middle, and posterior areas. Tergites of the anterior and posterior areas are fused into rigid plates, whereas those of the middle area are movable upon each other, generally articulating freely. Compound eyes generally are present on the dorsal side of the head. Ventral appendages consist of an anterior pair of multijointed uniramous antennae and behind these a variable number of undifferentiated paired biramous appendages, 4 of which are cephalic, with a pair of appendages corresponding to each postcephalic somite. Caudal antenniform cerci occur in some forms. Respiration is by means of branchial fringes on the limbs called preepipodites. Ontogenetic development is marked by progressive metamorphoses proceeding from a free larva that shows only cephalic segments, although some authors claim the hindmost segment to be the anal.

OCCURRENCE

Trilobites are exclusively marine animals, remains of which are restricted to rocks of the Paleozoic Era. They first appeared in the Early Cambrian, already diversified in many families and genera, and attained maximum development in Late Cambrian time. They were still very numerous in the Ordovician but the Silurian witnessed the beginning of their decline, with disappearance of many "archaic" types. Still fairly abundant in the Devonian Period, where only a few families are represented, they dwindled rapidly during the late Paleozoic and completely disappeared by the close of Permian time.

Though they form a morphologically compact group, the trilobites diversified from the outset into different stocks which, during the 250-million-year life span of the class, gave rise to numerous genera and species. VOGDES, in 1923, estimated that about 450 genera and 3,970 species of trilobites had been described. Since then, the number of described forms has increased greatly, so that at present about 1,500 genera and a total of about 10,000 species are recognized.

DEVELOPMENT OF STUDIES

The first known descriptions and figures of trilobites were published by LHWYD in 1698, who called them Trinuclei. In 1745 LINNÉ described several species under the collective name of *Entomolithus paradoxus,* regarding them as a division of his Insecta (by modern standards, Arthropoda). The name Trilobitae was proposed by WALCH in 1771, and though WAHLENBERG (1821) preferred Entomostracites and DALMAN (1826) used Palaeades, WALCH's term (modified to "Trilobita"), alluding to the longitudinal trilobation of the exoskeleton, is now universally accepted.

The number of monographs dealing with description of trilobites is large, and during the last 130 years many paleontologists have added greatly to our knowledge of the class. Pioneers in the description of these fossils are BRONGNIART (1822), DALMAN (1827), GREEN (1832), EMMRICH (1839), MILNE EDWARDS (1840), BURMEISTER (1843), GOLDFUSS (1843), BEYRICH (1846), HAWLE & CORDA (1847), and M'COY (1849). Since the middle 1800's fundamental monographs have been published on trilobites of various regions: (1) Bohemia by BARRANDE, NOVÁK, and PRANTL & PŘIBYL; (2) Germany by

Gürich, Pompeckj, and Rudolf & Emma Richter; (3) Scandinavia by Angelin, Brøgger, Warburg, Størmer, and Westergård; (4) Baltic region of Russia by Nieszkowski, Eichwald, Schmidt, Öpik, and Lermontova; (5) Great Britain by Salter, Woodward, Hicks, Reed, Cobbold, and Lake; (6) France by Rouault, Oehlert, Bergeron, Barrois, and Thoral; (7) Italy by Meneghini; (8) North America by Hall, Ford, Clarke, Billings, Matthew, Beecher, Walcott, Resser, Rasetti, Raymond, Whittington, and Poulsen (Greenland); (9) South America by Kayser, Clarke, Kozlowski, Knod, Ulrich, Kobayashi, and Harrington & Leanza; (10) Asia by Lorenz, Mansuy, Walcott, Resser, Endo, Reed, Kobayashi, and Sun; (11) Africa by Salter and Hupé; and (12) Australia by Whitehouse.

Up to 1870 only the hard exoskeleton of trilobites was known, and the zoological position of these organisms remained a matter of considerable uncertainty. They were variously regarded as related to quite different groups of Arthropoda, such as the Xiphosura, Branchiopoda, and Isopoda, and even to the Mollusca (Amphineura).

The ventral appendages were first described by Billings in 1870 from North American Ordovician specimens of *Isotelus.* Between 1895 and 1920, excellently preserved specimens of several Cambrian and Ordovician species, showing all ventral appendages, were described by Beecher, Walcott, and Raymond, and in 1930 Broili described those of 2 species from Lower Devonian rocks. In recent years, our understanding of the trilobite appendages has greatly increased, thanks largely to Størmer's outstanding investigations.

Trilobite larvae were first described by Barrande (1852) and the name "protaspis" was given by Beecher (1895) to the initial larval stage. The postembryonic development of some 50 species now is known, although only a few complete series of larval stages have been described.

MODE OF PRESERVATION

Trilobites are found in different types of marine sediments either (1) with their mineralized exoskeleton preserved, or (2) as external or internal molds. Fossils consisting of preserved hard parts may show little or no change in composition of the original exoskeleton, or alternatively, the substance of the exoskeleton may be replaced partly or wholly by silica, pyrite, or other mineral substances.

Complete specimens of trilobites are found frequently, either outstretched or enrolled, but commonly the remains consist of detached parts of the exoskeleton. These may represent exuviae shed during molting or the disarticulated parts of exoskeletons which became disjointed after death of the animals.

Exceptonally well-preserved complete specimens, with their fragile ventral appendages preserved, have been found both in black shales and in extremely fine-grained limestones. During recent years our knowledge of minute details of the exoskeleton of many species has grown through study of silicified specimens found in limestones, which can be completely detached from the matrix by dissolving away the limestone with hydrochloric, formic, or other acids.

MORPHOLOGY OF EXOSKELETON

SHAPE AND SIZE

Trilobites are typically ovoid to subelliptical in outline when seen in dorsal view, but this basic shape may be substantially modified in progressive and aberrant genera *(Deiphon, Ceratarges, Odontopleura).* The exoskeleton is usually moderately convex but in some *(Dionide)* it is almost flat, whereas in other *(Leiagnostus)* it is highly arched or globose.

The average length of trilobites ranges from 3 to 10 cm. Minute forms, however, are numerous, entire families (Shumardiidae, Eodiscidae) and even orders (Agnostida) being characterized by very small size. Some species of *Shumardia* are less than 5 mm. long, and many Agnostida measure less than 6 mm. The Eodiscidae are usually about 12 to 15 mm. long. Among the Agnostida, a species measuring 25 mm. in length is regarded as huge.

Truly gigantic forms, measuring more than 20 cm. in length, are scarce and restricted to a very few families. Outstanding examples are *Paradoxides harlani* (45 cm.), Paradoxididae, of Middle Cambrian age; *Megistaspis heros* (36 cm.), *Isotelus gigas* (44 cm.), and *Thysanopyge argentina* (45 cm.), all Asaphidae, of Ordovician age; *Illaenus giganteus* (40 cm.), Illaenidae, of Ordovician age; *Arctinurus boltoni* (30 cm.) and *Terataspis grandis* (60 cm.), Lichidae, from the Ordovician and Devonian, respectively; *Trimerus major* (38 cm.), Homalonotidae, of Devonian age; and *Coronura myrmecophora* (40 cm.), Dalmanitidae, of Devonian age. The largest known trilobite is *Uralichas riberoi* (70 cm.), a lichid from Ordovician rocks of Portugal. The measurements given, representing recorded maxima, do not take account of appendages such as antennae and possibly caudal rami that projected beyond the front and rear margins of the exoskeleton.

ORIENTATION

Orientation of trilobites is self-evident, with exception of the Agnostina. In these small blind trilobites, having only 2 thoracic segments separating 2 subequal "shields," it is difficult to decide, on purely morphological grounds, which is the front and which is the rear part of the animal. Only 2 morphological features of the Agnostina furnish some indications in this regard but, unfortunately, they provide contradictory evidence. One is the direction of curvature of thoracic pleural extremities, and the other is the direction of paired marginal spines commonly carried by one of the "shields." These 2 directions are opposite. Since the earliest descriptions of agnostid trilobites, virtually all authors have accepted the conclusion that the marginal spines are carried by the "tail shield" and that, therefore, the spines are directed backward as posterolateral projections of the margin. RAYMOND, however, was an exception. Reasoning that in the Agnostina, as in all other trilobites, the pleural extremities should curve backward, he oriented the agnostid dorsal exoskeleton accordingly, regarding as rear extremity what all other authors consider to be the anterior end. He overlooked, however, the fact that the ontogenetic development of the Agnostina, as described by BARRANDE as far back as 1852 for several Bohemian species, is opposed to this interpretation. If RAYMOND's views on orientation were to be accepted, this would imply admitting that the agnostids differ from all other known Arthropoda in the manner in which new thoracic segments are developed in the successive larval stages (see "Ontogeny of Trilobita"). Accordingly, the accepted orientation of these trilobites is such that when the animal faces forward, the pleural extremities also curve forward, the marginal spines (if present) being carried by the "tail shield" as backwardly directed projections of the posterolateral margins.

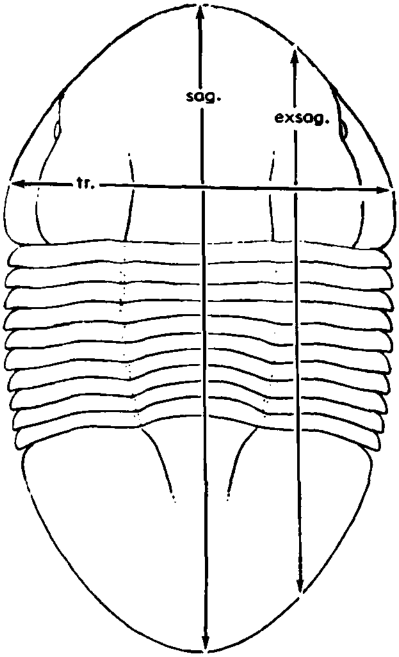

FIG. 27. Orientation of trilobite exoskeleton. *Ectillaenus katzeri* (BARRANDE) JAANUSSON, U.Ord., Boh., ×1 (*sag.*, sagittal line; *exsag.*, exsagittal line; *tr.*, transverse line) (79, 1954).

For the purpose of describing without ambiguity the length and width of trilobite parts, the descriptions are referred to the longitudinal and transverse directions of the whole animal (Fig. 27). Longitudinal measurements, however, can be taken either along the axial (sagittal) line of the body (abbreviated "*sag.*"), or along lines running parallel to it on either side and, therefore, "exsagittal" in position (abbreviated "*exsag.*"). When a given part, such as an axial ring or occipital ring, is said to be "wide *(sag.)*," the meaning is that its width has been measured along the sagittal line of the body. When "*exsag.*" is used, as in referring to width of a pleural segment, this means that the measurement has been taken along an "exsagittal line," namely, along a line running parallel to the sagittal line on either side of the body. Transverse measurements (abbreviated "*tr.*") are always taken along lines transverse to the whole body.

For the purpose of describing directions away from or toward the line of symmetry of the body, the terms **abaxial** and **adaxial** are used, respectively, in preference to the ambiguous expressions "outer" and "inner." **Distal** and **proximal** are used almost in the same sense.

Ventral and **dorsal** are self-explanatory terms, but in description of exoskeletal parts of trilobites, the injudicious use of these terms may lead to confusion. The name "dorsal exoskeleton," for instance, is applied by some paleontologists to that part of the mineralized exoskeleton which other authors prefer to call "carapace." As the "dorsal exoskeleton" has a discrete thickness, it obviously has a dorsal or external, and a ventral or internal surface. Moreover, the so-called dorsal exoskeleton is not wholly dorsal in position, having a reflected rim (doublure) extending onto the ventral side of the animal. Clearly, the downwardly facing ventral side of the doublure is also its external surface, conditions being exactly the opposite to those obtaining in the truly dorsal part of the "dorsal exoskeleton." This may lead to descriptive expressions such as "dorsal side of the ventral extension of the dorsal exoskeleton" which, though perfectly correct, should be avoided as confusing, its far simpler equivalent "internal surface of the doublure of the carapace" being preferable. The term "dorsal exoskeleton" is not fortunate, since its reflected doublure is ventral in position. This would not be too objectionable if the doublure invariably were a very narrow rim, but in many trilobites it is actually a broad band extending a considerable distance adaxially. In some Illaenidae, for instance, the pygidial doublure covers more than 0.7 of the ventral side of the pygidial region. For these reasons, the term "carapace," despite its different connotation in crustacean morphology, is preferred to "dorsal exoskeleton" by some authors, including me.

STRUCTURAL ELEMENTS

The exoskeleton of trilobites consists both of hard mineralized integument and comparatively soft chitinous parts. The mineralized integument covered the dorsal side of the body and parts of its ventral side, whereas the nonmineralized chitinous integument covered the ventral appendages. The remainder of the ventral side of the body was covered by a soft membrane. Most trilobites were capable of enrollment, and thus the vulnerable ventral side could be protected.

The chitinous covering of the appendages is very rarely preserved, all that usually remains of the trilobites being the hard mineralized exoskeleton that covered the dorsal side of the body and certain areas of the ventral side.

The **carapace (dorsal exoskeleton)** consists of the separate or fused areas of mineralized integument **(sclerites)** covering successive body segments. Each individual covering of this sort is a **tergite**. The tergites are longitudinally trilobed into an axial region (mesotergite) and 2 side regions (pleurotergites), which should be regarded as lateral extensions of the axial portion. The anterior tergites and their lateral extensions are fused together into a single rigid tagma, called the **cephalon.** Similarly, the posterior tergites normally are fused into a single plate called the **pygidium.** The part of the carapace interposed between cephalon and pygidium is termed **thorax,** being formed of individual tergites that are movable upon each other, articulating along their axial portions (Fig. 28).

Ventral sclerites, consisting of separate areas of mineralized integument **(sternites),** are restricted to the cephalic region. Trilobites have a maximum of 3 such sternites, which are known as **rostral plate, hypostoma,** and **metastoma,** the first 2 being preoral and the last postoral in position.

The external surface of the trilobite exoskeleton is usually smooth, but it may be sculptured by pits, granulations, tubercles, radial crests, and "terrace lines." The terrace lines, running subparallel to the margins of the exoskeleton and usually arranged in a Bertillon pattern, seem to represent

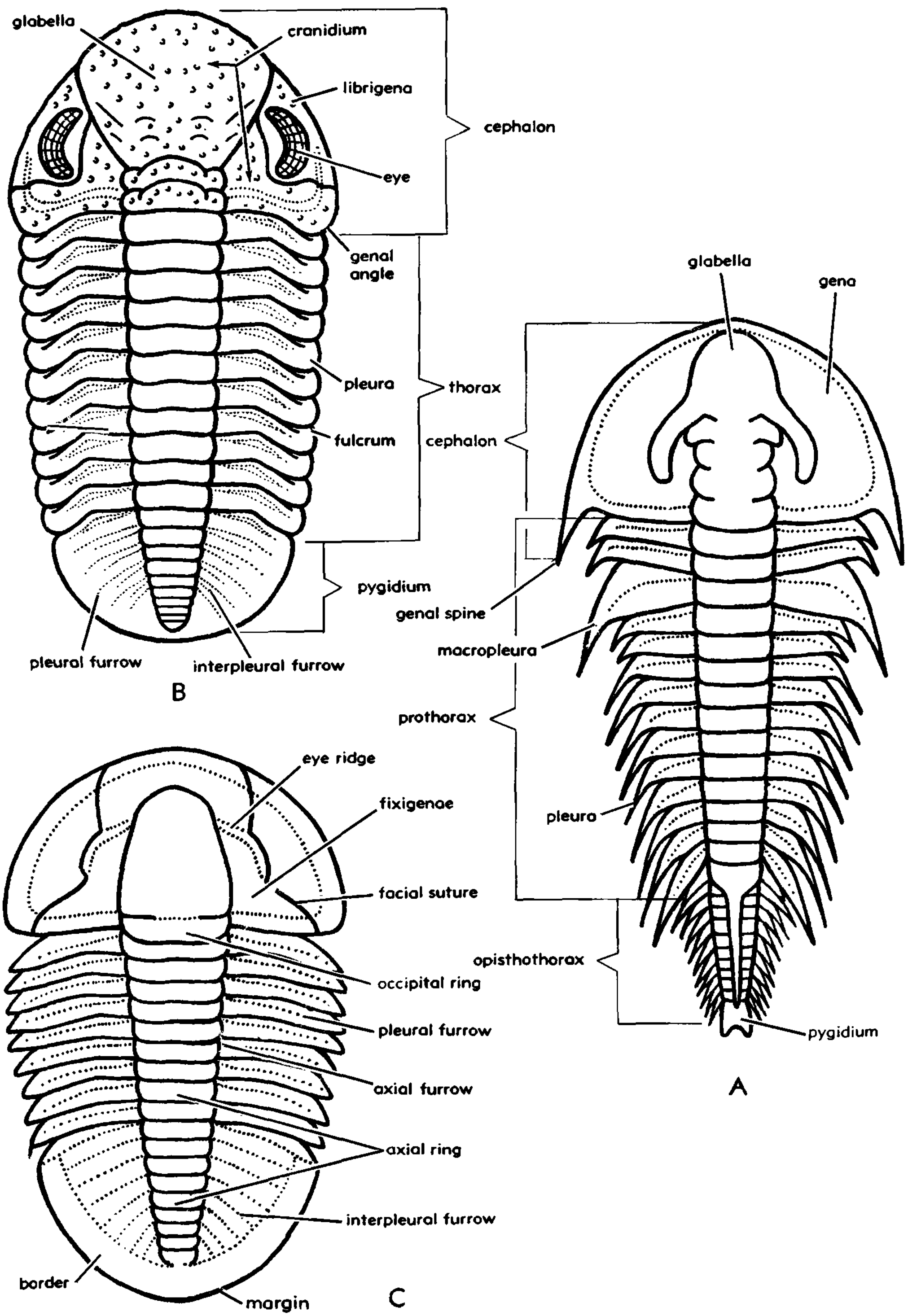

Fig. 28. Nomenclature of exoskeleton.——*A. Olenellus vermontanus* (Hall) Hall, L.Cam., USA(Vermont), ×1 (64).——*B. Phacops fecundus* Barrande, Dev., Bohemia, ×1 (2).——*C. Asaphiscus wheeleri* Meek, U.Cam., USA(Utah), ×1 (488).

folds of the integument comparable to those seen in living Arthropoda (Schulze, 1937). The granulations and tubercles may be perforated, as in some Calymenidae and Cheiruridae (noted in description of integumentary sensory organs).

CEPHALIC REGION

The term "cephalon" is properly applied to the rigid plate formed of fused anterior tergites of the trilobite exoskeleton.[1] However, the term is sometimes loosely extended to embrace the internal organs, appendages, and other parts located beneath the exoskeletal covering or "cephalon proper." This is a case of the name of a part being extended to designate the whole, being strictly comparable to the incorrect use of "skull" or "cranium" to designate the head of mammals, birds, and other vertebrates. To avoid confusion it is preferable to use different terms to designate the ensemble of fused anterior somites and the ensemble of their fused exoskeletal coverings.

The name **cephalic region** is here specifically applied to that area of the trilobite body formed by fusion of several anterior somites. The term embraces, by definition, the dorsal and ventral integuments (mineralized or not), internal organs, and ventral appendages borne by the somites. The term **cephalon** is here restricted, following common usage, to the rigid tagma formed of fused tergites of the cephalic region. It should be apparent that though the rostral plate, hypostoma, and metastoma are parts of the cephalic region, they are not parts of the cephalon.

The cephalon, being formed of fused tergites, is essentially dorsal in position, but it extends ventrally into a more or less wide reflected rim or **doublure.** Typically, it is semielliptical in outline, but considerable departure from this basic shape is seen frequently. In some Agnostida the cephalic outline is almost circular, whereas in other trilobites it may be semicircular, crescentic, subtrapezoidal, or subtriangular (Fig. 29). The size of the cephalon varies considerably in relation to that of the thorax and pygidium. Usually the cephalon is shorter than

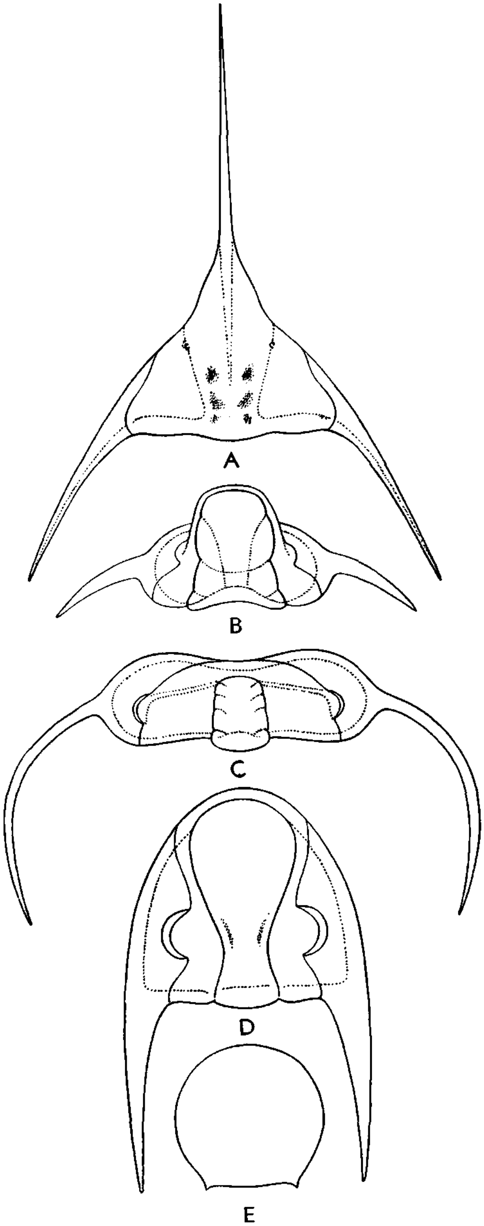

Fig. 29. Different cephalic shapes among trilobites.——*A. Lonchodomas rostratus* (Sars) Angelin, L. Ord., Norway, ×2.65 (reconstr. from 99, 1950).——*B. Dicranopeltis scabra* (Beyrich), Ord., Bohemia, ×0.65 (after 2).——*C. Eurycare latum* (Boeck) Angelin, U.Cam., Swed., ×4 (after 97, 1922),——*D. Phillipsinella parabola* (Barrande) Novák, U.Ord., Scot., ×4 (after 99, 1950).——*E. Ciceragnostus iruyensis* (Kayser) Harrington & Leanza, L.Ord., Arg., ×4.8 (after 19).

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[1] Noting that the rostral plate is commonly (though not invariably) part of the cephalic doublure and that the hypostoma almost universally is joined by suture or fusion to the rostral plate (as subsequently described), C. J. Stubblefield holds that these ventrally placed skeletal elements are correctly classed as parts of the cephalon.—R.C.M.

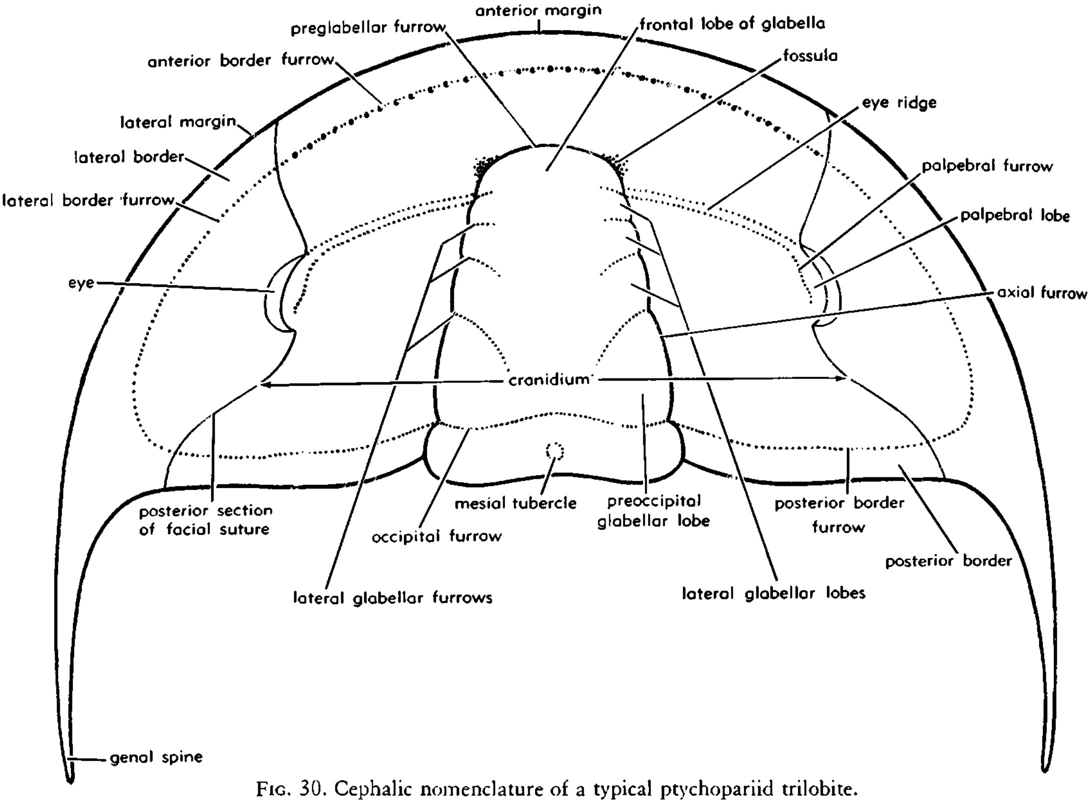


FIG. 30. Cephalic nomenclature of a typical ptychopariid trilobite.

the thorax and longer than the pygidium, but in many genera cephalon and pygidium are of about equal size.

The cephalon is usually convex both longitudinally and transversely. The convexity ranges from very slight *(Dionide)* to exceptionally great *(Deiphon, Sphaerexochus)*.

Longitudinal trilobation of the cephalon gives rise to an axial raised region **(glabella** and **occipital ring)** and 2 lateral **(genal)** regions which carry the compound eyes, if present. In some so-called smooth trilobites *(Leiagnostus, Illaenus)* the trilobation is obsolete and the cephalon then appears as a single evenly convex structure. In the great majority of trilobites, the cephalon is transected by paired facial sutures that separate a middle portion **(cranidium)** from 2 side regions (**librigenae,** "free cheeks"), which carry the visual surface of the eyes (Fig. 30).

GLABELLA

Typically, the glabella forms a distinctly raised area along the axis of the cephalon, being bounded laterally by **axial furrows.** These usually converge forward and grade into a transverse **preglabellar furrow** that bounds the anterior extremity of the glabella. In some genera, a pair of anterior pits **(fossulae)** are developed at the bottom of the axial furrows close to the anterolateral corners of the glabella. In "smooth" trilobites the axial and preglabellar furrows may be very shallow and indistinct. In extremely modified forms they disappear entirely, the glabella being then undifferentiated from the rest of the cephalon. The glabella is bounded posteriorly by the **occipital furrow,** which separates it from the **occipital ring.** In some trilobites *(Illaenus, Ectillaenus, Stenopareia, Dysplanus)* the occipital furrow is obsolete, the occipital ring coalescing with the glabella proper (Fig. 27).

Size, shape, and convexity of the glabella are highly variable. In some genera, the glabella is moderately convex, usually extending along the posterior 0.7 of the cephalon. In progressive genera it may become inflated or globose and very large, even extending for a considerable distance beyond the anterior margin of the cephalon *(Lon-*

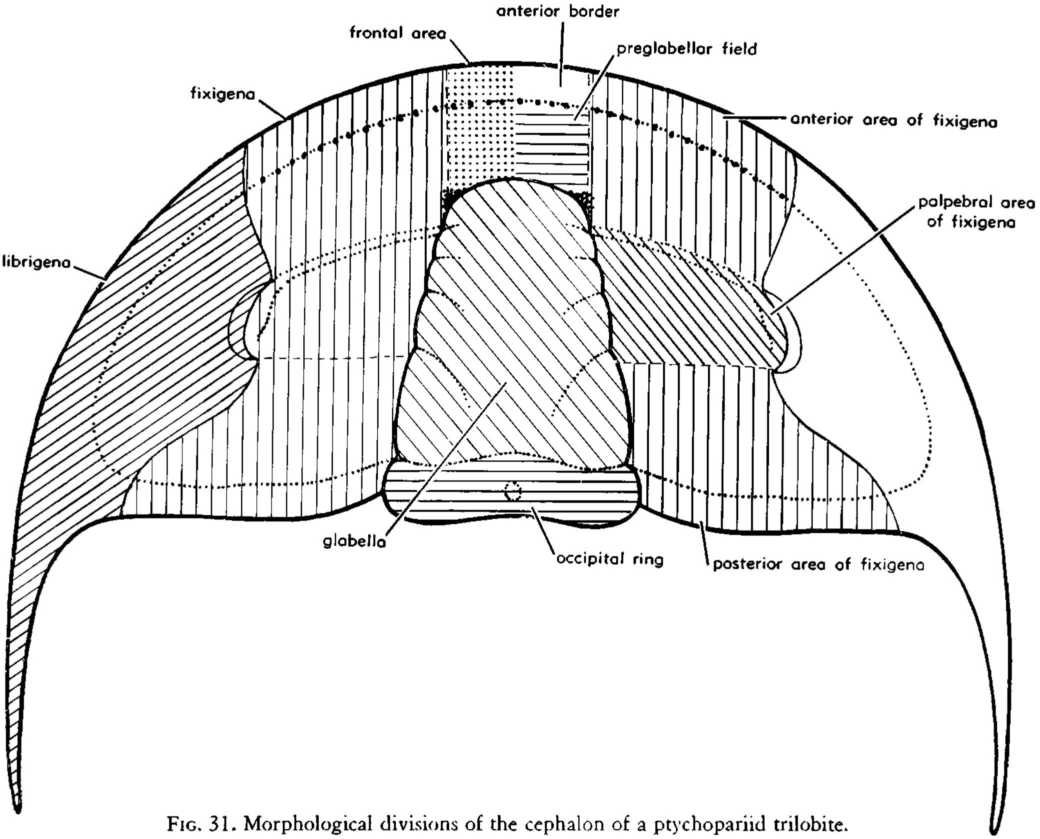


FIG. 31. Morphological divisions of the cephalon of a ptychopariid trilobite.

chodomas, Fig. 29*A; Raphiophorus,* Fig. 32*R*). The shapes of glabellae are commonly diagnostic characters of different genera (Fig. 32).

The glabella usually retains traces of the original cephalic segmentation. This is evidenced by paired **lateral glabellar furrows** which may vary in different genera from 5 pairs to a single pair (Fig. 33). In many trilobites, however, the glabella lacks furrows, being completely smooth. The lateral glabellar furrows may or may not reach the axial furrows. Their direction varies from inward-forward to inward-backward and their adaxial extremities may unite across the glabella so that a pair of furrows may form a single **transglabellar furrow.** For purposes of description, the lateral glabellar furrows are numbered by some paleontologists from front to back. When only 3 pairs are present they are termed anterior, middle, and preoccipital (or posterior). An alternative method is to number the furrows from back to front, in which case the preoccipital furrows are termed *1p* (1st from the posterior extremity of the glabella), the next forward pair are designated as *2p,* and so on to the foremost furrows.

In some genera *(Parabolinella)* the preoccipital furrows may bifurcate at their abaxial extremities, whereas in others *(Hedinaspis, Hypermecaspis)* an intercalary pair may be present between the occipital and preoccipital furrows.

The paired side portions of the glabella between successive lateral glabellar furrows are called **lateral glabellar lobes.** They are numbered either from front to back or from back to front, much as the lateral glabellar furrows; using the latter method, *1p* corresponds to the preoccipital lobes. The portion of the glabella between the preglabellar furrow and the 1st (anterior) pair of lateral glabellar furrows is called **frontal glabellar lobe.** This may be continued backward along the axial line of the glabella into a **central area** delimited by the adaxial extremities of the lateral furrows. When frontal lobe and central area are confluent, they form a **frontomedian lobe.** In some special-

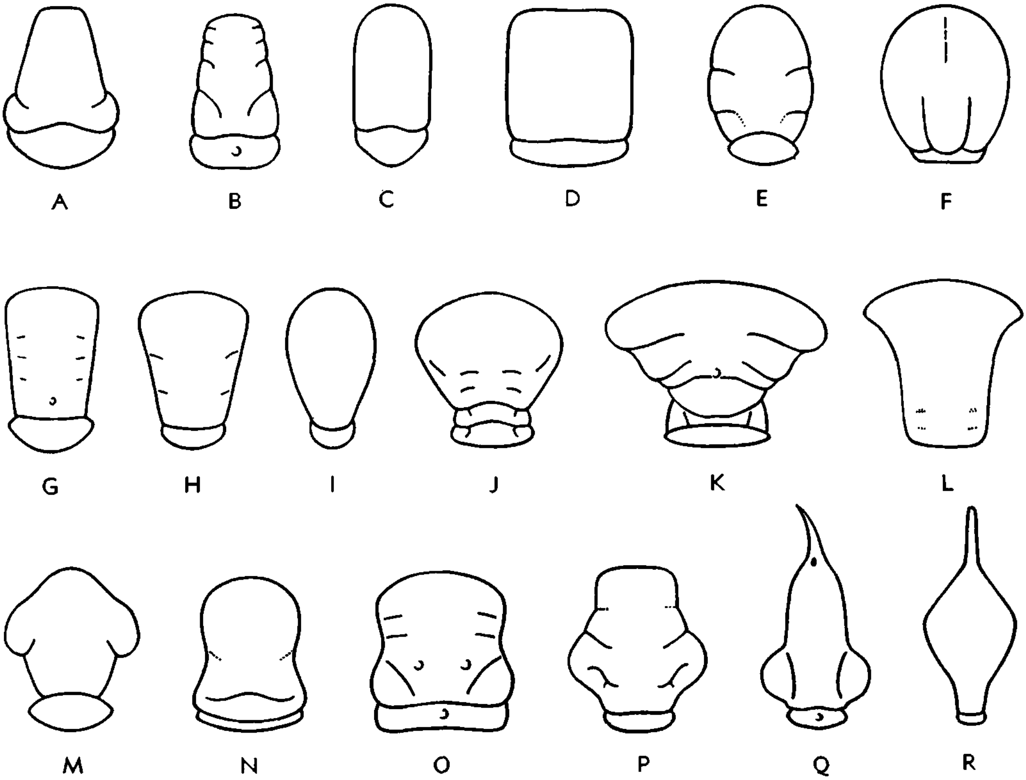


FIG. 32. Different outlines of trilobite glabellae and occipital lobes.——*A,B.* Tapering forward; *A,* truncate anteriorly *(Harpides); B,* rounded anteriorly *(Ptychoparia).*——*C.* Parallel-sided, rounded anteriorly *(Brassicicephalus).*——*D.* Subquadrate *(Lloydia).*——*E,F.* Elliptical; *E, Isocolus; F, Seleneceme.*——*G,H.* Evenly expanded forward, axial furrows straight; *G, Ceratopyge; T, Theamataspis.*——*I.* Pyriform *(Famatinolithus).*——*J-M.* Expanded forward; *J, Phacops; K, Scutellum; L, Illaenopsis; M, Shumardia.*——*N,O.* Contracted at middle; *N, Birmanites; O, Phaetonellus.*——*P,Q.* Bell-shaped; *P, Apatokephalus; Q, Teratorhynchus.*——*R.* Rhomboidal *(Raphiophorus).* (All diagrammatic, not to scale.)

ized genera (Lichidae, Odontopleuridae) the anterior lateral glabellar furrows are continued backward in longitudinal furrows more or less parallel to the axial furrows. Coincidently, one or more of the lateral glabellar furrows may disappear, causing the lateral glabellar lobes to coalesce so as to form bicomposite and tricomposite glabellar lobes (Fig. 34).

The frontal glabellar lobe may carry a **mesial spine,** usually directed forward *(Lonchodomas)* or upward-forward *(Paracalmonia).* In some trilobites *(Telephina bicornis,* Fig. 37*D*) paired glabellar spines are developed. In many forms (Asaphidae, Ceratopygidae), the central area of the glabella bears a small **mesial node** that usually is located near the occipital furrow.

The paired preoccipital glabellar lobes may become a single preoccipital lobe when the preoccipital furrow becomes transglabellar. In some genera (*Ditomopyge,* Fig. 35*A*) the preoccipital lobe is longitudinally trisected into a median preoccipital and 2 lateral preoccipital lobes, whereas in others (*Schizoproetus,* Fig. 35*B*) a pair of small triangular lateral lobes may be developed close to the posterolateral corners of the glabella. These are termed **basal glabellar lobes.** In the Agnostida (Fig. 35*C*), which lack a differentiated occipital ring, the basal lobes reach the posterior margin of the cephalon.

OCCIPITAL RING

In most trilobites the rear part of the cephalic axis is differentiated into a distinct

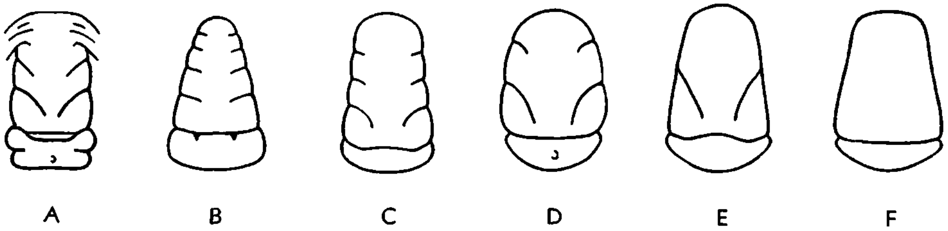


FIG. 33. Glabellar segmentation in different genera, showing decreasing number of lateral glabellar furrows from 5 pairs to none. *A, Fallotaspis; B, Daguinaspis; C, Latiredlichia; D, Talbotina; E, Elrathiella; F, Plethopeltis.*

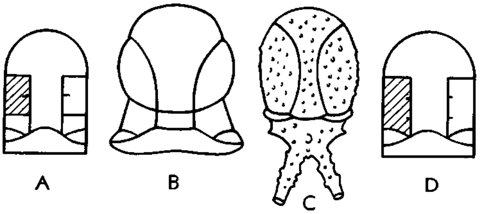


FIG. 34. Composite lateral glabellar lobes in the Lichidae.——*A,B.* Bicomposite lobes *(Dicranopeltis)*; shaded area in schematic interpretation *(A)* represents bicomposite lateral lobe resulting from fusion of 1st *(4p)* and 2nd *(3p)* lateral glabellar lobes.——*C,D.* Tricomposite lobes *(Hoplolichas)*; shaded area in schematic interpretation *(D)* represents tricomposite lateral lobe resulting from fusion of 1st *(4p)*, 2nd *(3p)*, and 3rd *(2p)* lateral glabellar lobes.

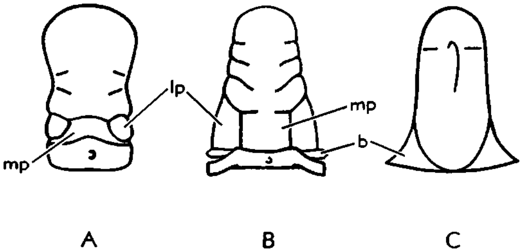


FIG. 35. Preoccipital and basal glabellar lobes. *A, Ditomopyge; B, Schizoproetus; C, Geragnostus.* (Explanation: *bl*, basal lobes; *mp*, median preoccipital lobes; *lp*, lateral preoccipital lobes).

area called **occipital ring,** separated from the posterior extremity of the glabella by the occipital furrow. In many species, however, the furrow may be shallow and indistinct, disconnected at the middle or even effaced completely, in which condition (Illaenidae, Fig. 27) an occipital ring is not distinguished.

The occipital ring may be smooth or more or less trisected into a middle and 2 side portions *(Hypermecaspis)*. It may carry mesial or paired tubercles or spines and, in some genera *(Pagetia)*, the whole ring may be drawn into a stout spine. In *Fallotaspis* (Fig. 45*J*) and some other forms, the ring may be more or less subdivided into anterior and posterior bands by short lateral intra-occipital furrows directed more or less at right angles to the sagittal line of the cephalon.

FRONTAL AREA

In most Cambrian trilobites and in many later genera, the glabella does not extend to the anterior margin of the cephalon but ends in a depressed region called **frontal area.** The lateral and posterior boundaries of the frontal area are not always easy to define. In most Cambrian trilobites having a comparatively short glabella, submedian to subanterior eyes, and well-developed eye ridges, there is usually no difficulty in delineating the frontal-area boundaries. The area is bounded laterally by anterior sections of the facial sutures and posteriorly by the eye ridges (facial sutures and eye ridges described in subsequent paragraphs), or, if these are absent, by imaginary lines connecting the anterolateral corners of the glabella with the anterior extremities of the raised areas called **palpebral lobes.** In many other trilobites, particularly in those possessing a long glabella, submedian to posterior eyes, and no eye ridges, the boundaries are difficult to define. In these the frontal area is reduced to the part of the cranidium directly in front of the preglabellar furrow and bounded laterally by imaginary lines parallel to the cephalic axis extending from the anterolateral corners of the glabella to the anterior margin. Sides of the cranidium lying between these imaginary lines and anterior sections of the facial sutures and situated in front of the anterior extremities of the palpebral lobes must be regarded as parts of the lateral areas of the cranidium called fixigenae. In trilobites devoid of facial sutures, such as the agnostids and olenellids, the frontal area is also reduced to the cephalic portion lying directly in front of the glabella between the preglabellar furrow and anterior margin.

In trilobites having an anterior border furrow, the frontal area is subdivided into a **preglabellar field,** between the preglabellar and anterior border furrows, and an **anterior cephalic border,** between the border furrow and cephalic margin. Typically, the preglabellar field is depressed and flat, but in some genera it may be strongly curved forward-downward, globose, or concave. The width *(sag.)* of the preglabellar field ranges from very wide to quite narrow. In many trilobites it is wholly absent, the preglabellar furrow becoming part of the anterior border furrow.

The preglabellar field may be transected by a mesial longitudinal ridge or furrow. In some genera it is crossed by raised radiating ridges that bifurcate and anastomose more or less irregularly.

The anterior border furrow may bear a row of small pits *(Kainella, Angelina).* The anterior cephalic border may be flat and depressed or raised and wirelike. It may be either wider or narrower than the preglabellar field. In some trilobites it is produced into a median process, which may bifurcate or trifurcate, or may be developed as a mesial spine that is actually a projection of both the border and ventral doublure. Also, the border may bear a row of small spines.

FIXIGENAE

In trilobites devoid of facial sutures (agnostids, olenellids) side portions of the cephalon, comprising areas between the glabella and the lateral and posterior cephalic margins, are called **genal regions.** If facial sutures are present, the genal regions are subdivided into fixigenae and librigenae. The **fixigenae** ("fixed cheeks") are the lateral parts of the cranidium lying between the glabella, facial sutures, and posterior cephalic margin. Their anterior boundaries in some forms are rather ill defined.

Three areas may be distinguished in each fixigena: (1) anterior, in front of the palpebral lobe; (2) palpebral, between the abaxial edge of the palpebral lobe and the glabella; and (3) posterior, from the palpebral lobe to the posterior margin of the cranidium. The posterior areas may be very small and triangular *(Kainella),* long *(tr.)* and narrow *(exsag.) (Hungaia),* or wide *(tr.)* and large, as in most trilobites classed as proparian. The posterior border of the fixigenae is usually differentiated by a posterior border furrow. The posterior border and ventral doublure may be produced at some point between the axial furrows and posterolateral corners of the genae into paired spines termed metafixigenal, or into a row of small spines. Spines developed at the posterolateral angles of the cephalon are called genal spines.

PALPEBRAL LOBES

The palpebral lobes are lateral extensions of the abaxial edge of the palpebral areas of the fixigenae that may rise obliquely or even vertically above the main fixigenal surface. Their abaxial margin, separated from the visual surface of the eye by the facial suture, may have semicircular, semielliptical, or crescentic outline. The palpebral lobes may be marked off distinctly from the rest of the fixigenae by a **palpebral furrow** running parallel to the outer edge of the lobe. In many trilobites this furrow is absent, the palpebral lobe grading into the palpebral areas of the fixigenae without marked boundary. In a few forms *(Asaphus, Encrinurus)* the palpebral lobe of the fixigenae and the area beneath the eye (eye platform) of the librigenae may form a more or less tubular stalk supporting the visual surface of the eye, which is located near the tip of the peduncle.

EYE RIDGES

The eye ridges are raised, generally narrow bands running across the fixigenae from the vicinity of the anterolateral corners of the glabella to anterior extremities of the palpebral lobes. In most trilobites the eye ridges spring from the axial furrows close to the glabella, but in some Cambrian forms (Protolenidae, Daguinaspididae) they are direct extensions of the anterolateral portions

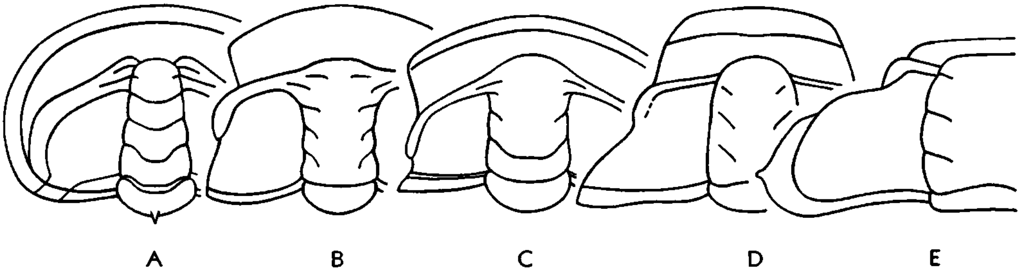


FIG. 36. Different types of eye ridges.——*A,B.* Trifid; *A, Choubertella spinosa* HUPÉ, L.Cam., Morocco, ×1.2; *B, Kingaspis campbelli* (KING) KOBAYASHI, L.Cam., Morocco, ×1.8 (both after 24).——*C.* Bifid; *Bigotina bivallata* COBBOLD, L.Cam., Fr.(Normandy), ×4 (after 24).——*D.* Normal unsegmented ptychopariid type; *Elrathina fecunda* DEISS, M.Cam., USA(Montana), ×2.2 (after 24).——*E.* Palpebro-ocular ridge; *Rossaspis superciliosa* (ROSS) HARRINGTON, L.Ord., USA(Idaho), ×5.3 (after 49).

of the glabella. In these trilobites, the adaxial extremity of the eye ridges may be divided into two *(Bigotina,* Fig. 36*C*) or three (*Kingaspis, Choubertella,* Fig. 36*A,B*) segments, which are direct lateral extensions of the frontal glabellar and anterior lateral glabellar lobes. The eye ridges may end at the anterior extremity of the palpebral lobes or continue backward-outward so as to form the whole palpebral lobe or only its raised outer rim. The length and direction of the eye ridges is variable according to size and location of the palpebral lobes and width of the palpebral area of the fixigenae. In some Pliomeridae (*Rossaspis,* Fig. 36*E*) with anterior eyes and narrow *(tr.)* palpebral areas of the fixigenae, the eye ridges and the palpebral lobes form units termed **palpebro-ocular ridges.**

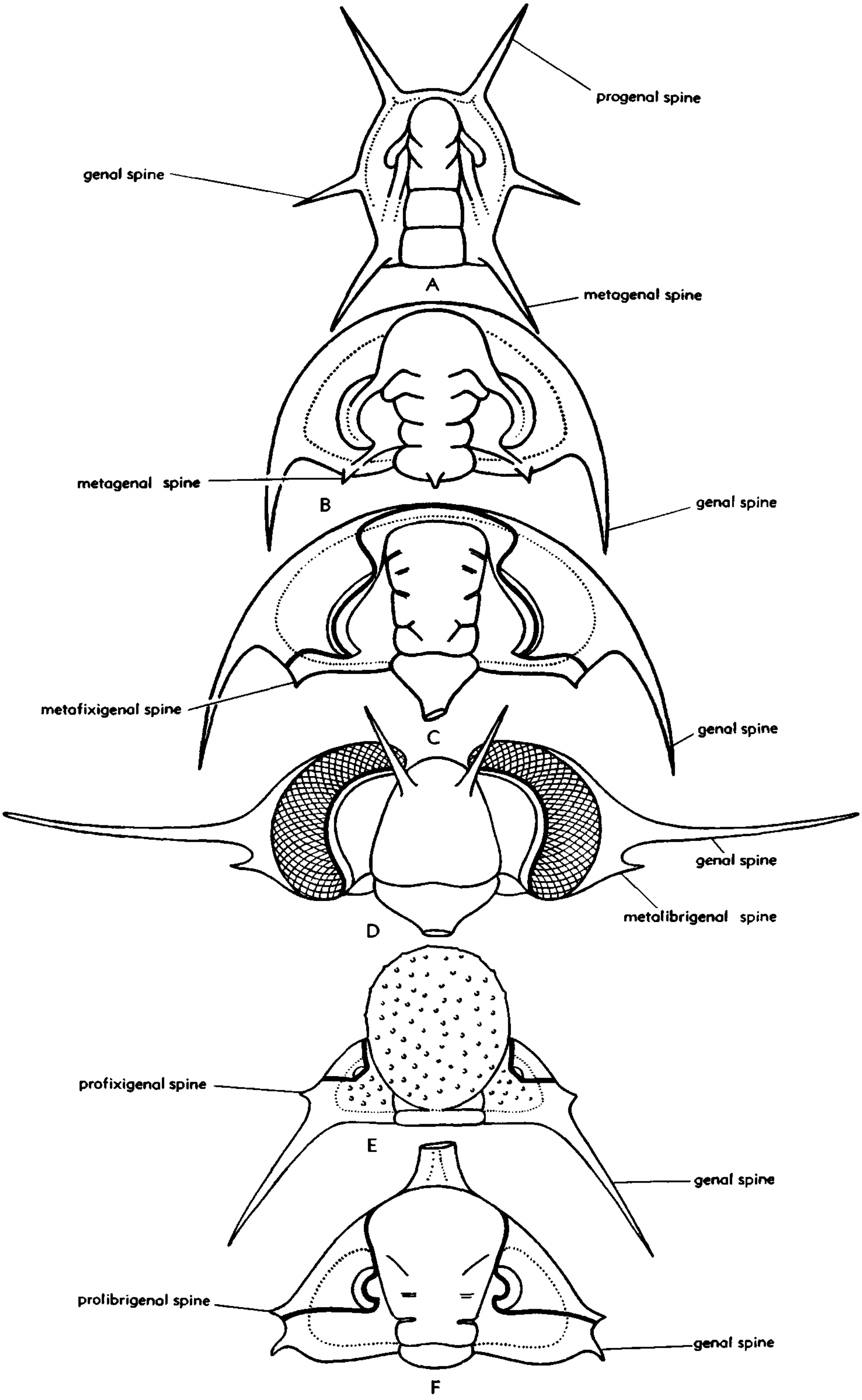
LIBRIGENAE

The **librigenae** ("free cheeks") are paired cephalic areas extending between the facial sutures and lateral margins. They are usually crescentic, but variation in their shape depends mostly on the course of the facial sutures. In some opisthoparian trilobites *(Basiliella)* they are very large, whereas in most proparian genera they are moderately to very small *(Pagetia).* In such genera as *Entomaspis, Pteroparia,* and *Loganopeltis,* as well as in the Trinucleidae, the librigenae are almost wholly ventral in position, practically coinciding with the cephalic doublure.

The librigenae carry the visual surface of the eyes, which are usually semielliptical, crescentic, or reniform areas circling the outer edge of the palpebral lobes. In many trilobites the surface of the librigenae rises more or less abruptly close to these areas, forming a sharp-curved tract or sort of socle **(eye platform)** at the base of the visual surface of the eye.

CEPHALIC SPINES

Numerous species of trilobites are characterized by cephalic spines. These may spring from the glabella, occipital ring, or genae as projections of the dorsal integument, or from the cephalic margins, as projections of both the dorsal integument and doublure. In many odontopleurids *(Miraspis, Ceratocephala, Acidaspis, Odontopleura, Radiaspis),* as well as in some telephinids *(Glaphurus),* there are numerous pairs of marginal cephalic spines produced from the lateral and anterior margins, whereas in some lichids *(Terataspis)* similar spines are found also along the posterior cephalic margin. These spines, which probably had a defensive purpose that was effective during enrollment, are secondary outgrowths having no relation to the primitive cephalic segmentation. Therefore, they have little taxonomic value. Of considerable importance, on the other hand, are the so-called **genal spines** that characterize many trilobites. These are projections of the border and doublure of the posterolateral extremities of the cephalon, the **genal angles,** which may be either carried by the librigenae (opisthoparian condition) or carried by the fixigenae (proparian condition). These spines, usually hollow and circular or subtriangular in section, may diverge


progenal spine
genal spine
A
metagenal spine
metagenal spine
B
genal spine
metafixigenal spine
C
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D
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E
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genal spine
F

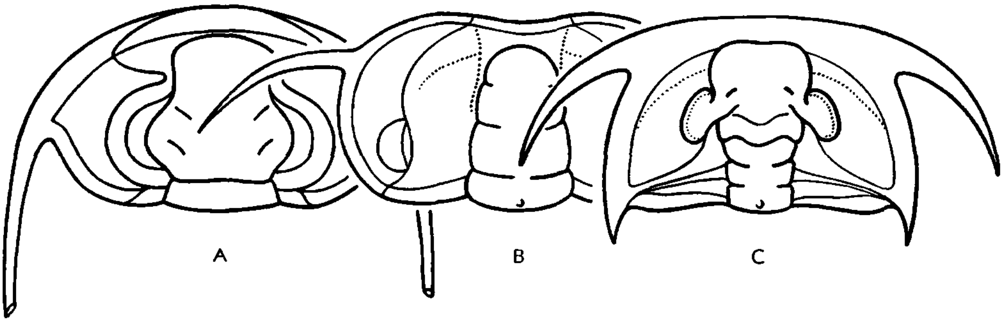

FIG. 38. Advanced cephalic spines.——*A. Menoparia genalunata* Ross (Remopleurididae), L.Ord., USA (Utah), ×7.2 (after 88, 1952).——*B. Sphaerophthalmus alatus* (BOECK) ANGELIN (Olenidae), U.Cam., Swed., ×10 (after 97, 1923).——*C. Laudonia bispinata* HARRINGTON (Olenellidae), L.Cam., Can.(B.C.), ×2.5 (new).

abruptly sideward from the genal angles or they may extend backward as continuations of the curved cephalic margins.

In addition to the genal spines, some trilobites bear 1 or 2 more pairs of marginal spines springing from the lateral and posterior margins. These spines, which are of considerable importance for taxonomic purposes, may be classified on the basis of their placement with reference to the genal angle and posterior sections of the facial sutures (Fig. 37). Proposed classification of these marginal spines of the cephalon is given in the following table.

Classification of Paired Marginal Spines of Trilobite Cephala

Located at genal angles	Genal
Located in front of genal angles.	
Carried by genal region (no facial sutures)	Progenal
Carried by fixigenae	Profixigenal
Carried by librigenae	Prolibrigenal
Located behind genal angles.	
Carried by genal regions (no facial sutures)	Metagenal
Carried by fixigenae	Metafixigenal
Carried by librigenae	Metalibrigenal

Fixigenal and **librigenal** spines are appropriate general terms to distinguish paired marginal spines carried by the fixigenae and librigenae, respectively. It should be pointed out in this connection that the metagenal and metafixigenal spines often have been referred to in literature on trilobites as intergenal spines. The term "intergenal," as applied to these spines, is a confusing misnomer, because the only spines carried "between the genae" very evidently are those borne by the occipital ring or glabella.

Typically, the genal spines spring from the posterolateral angles of the cephalon, but in some trilobites these and other marginal spines show a marked tendency to occupy a forward position. This tendency is already present in the Lower Cambrian Olenellidae. In such genera as *Laudonia* (Fig. 38*C*) what appear to be the genal spines actually are metagenal spines that have migrated outward, the true genal spines being located far forward. This tendency appeared independently in many other families, such as the Redlichiidae, Neoredlichiidae, Saukiandidae, Paradoxididae, Zacanthoididae, Damesellidae, Olenidae, Remopleurididae, Telephinidae, Lichidae, and Harpidae (Fig. 38).

DOUBLURE

The cephalic exoskeleton is continued on to the ventral side as a reflected rim or

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(See facing page)

FIG. 37. Nomenclature of paired cephalic spines.——*A. Olenelloides armatus* PEACH, L.Cam., Scotland, ×10 (after 83, 1894).——*B. Holmia kjerulfi* (LINNARSSON) MARCOU, L.Cam., Swed., ×1.5 (after 78, 1887).——*C. Zacanthoides romingeri* RESSER, M.Cam., Can.(B.C.), ×1 (after 84, new).——*D. Telephina bicornis* (ULRICH), M.Ord., USA(Virginia), ×2.9 (after 94, 1930).——*E. Sphaerocoryphe* cf. *granulatus* (ANGELIN), Ord., Estonia, ×3 (after 24).——*F. Paracalmonia cuspidata* (CLARKE), L.Dev., S.Am.(Brazil), ×0.75 (after 73, 1913).

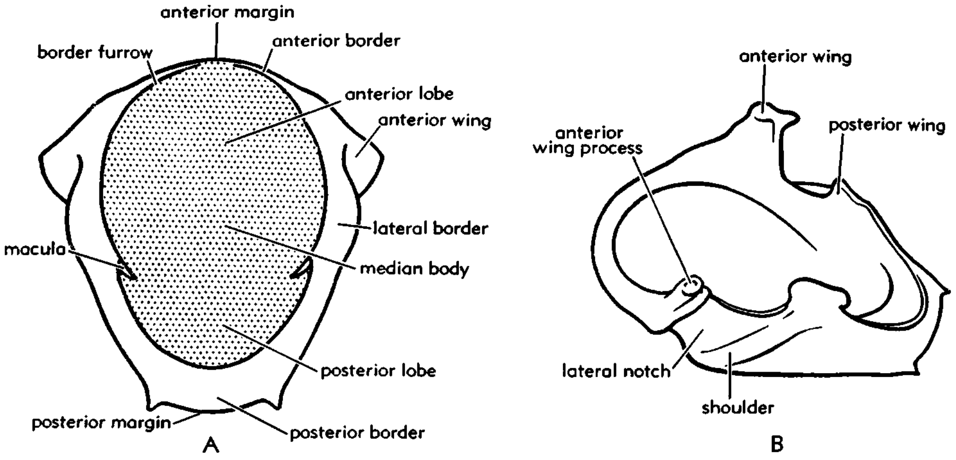

FIG. 39. Nomenclature of hypostoma, illustrated by *Ceraurinella typa* B.N. COOPER, M.Ord., USA(Virginia), ×5. *A*, Exterior view; *B*, oblique interior view (after 71).

doublure of variable width (Figs. 43,48). The doublure is usually marked by terrace lines, which run subparallel to the margins of the cephalon, being arranged in a Bertillon pattern. The soft ventral membrane was attached to the inner edge of the doublure.

ROSTRAL PLATE

In addition to the doublure, 3 sternites may be present on the ventral side of the cephalic region. The most anterior of these is the **rostral plate,** which may be separated from the doublure by a transverse rostral suture and by paired longitudinal connective sutures. The other sternites are named hypostoma and metastoma.

The rostral plate may be a large crescentic plate extending from the vicinity of one genal angle to the other, as in Olenellidae (Fig. 48*B-D*); a moderately wide *(tr.)* and short *(sag.)* plate, as in most ptychopariids (Fig. 48*E*); a small, narrow *(tr.)* band, as in many Pliomeridae; or a small subtriangular plate, as in the Homalonotidae (Fig. 48*H*). In the last-mentioned family, the rostral plate is partly dorsal in position. In progressive trilobites (Asaphidae, Nileidae, Phacopidae), a rostral plate is absent.

HYPOSTOMA

The 2nd sternite, called the **hypostoma,** covers the mouth region. Typically, it has a general ovoid outline (Figs. 39-41), consisting of a **median body** convex adventrally, and a surrounding flat, convex, or concave border that is bent into a dorsal doublure. The median body may be subdivided by a more or less distinct median furrow into a larger, more convex anterior lobe and a smaller, flatter posterior lobe. Also, the median body may bear a pair of varyingly elongated protuberances, termed **maculae,** usually located near the abaxial extremities of the median furrow.

The hypostomal border, subdivided into anterior, lateral, and posterior parts, is ususually separated from the median body by a shallow border furrow. The anterior border is narrow mesially, widening laterally into a pair of **anterior wings,** each of which may carry a rounded boss or thornlike structure (wing process), located on the interior (dorsal) surface near their abaxial tips. A corresponding pit is located on the exterior (ventral) surface of the wings. The anterior wings are separated from the lateral borders

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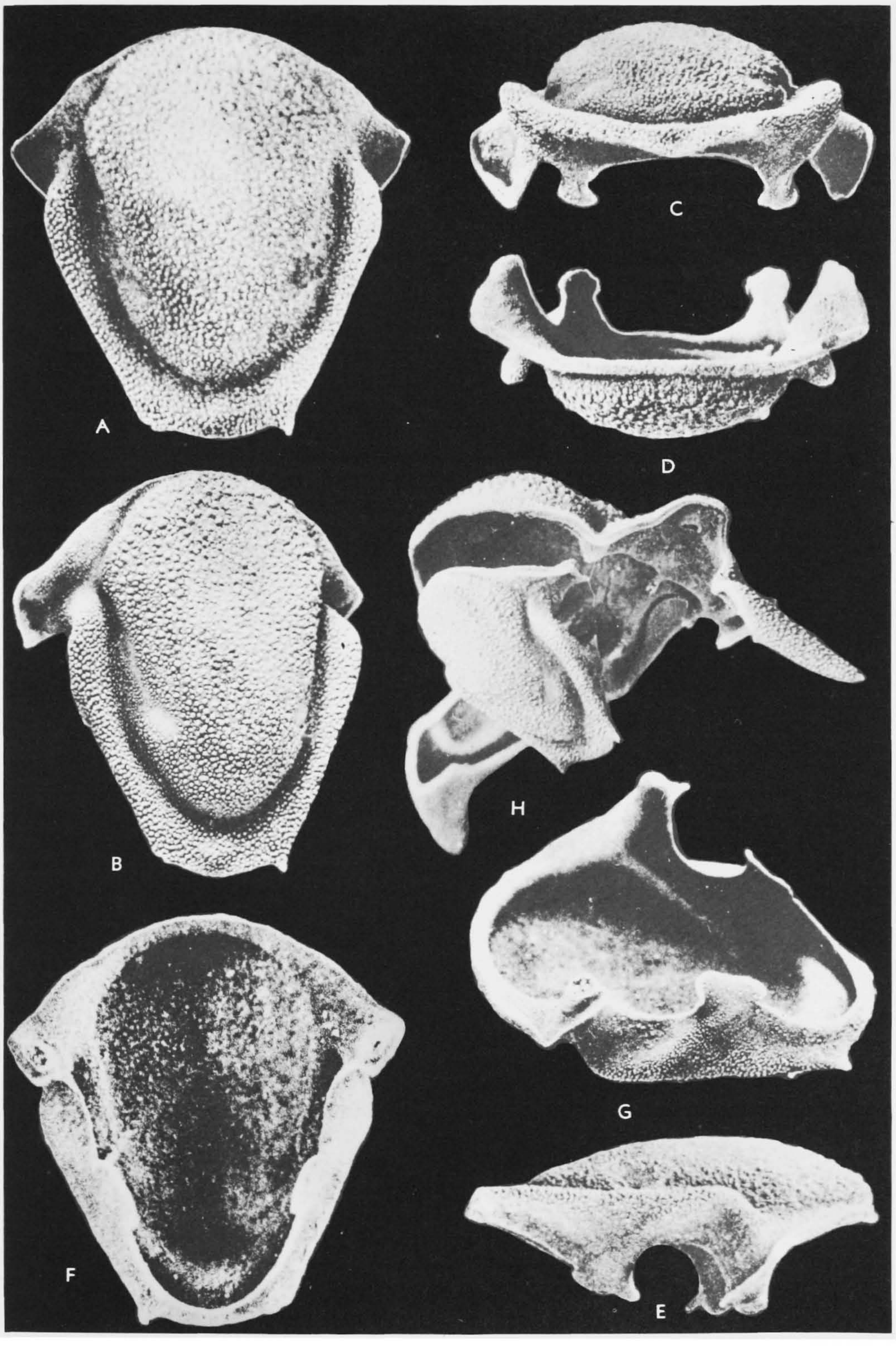
(See facing page)

FIG. 40. Different views of the hypostoma of *Ceraurinella typa* COOPER, M.Ord., USA(Virginia) (after 71). *A,B,* Exterior ventral and oblique view; *C-E,* posterior, anterior, and lateral views; *F,G,* interior dorsal and oblique view; *H,* cranidium and hypostoma mounted in approximate relative natural position, oblique ventral view (*A-G,* ×6.7; *H,* ×5.8).


A
C
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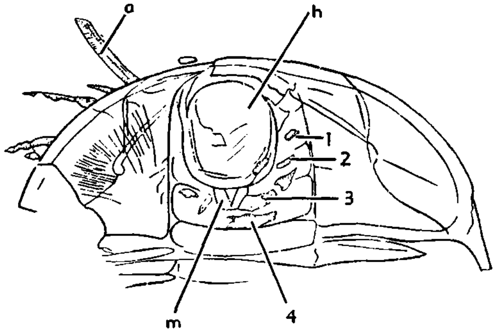


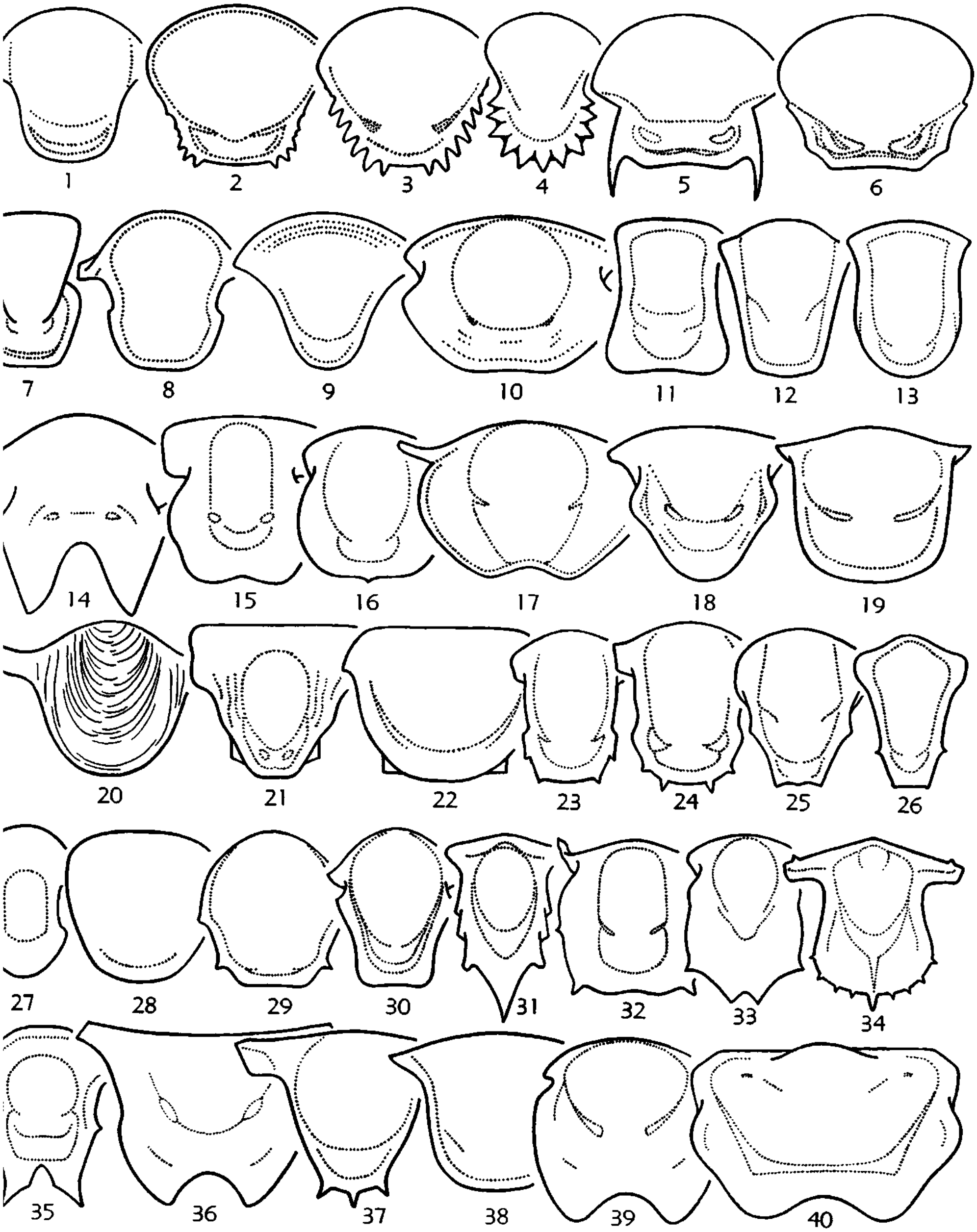
Fig. 41. Cephalic region of *Olenoides serratus* (Rominger) Kobayashi, M.Cam., Can.(B.C.), ×1 (after 60) (Explanation: *h*, hypostoma; *m*, metastoma; *a*, antenna; *1-4*, ?fragments of the 4 biramous cephalic appendages).

by deep **lateral notches.** Immediately behind the notches, the lateral border usually reaches maximum width in a somewhat inflated area **(shoulder)** that projects ventrally. Behind the shoulder, the doublure of the lateral border may be projected into a pair of **posterior wings.** These are extensions of the doublure and not parts of the border. The notches have been interpreted (Whittington & Evitt, 1953) as passageways for the forwardly directed antennae of the trilobites, and the ventral bosses on the tips of the anterior wings are thought to be places of attachment of the antennary muscles.

The posterior border of the hypostoma may be very wide (*Kanoshia,* Fig. 42,*33*), or narrow (*Nileus,* Fig. 42,*17*), and the corresponding posterior margin may be evenly rounded (*Callavia, Scutellum,* Fig. 42,*18*), pointed (*Pseudocybele,* Fig. 42,*31*), or serrated (*Fremontella,* Fig. 42,*4*). The lateral margins may grade into the posterior margin in an uninterrupted curve (*Dalmanitina,* Fig. 42,*38*), or the posterolateral angles of the hypostoma may be produced into a pair of spinelike projections (*Hypodicranotus,* Fig. 43*D*; *Asaphus,* Fig. 42,*14*). In the first case the hypostoma is said to be "entire" or to have an "entire posterior margin," whereas in the second it is said to be "bifurcated" or to have a "bifurcated posterior margin."

Hypostomas have been described in less than a third of known species of trilobites. In most they are detached plates found associated with other parts of a given species. Only in comparatively few fossils has the hypostoma been found *in situ,* preserving its original relation to other cephalic parts. The study of these specimens shows that 3 different types of hypostomal attachment existed among trilobites: (1) fused with the

Fig. 42. Different shapes of hypostomata.——*1. Callavia broeggeri* (Walcott) Matthew (Olenellidae), L.Cam., Can., ×1 (after 64).——*2. Olenellus thompsoni* (Hall) Hall (Olenellidae), L.Cam., USA (Tenn.), ×2.8 (after 64).——*3. Wanneria walcottana* (Wanner) Walcott (Olenellidae), L.Cam., USA (Pa.), ×1 (after 64).——*4. Fremontella halli* (Walcott) Harrington (Olenellidae), L.Cam., USA(Ala.), ×12 (after 64).——*5. Paradoxides oelandicus* Angelin (Paradoxididae), M.Cam., Swed., ×3 (after 31).——*6. Paradoxides harlani* Green (Paradoxididae), M.Cam., USA(Mass.), ×1.2 (after 91, 1944).——*7. Strenuaeva primaeva* (Brøgger) Kiaer, L.Cam., Norway, ×10.7 (after 28).——*8. Kootenia lakei* (Cobbold) (Dorypygidae), M.Cam., Eng., ×2.5 (after 30, 1938).——*9. Mexicaspis stenopyge* Lochman (Zacanthoididae), M.Cam., Mexico, ×4 (after 81, 1948).——*10. Dikelocephalus minnesotensis* Owen (Dikelocephalidae), U.Cam., USA, ×1.1 (after 95, 1930).——*11. Damesella blackwelderi* Walcott, (Damesellidae), M.Cam., China, ×1.1 (after 96, 1913).——*12. Saukiella indenta* Ulrich & Resser (Saukiidae), U.Cam., USA(Wis.), ×2.8 (after 95, 1930).——*13. Parabolina jemtlandica* Westergård (Olenidae), U.Cam., Swed., ×5 (after 97, 1922).——*14. Asaphus (Neoasaphus) ludibundus* Törnquist (Asaphidae), M.Ord., Swed., ×1.65 (after 79, 1953).——*15. Megistaspis (Megistaspis)* cf. *elongata* (Schmidt) Jaanusson (Asaphidae), M.Ord., Estonia, ×1.9 (after 31).——*16. Asaphellus homfrayi* (Salter) Callaway (Asaphidae), L.Ord.(Tremadoc.), Eng., ×1.22 (after 30, 1942).——*17. Nileus armadillo* Dalman (Nileidae), Ord., Swed., ×3 (after 31).——*18. Scutellum polyactin* (Angelin) (Thysanopeltidae), U.Sil., Swed., ×2.8 (after 31).——*19. Eobronteus lunatus* (Billings) Wilson (Thysanopeltidae), M.Ord., Can., ×3 (after 92, 1949).——*20. Platillaenus ladogensis* (Holm) Jaanusson (Illaenidae), L.Ord., Swed., ×2.3 (after 31).——*21. Illaenus sarsi* Jaanusson (Illaenidae), Ord., Norway, ×1.75 (after 79, 1954).——*22. Stenopareia linnarssoni* (Holm) Holm (Illaenidae), M.Ord., Swed., ×2.5 (after 79, 1954).——*23. Proetus signatus* Lindström (Proetidae), Sib., Swed., ×4 (after 31).——*24. Proetus (Proetus) concinnus* (Dalman) (Proetidae), Sib., Swed., ×4 (after 87, new).——*25. Paladin (Paladin) helmisensis* Whittington (Phillipsiidae), U.Miss., USA(Tex.), ×5.6 (after 99, 1954).——*26. Lioharpes venulosus* (Hawle & Corda) (Harpidae), L.Dev., Bohemia, ×1.85 (after 99, 1950).——*27. Eoharpes primus* (Barrande) Raymond (Harpidae), L.Ord., Bohemia, ×3.4 (after 99, 1950).——*28. Cryptolithus tesselatus* Green (Trinucleidae), M.Ord., USA(N.Y.), ×10.5 (after 41).——*29. Ampyx linleyensis* Whittard (Raphiophoridae), L.Ord., Eng., ×3.35 (after 98, 1955).——*30. Cheirurus insignis* Beyrich (Cheiruridae),



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.Ord., Bohemia, ×1.25 (after 2).——*31. Pseudocybele nasuta* Ross (Pliomeridae), L.Ord., USA(Utah), 8.3 (after 49).——*32. Tesselacauda depressa* Ross (Pliomeridae), L.Ord., USA(Idaho), ×7 (after 49). —*33. Kanoshia kanoshensis* (Hintze) Harrington (Pliomeridae), L.Ord., USA(Utah), ×4 (after 77, 52).——*34. Cybeloides virginiensis* B.N. Cooper (Encrinuridae), M.Ord., USA(Virginia) ×3.7 (after 74, 53).——*35. Flexicalymene senaria* (Conrad) Whittington (Calymenidae), M.Ord., USA(N.Y.), ×6 fter 75, 1953).——*36. Homalonotus knighti* König (Homalonotidae), U.Sil., Eng., ×2.5 (after 89, 65).——*37. Phacops fecundus* Barrande (Phacopidae), Sil., Bohemia, ×1.1 (after 2).——*38. Dalanitina socialis* (Barrande) Reed (Dalmanitidae), Ord., Bohemia (after 2).——*39. Lichas laciniatus* Vahlenberg) Hisinger (Lichidae), U.Ord., Swed., ×1.4 (after 67).——*40. Ceratocephala laciniata* Whittington & Evitt (Odontopleuridae), M.Ord., USA(Virginia), ×9 (after 71).

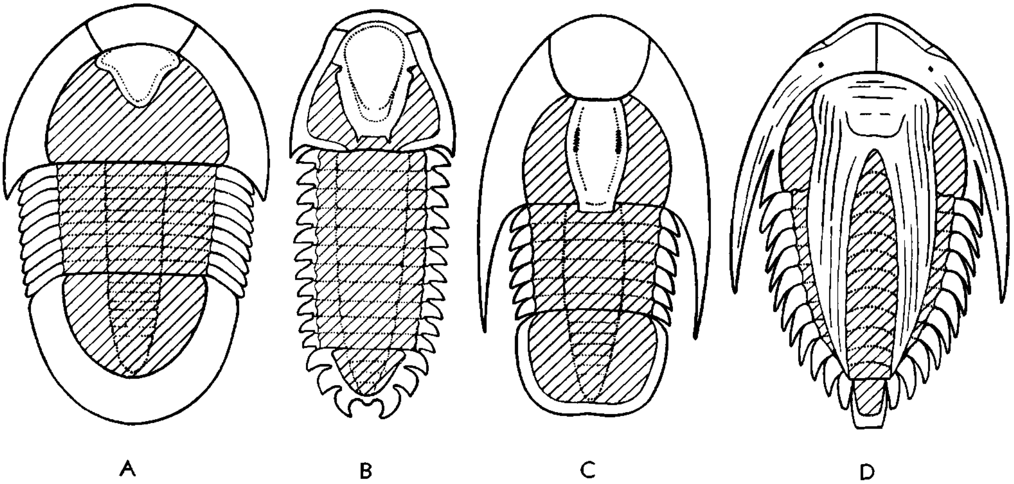


Fig. 43. Relative lengths of hypostomata in different genera, shown by carapaces and hypostomata in ventral view, with doublure, rostral plate, and hypostoma in white, and ventral (internal) surface of carapace shaded.——*A. Stygina latifrons* Portlock (Styginidae), U.Ord., Ireland, ×1.7 (after 99, new).——*B. Cheirurus gibbus* Barrande (Cheiruridae), Sil., Bohemia, ×0.65 (after 2).——*C. Phillipsinella parabola* (Barrande) Novák (Phillipsinellidae), U.Ord., Scot., ×4 (after 99, 1950).——*D. Hypodicranotus striatulus* (Walcott) Whittington (Remopleurididae), U.Ord., USA(N.Y.), ×1.6 (after 99, 1952).

rostral plate, forming a single "rostral-hypostomal plate" (Fig. 44); (2) attached to the rostral plate or anterior cephalic doublure (if rostral plate was lacking) by means of a hypostomal suture that could be either functional or in a state of complete or partial symphysis; and (3) attached to the rostral plate or anterior cephalic doublure by a stalk or peduncle. In some trilobites the hypostoma was "free," not attached by any plate to the cephalon, but supported by the soft ventral membrane.

No hypostomas have been found associated with any agnostid and only in *Pagetia* among eodiscid trilobites. Rasetti has mentioned that in enrolled silicified specimens of agnostids, no hypostoma is to be found inside the tightly closed "box" formed by the enrolled specimen. The absence of a hypostoma, however, may be due to the fact that the plate was not mineralized in the agnostids and, therefore, not preserved. In the Eodiscidae, the apparent lack of hypostomas probably is due to faulty records. Judging by the close relationship between Eodiscidae and Pagetiidae, it is only natural to suppose that the Eodiscidae possessed a small hypostoma, just as in the Pagetiidae.

METASTOMA

The 3rd sternite is postoral in position. It consists of a very small concave plate that seems to have been supported by the ventral membrane immediately behind the mouth. The metastoma is known only in a few genera, notably *Olenoides* (Fig. 41), *Triarthrus,* and *Phacops* (Fig. 57*B*).

SUTURES

Trilobites are typically distinguished by the presence of cephalic sutures. These are very narrow, almost lineal bands where the exoskeleton remained soft and uncalcified. They transect the mineralized integument of the cephalon and its ventral doublure. Typically, the sutures were lines of weakness along which the cephalic exoskeleton could break apart into isolated pieces at times of molting (ecdysis). Cephalic sutures are wholly lacking in some trilobites, particularly the agnostids and eodiscids, and in many others they are in such a state of partial or complete symphysis that obviously they could not have functioned in ecdysis.

FACIAL SUTURES

The name **facial suture** *(sutura facialis)* was introduced by Dalman (1827) for the

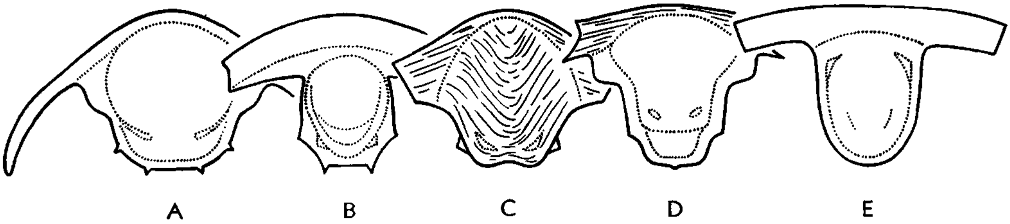


Fig. 44. Rostral-hypostomal plate resulting from ankylosis of hypostomal suture.——*A. Holmia kjerulfi* (Linnarsson) Marcou (Olenellidae), L.Cam., Norway, ×0.4 (after 28).——*B. Redlichia noetlingi* (Redlich) Cossman (Redlichiidae), L.Cam., W.Pakistan, ×2.7 (after 90, 1955).——*C. Paradoxides davidis* Salter (Paradoxididae), M.Cam., G.Brit., ×2.65 (after 30, 1935).——*D. Fieldaspis furcata* Rasetti (Zacanthoididae), M.Cam., Can., ×3 (after 84, new).——*E. Oryctocephalus walcotti* Resser (Oryctocephalidae), M.Cam., USA(Idaho), ×6.65 (after 39).

most conspicuous and typical of all cephalic sutures. They appear as a pair of fine impressed lines that start symmetrically on the posterior or lateral doublure, cross the cephalic border, and take symmetrical courses along the dorsal surface of the cephalon bounding the adaxial side of the visual surface of the eyes; thence they continue forward to unite anteriorly on the dorsal side, along the margin, or on the ventral side (doublure) of the cephalon. If the sutures meet anteriorly on the dorsal side, they are said to be **dorsal-intramarginal** anteriorly. If they meet along the margin, the sutures are described as **marginal** anteriorly. If they meet along the ventral side, the sutures are **ventral-intramarginal** anteriorly. So far as known, the pairs of facial sutures invariably meet anteriorly. Resser's unpublished reference, mentioned by Richter (1933) and Stubblefield (1936), of a type of facial sutures in which individuals of the pair extend onto the anterior doublure without connection between them has not been substantiated. Rasetti (1952) pointed out that this condition may exist in the Pagetiidae, but it seems likely that even in these trilobites the anterior parts of the facial sutures were connected by a transverse marginal suture.

Each of the symmetrical pair of facial sutures is subdivided for descriptive purposes into an **anterior section** (incorrectly called "anterior branch"), extending from the anterior margin to the eye, and a **posterior section** ("posterior branch"), extending from the eye to the posterior or lateral margins. Facial sutures are classed as opisthoparian, proparian, and gonatoparian, according to whether the posterior sections intersect the posterior margin, lateral margin, or genal angle of the cephalon. In **opisthoparian sutures** the posterior sections cut the posterior cephalic margins in a manner that makes the genal angles or spines carried by the librigenae. In **proparian sutures,** the posterior sections cut the lateral cephalic margins in front of the genal angles, which, therefore, are carried by the fixigenae. In **gonatoparian sutures,** the posterior sections of the facial sutures bisect the genal angles.

The course of both the anterior and posterior sections of the facial sutures shows considerable variation in different genera of trilobites. The anterior sections may diverge in forward direction (*Ptychoparia,* Fig. 45*E*), run subparallel (*Odontochile,* Fig. 45*C*), converge (*Flexicalymene,* Fig. 45*D*), or be retrodivergent (directed outward-backward, as in *Entomaspis,* Fig. 45*I*). The posterior sections may vary from very short, directed outward-backward, cutting the posterior margin very close to the occipital ring (*Kainella,* Fig. 45*F*), to long, directed outward-forward, cutting the lateral margin well in front of the genal angles (*Burlingia,* Fig. 45*B*).

No attempt has been made to classify all possible variations of the facial sutures, but certain recurrent patterns found in different trilobites have received special names. Only 2 types of proparian sutures deserve such designations. (1) One of these is the **burlingiiform** type, in which the anterior and posterior sections of the sutures are subparallel, diverging outward-forward at an angle of about 45° to the axial line of the cephalon (*Burlingia,* Fig. 45*B*). (2) The other is the **dalmanitiform** type, in which the anterior sections of the sutures meet on the dorsal side of the cephalon, being wholly dorsal-intramarginal (*Odontochile,* Fig. 45*C*).

Several types of opisthoparian sutures have received special names. (3) The term **cedariiform** (or pseudoproparian) is applied to the type in which the posterior sections of the sutures swing behind the eyes so as to intersect the adaxial portions of the lateral borders and thence swing inward-backward to the posterior margin of the cephalon (*Cedaria,* Fig. 45*G*). When the librigenae of species possessing cedariiform sutures are not preserved, it is often difficult to dis-

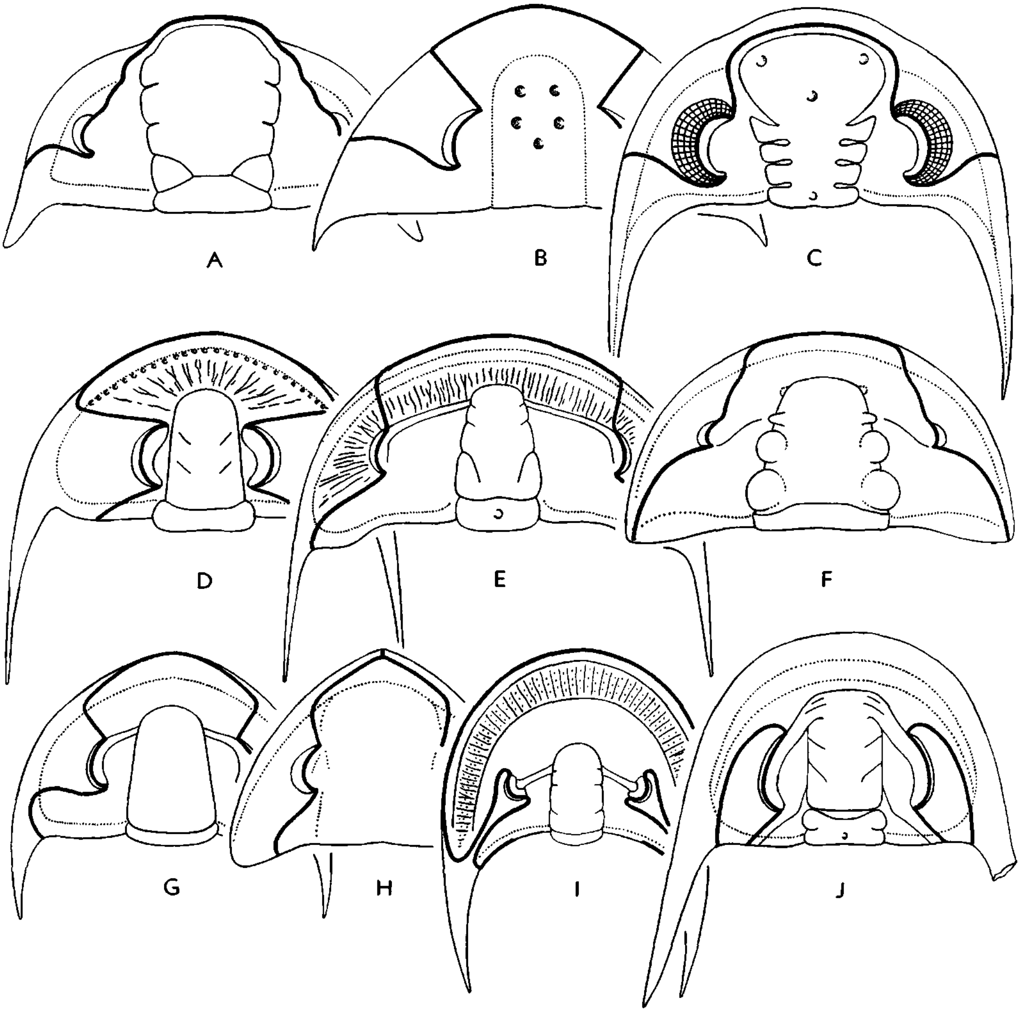


FIG. 45. Types of facial sutures.——*A-C.* Proparian sutures; *A,* cheirurid type, *Ceraurinella typa* B. N. Cooper, M.Ord., USA(Virginia), ×3.5 (after 71),*B,* burlingiiform type, *Burlingia hectori* Walcott, M. Cam., Can., ×9.3 (after 96, 1908); *C,* dalmanitiform type, *Odontochile hausmanni* (Brongniart) Hawle & Corda, Dev., Boh., ×1 (after 2).——*F.* Gonatoparian suture; *Flexicalymene senaria* (Conrad) Whittington, M.Ord., USA(N.Y.), ×3.5 (after 70).——*D,E,G-I.* Opisthoparian sutures; *D,* kainelliform type, *Kainella meridionalis* Kobayashi, L.Ord., S.Am.(Arg.), ×0.73 (after 19); *E,* ptychopariid type, *Ptychoparia striata* (Emmrich) Hawle & Corda, L.Ord., Boh., ×1 (after 2); *G,* cedariiform type, *Cedaria prolifica* Walcott, U.Cam., USA(Ala.), ×1.6 (after 81, 1948); *H,* isoteliform type, *Isotelus gigas* DeKay, M.Ord., Can., ×1.2 (after 84, 1912); *I,* entomaspidiform type, *Entomaspis radiatus* Ulrich, U.Cam., USA(Mo.), ×5.6 (after 448, 1952).——*J,* Metaparian sutures; *Fallotaspis taxemmourtensis* Hupé, L.Cam., Afr. (Morocco), ×1.33 (after 24).

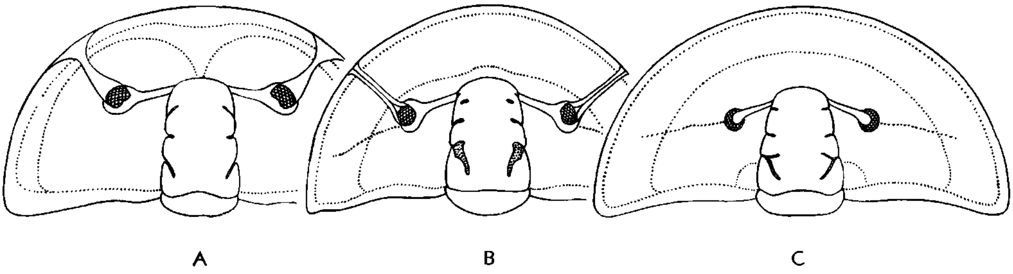


FIG. 46. Evolution of the facial sutures in the loganopeltid stock of the Harpidae.——*A. Loganopeltoides kindlei* RASETTI, U.Cam., Can. (Newf.), X5.4.——*B. Loganopeltoides zenkeri* (BILLINGS) RASETTI, U.Cam., Can.(Que.), X4.65.——*C. Loganopeltis depressa* RASETTI, L.Ord., Can.(Que.), X3.3 (All after 38).

tinguish this kind of opisthoparian sutures from the true proparian type. (4) In the **ptychopariiform** type, anterior sections of the facial sutures have a more or less straight course from the eyes to the anterior margin of the cephalon, where adaxially they become marginal or ventral-intramarginal to the mid-line (*Ptychoparia,* Fig. 45*E*). (5) In the **kainelliform** type the anterior sections first diverge strongly in front of the eyes and then bend sharply inward-forward, cutting very obliquely the anterior border of the cephalon and meeting mesially either on the dorsal side or marginally (*Kainella,* Fig. 45*F*). (6) The terms **isoteliform** and **niobiform** formerly were used to distinguish 2 supposedly different types of opisthoparian sutures within the family Asaphidae. In isoteliform sutures the anterior sections meet in a more or less pointed ogive at the mid-point of the anterior margin of the cephalon and are, therefore, wholly dorsal-intramarginal (*Isotelus,* Fig. 45*H*). Niobiform sutures were regarded as being marginal anteriorly, that is, with anterior sections along the margin for a certain length. This type of sutures was believed to characterize the genus *Niobe* (hence niobiform), but LAKE (1942) was able to prove that in this genus the anterior suture sections are wholly dorsal-intramarginal even if they run very close to the cephalic margin. Clearly, then, the term niobiform is inappropriate. (7) Lastly, the name **entomaspidiform** may be applied to the peculiar type of opisthoparian sutures in which the anterior sections are retrodivergent, running outward-backward from the eyes to the lateral margins (*Entomaspis,* Fig. 45*I*). In such genera as *Entomaspis* and *Hypothetica,* the anterior sections of the sutures reach the lateral cephalic margins just in front of the genal spines and then run marginally to the anterior mid-point of the cephalon. In these genera, the librigenae are reduced mostly to the ventral side (doublure), with a narrow dorsal extension between the eyes and the posterolateral areas of the cephalon.

In some genera of trilobites belonging to families in which the presence of well-developed facial sutures is the general rule, the sutures may become ankylosed and nonfunctional, and eventually traces of them may disappear entirely. This is frequently the case with blind trilobites, but many genera characterized by normal eyes also show this "regression" which, as in some Conocoryphidae and Proetidae, clearly preceded the reduction and final disappearance of the eyes.

The disappearance of facial sutures is accomplished in 2 different ways: (1) by migration of the anterior and posterior sections preceding ankylosis, and (2) by direct ankylosis without previous migration of the sections. The 1st mode is excellently illustrated in the Harpididae. RASETTI (1945, 1948) has shown that in *Loganopeltoides kindlei* (Fig. 46*A*) and *L. minutus,* from the Upper Cambrian of Newfoundland and Quebec, respectively, the sutures are burlingiiform, the anterior and posterior sections running outward-forward, initially approaching each other but not coming together, then diverging slightly and curving near the lateral margins to become marginal, the anterior section running forward in the mid-line and the posterior section running backward to the genal angle. Thus, the librigenae are ventral in position, corre-

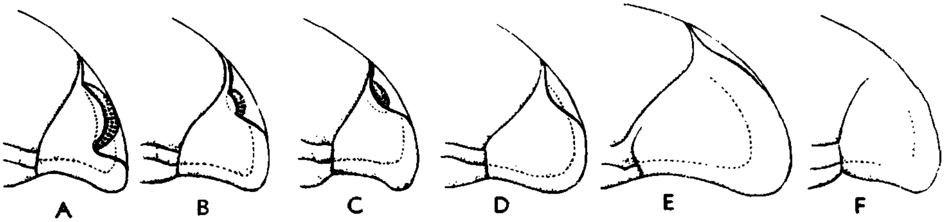


FIG. 47. Lateral migration of the facial sutures accompanying migration, reduction, and disappearance of the eyes in the Phacopidae.——*A. Phacops circumspectans* PORTLOCK, U.Dev., Ger.——*B. Phacops wedekindi* RICHTER & RICHTER, U.Dev., Ger.——*C. Cryphops? ensae* (RICHTER & RICHTER), U.Dev., Ger.——*D. Trimerocephalus mastophthalmus* (REINH. RICHTER), U.Dev., Ger.——*E. Dianops limbata* (REINH. RICHTER), U.Dev., Ger.——*F. Ductina ductifrons* (RICHTER & RICHTER), U.Dev., Ger. (All after 47.)

sponding to the cephalic doublure, with a narrow bandlike extension on to the dorsal side between the eyes and anterolateral margins of the cephalon. In *L. zenkeri,* from the Upper Cambrian of Quebec (Fig. 46*B*), the 2 sections have fused into a single suture running outward-forward along a narrow crest extending from the eye to the anterolateral margin of the cephalon. Lastly, in *Loganopeltis depressa,* from lowermost Ordovician rocks of Quebec (Fig. 46*C*), all traces of facial sutures have disappeared and, presumably, all that remains of them is an entirely marginal suture running all along the edge of the cephalon from one genal angle to the other.

In many other trilobites regression of facial sutures was accomplished *"in situ,"* without previous migration of the sections. In many Phacopidae, for instance, where the facial sutures are apparently continuous and well developed, they were evidently nonfunctional in ecdysis. This seems clear from the fact that the cephalic exuviae of many species (hard cephalic exoskeleton shed during molting) consist of a single piece, the librigenae being still firmly attached to the cranidium (Fig. 83). Therefore, although the sutures are still clearly observable, they must be regarded as in a state of symphysis. Curiously enough, in certain Phacopidae the nonfunctional sutures disappeared by outward migration of the sections, accompanying outward migration, reduction, and final disappearance of the eyes. This is seen in the *Phacops circumspectans-Ductina ductifrons* series of Late Devonian age, as shown by RICHTER & RICHTER (1926) (Figs. 47, 291).

The nonfunctional character of the sutures leading to final disappearance is beautifully shown by the blind proetid *Typhloproetus,* in which the facial sutures are well developed except for the rear extremities of the posterior sections that have vanished. Though it is generally true that in blind trilobites, like the Conocoryphidae and Raphiophoridae, the facial sutures tend to migrate outward and become more or less dorsal-intramarginal, this migration and disappearance are not related necessarily to migration, reduction, and final disappearance of the eyes. This is clearly shown by such blind proetids as *Drevermannia, Carnicia, Palpebralia,* and *Formonia,* which, though lacking eyes, possess well-developed facial sutures, or, reversing the conditions, by *Brachymetopus,* which possesses well-developed eyes though generally lacking facial sutures.

METAPARIAN SUTURES

The Olenellidae and related trilobites have a functional wholly ventral-intramarginal suture separating the cephalon from a large crescentic or horseshoe-shaped rostral plate. The great majority of species lack facial sutures, but a few forms are characterized by the presence of peculiar lines or fine "ocular ridges" that spring from the anterior and posterior extremities of the eye lobes, curving backward toward the posterior margin of the cephalon. Some authors (FORD, WALCOTT in early papers, BEECHER, MOBERG, KIAER, WARBURG) have been inclined to regard these lines as the last traces of fused facial sutures of opisthoparian type, whereas others (LINDSTRÖM, WALCOTT in later papers, SWINNERTON, POULSEN, STUBBLEFIELD, STØRMER) have been prone to regard them as sutures in process of development, as wrinkles originated during entombment, or as structures with no sutural significance. Until 1953 the discussion was centered on a few European and North American forms, such as *Kjerulfia lata, Holmia kjerulfi,* and some species of *Paedeumias* and *Wanneria.* In all these trilobites, even in better-preserved specimens, only the posterior ("postocular") ridges, springing from the posterior extremity of the eye lobes, are completely developed and reach the posterior cephalic margin. The anterior ("preocular") ridges, springing from the anterior extremity of the eye lobes and swinging backward in a gentle curve, were found to vanish before reaching the posterior border of the cephalon. This led several authors to regard the preocular ridges as impressions left on the dorsal side of the cephalon by the inner edge of the rostral plate, an hypothesis which seemed substantiated by the well-known thinness of the olenellid exoskeleton and by the fact that in some species the structures regarded as preocular ridges, instead of springing from the anterior extremity of the eye lobes, originate in the axial furrows well in front of the eyes. The fact that both the preocular and postocular ridges are raised crests was also used as an argument against their sutural significance. However, Rasetti's studies on *Loganopeltoides* have shown that facial sutures in process of disappearance may run along the crests of fine raised ridges; also, Whittington & Evitt have shown that in silicified specimens of *Dimeropyge virginiensis* the facial sutures are located on narrow crests which they termed "sutural ridges." Though it is evident that in some olenellids (i.e., *Laudonia*) the anterior ridges are best regarded as impressions of the inner edge of the rostral plate, this explanation cannot be applied to fossils in which the ridges exactly join the anterior extremity of the eye lobes.

In recent years, Hupé's studies on the Lower Cambrian faunas of Morocco have led to discovery of several olenellid genera which seem to provide an acceptable answer to this much discussed problem. In such genera as *Fallotaspis* (Fig. 45*J*) and *Daguinaspis* both the preocular and postocular ridges are fully developed, the preocular ridges actually reaching the posterior cephalic margin adaxially from the genal angle. In these genera, the preocular and postocular ridges are independent structures from the "pseudo-preocular ridges" (impression of the inner edge of the rostral plate) and the metagenal ridges, respectively, and little doubt can remain that the preocular and postocular ridges actually represent completely ankylosed facial sutures. The name **metaparian** sutures was used by Raw (1925) to distinguish this peculiar type of nonfunctional opisthoparian sutures in which both sections are directed outward-backward and cut the posterior margin of the cephalon.

ROSTRAL AND PERROSTRAL SUTURES

In typical ptychopariid trilobites having a rostral plate and facial sutures, the anterior sections of the sutures become marginal on reaching the edge of the cephalon or continue on to the anterior doublure, becoming ventral-intramarginal and meeting at a point located on the sagittal line. This transverse marginal or ventral-intramarginal suture connecting the cranidium with the rostral plate is called **rostral suture.** However, it can be regarded as being an integral part of the dorsal cephalic suture system and the name *"grande suture"* was used by Barrande for the ensemble of facial and rostral sutures, which he regarded as forming a single structure. This is also the view of some modern authors (Rasetti, Hupé), and others (Kiaer, Warburg, Henriksen, Richter) believe that the rostral suture is a structure independent of the facial sutures.

Evidently, the rostral suture can be distinguished as such only if a rostral plate is present. If this plate is absent, as in the saukiids, asaphids, nileids, dalmanitids, and other trilobites, the facial sutures become indistinguishable from Barrande's *grande suture,* for it should be clear that in these forms rostral suture cannot be used as designation of the transverse anterior section (dorsal-intramarginal, marginal, or ventral-intramarginal) connecting the anterior sections of facial sutures.

The name **perrostral suture** was applied by Richter to the functional ventral-intramarginal suture of olenellids. This suture extends in a semicircle or semiellipse from the vicinity of one genal angle to the other, and becomes definitely ventral in the posterolateral areas of the cephalon where it

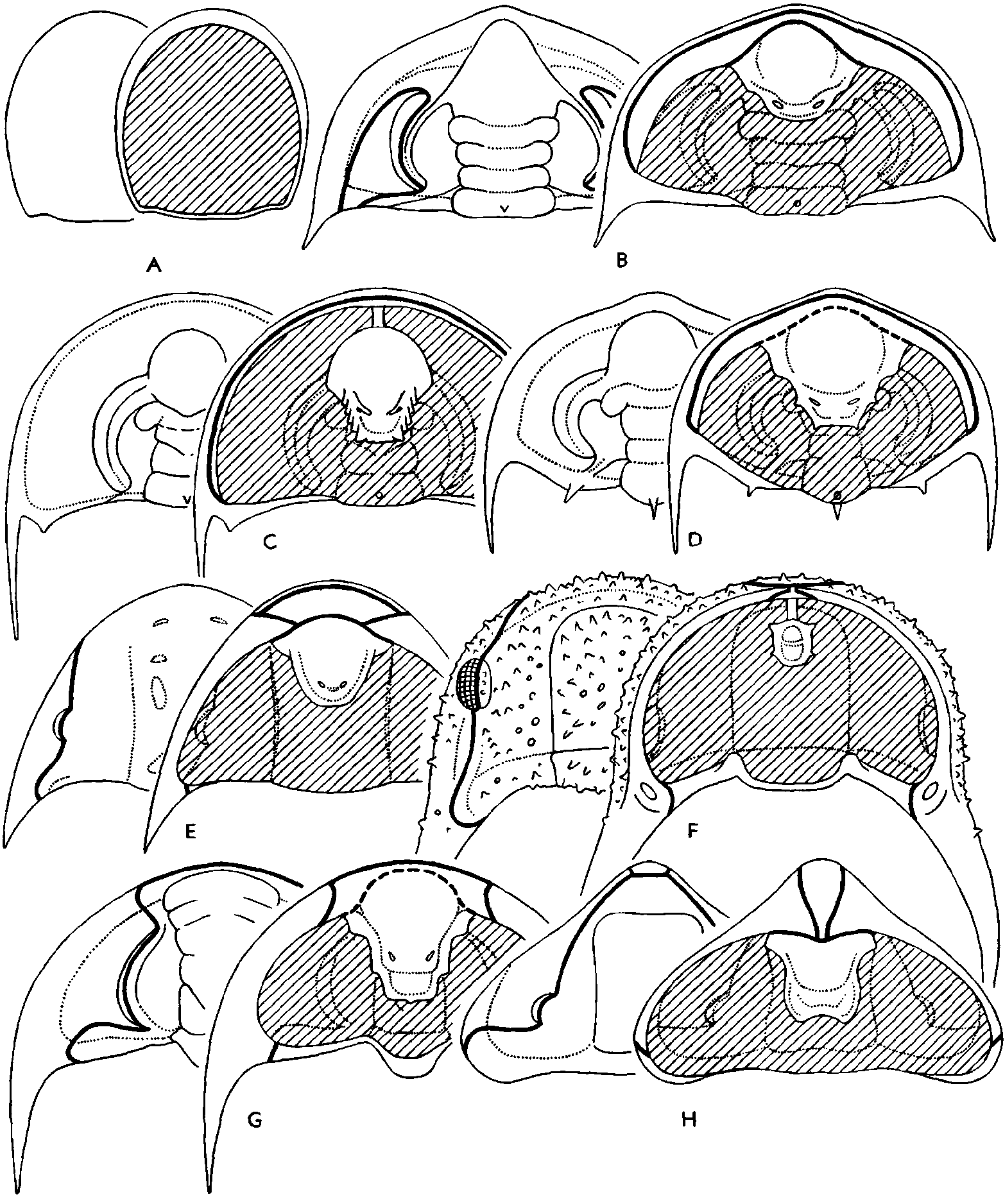


Fig. 48. Cephalic types defined by suture patterns.——*A.* Agnostid type, *Phalacroma glandiforme* (Angelin) Westergård, M.Cam., Swed., ×3.3 (after 97, 1946).——*B.* Olenellid type, *Kjerulfia lata* Kiaer, L.Cam., Swed., ×0.5 (after 28).——*C.* Paedeumiid type, *Paedeumias transitans* Walcott, L.Cam., USA (Vermont), ×2.5 (after 64).——*D.* Holmiid type, *Holmia kjerulfi* (Linnarsson) Marcou, L.Cam., Swed., ×1.85 (after 28).——*E.* Ptychopariid type, *Dysplanus centrotus* (Dalman) Burmeister, L.Ord., Swed., ×1.2 (after 79, 1954).——*F.* Dimeropygid type, *Dimeropyge virginiensis* Whittington & Evitt, M.Ord., USA(Virginia), ×21.7 (after 71).——*G.* Corynexochid type, *Fieldaspis furcata* Rasetti, M.Cam., Can. (B.C.), ×1.3 (after 84, 1951).——*H.* Homalonotid type, *Dipleura dekayi* Green, M.Dev., USA(N.Y.), ×0.8 (after 17).——*I.* Bathynotid type, *Bathynotus holopygus* (Hall) Hall, L.Cam., USA(Vermont), ×2 (after 81, new).——*J.* Asaphid type, *Lachnostoma latucelsum* Ross, L.Ord., USA(Utah), ×7.45 (after 49).——*K.* Nileid type, *Nileus armadillo* Dalman, Ord., Swed., ×1.5 (after 1, 1854, and 2).——*L.* Phacopid type, *Odontochile hausmanni* (Brongniart) Hawle & Corda, Dev., Bohemia, ×1.25 (after 2).——*M.* Trinucleid type, *Cryptolithus tesselatus* Green, M.Ord., USA(N.Y.), ×3 (after 70, and 85, 1930).——*N.* Harpid type, *Paraharpes hornei* (Reed) Whittington, U.Ord., Scot., ×2 (after 99, 1950).

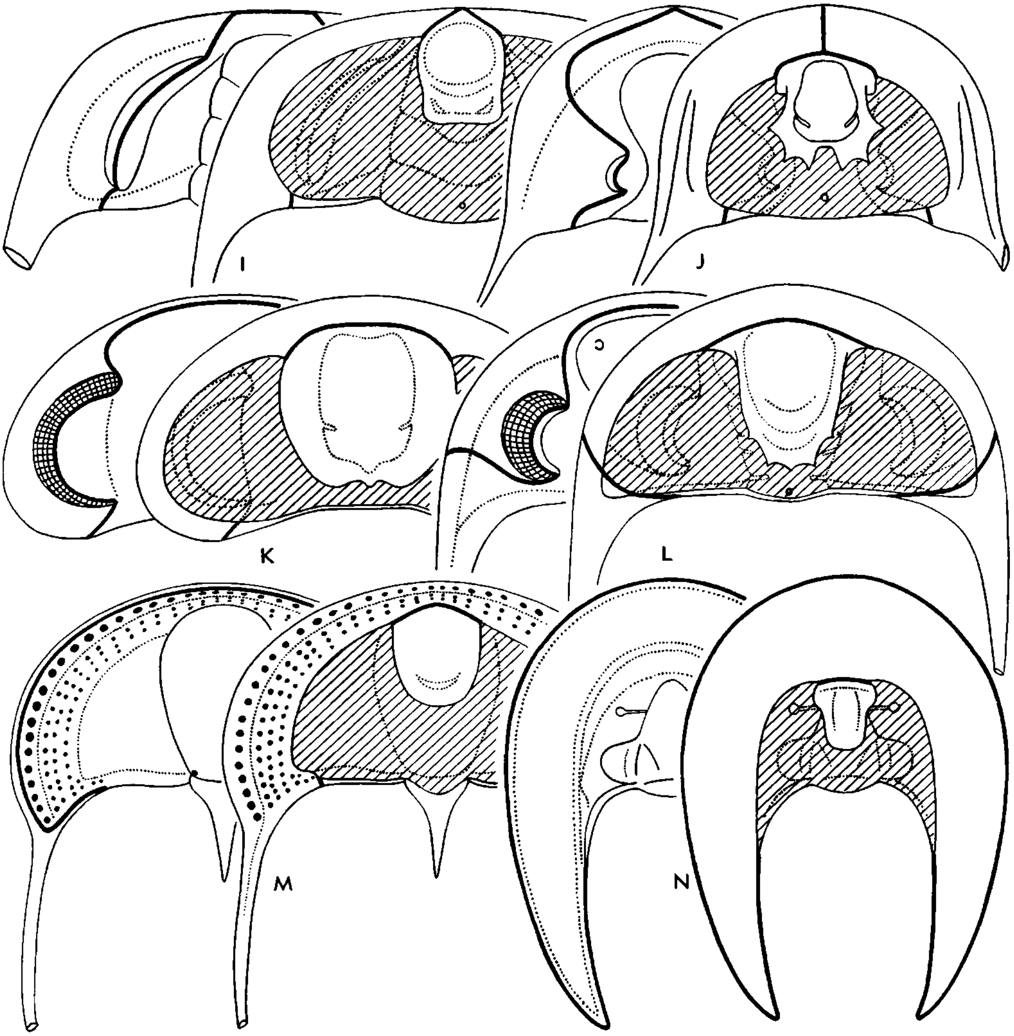


FIG. 48 *(Continued from facing page)*

swings inward-backward in a gentle curve across the base of the genal angle, finally ending at the inner edge of the ventral doublure (*Kjerulfia, Paedeumias, Holmia,* Fig. 48*B-D*). If the metaparian sutures of the olenellids is accepted as an ankylosed opisthoparian structure, the perrostral suture may be regarded as the equivalent of the rostral suture of most ptychopariid trilobites, and as the only part of the *grande suture* which has remained functional.

CONNECTIVE AND MEDIAN SUTURES

In most ptychopariids possessing a rostral plate, a pair of symmetrical sutures springs from the abaxial extremities of the rostral suture and crosses the anterior cephalic doublure so as to reach its inner edge. These are **connective sutures** that bound the rostral plate abaxially, separating it from the doublure of the librigenae. The connective sutures are usually wholly ventral, but in the Homalonotidae (Fig. 48*H*) they are partly dorsal. They may be (1) widely separated from each other (with rostral plate wide, *tr.*, as in *Dysplanus,* Fig. 48*E*); (2) very close to each other (rostral plate reduced to narrow band, as in Pliomeridae and Encrinuridae); or (3) they may converge to the mid-point of the internal edge of the doublure (rostral plate more or less triangular in outline, as in *Dipleura,* Fig. 48*H*).

In some trilobites, notably the Asaphidae (Fig. 48*J*), the connective sutures coalesce into a single **median** suture that runs along the sagittal line of the doublure, and the rostral plate disappears. In the Nileidae (Fig. 48*K*), which are closely related to the Asaphidae, the median suture disappears through ankylosis and the doublures of the librigenae are confluent along the sagittal line. The phacopid trilobites also lack a connective or median suture.

MARGINAL AND SUBMARGINAL SUTURES

Some trilobites, notably the Harpidae, which lack facial sutures, possess a **marginal suture,** which runs all along the outer edge of the cephalon separating the dorsal exoskeletal plate from the ventral doublure (Fig. 48*N*). In these trilobites, the suture is located along the mid-line of the cephalic rim, along the anterior and lateral margins, as well as adaxial margins of the prolongations. The suture is, therefore, wholly marginal.

In the Trinucleidae and Dionididae (*Cryptolithus,* Fig. 48*M*) the suture is marginal or dorsal-intramarginal almost all around the cephalon, but becomes dorsal near the posterolateral extremities of the shield, obliquely cutting over the base of the genal spines, which are connected directly with the ventral doublure (called "lower lamella" in the Trinucleidae). The suture, therefore, may be described as marginal to **submarginal** with dorsal posterior extremities. It is conceivable that the trinucleid suture may have been developed from facial sutures of cedariiform type, resembling those of *Orometopus,* suffering the following modifications: (1) backward migration of anterior sections of the sutures, passing through an entomaspidiform stage; (2) fusion of the anterior and posterior sections; and (3) ankylosis and final disappearance of the suture. This has been suggested by Rasetti (1952). The peculiar double metagenal ridges of *Dionide,* directed outward-backward toward the genal angles, suggest that they represent the ankylosed posterior and anterior sections of sutures of entomaspidiform type.

In the Raphiophoridae the suture is dorsal-intramarginal to submarginal with dorsal posterior extremities. In the Conocoryphidae it is submarginal to distinctly marginal, approaching the trinucleid condition (*Conocoryphe, Ctenocephalus*). This suture, however, is not homologous to the trinucleid suture, as it seems to have been derived from both the anterior and posterior sections of normal opisthoparian sutures that have migrated outward, as in the phacopid *Ductina* (Fig. 47*F*). The trinucleid suture, on the other hand, seems to have been developed almost exclusively from the anterior sections of opisthoparian sutures of entomaspidiform type.

HYPOSTOMAL SUTURE

The hypostoma of most trilobites was attached to the rostral plate or anterior cephalic doublure by means of a transverse **hypostomal suture** (Figs. 43, 48). Generally, this suture was functional in ecdysis, as indicated by the fact that hypostomas are usually found detached and isolated. Some authors, however, believe that the hypostomal suture may have had the character of a semirigid articulation, permitting slight movements of the hypostoma (such as rapid vibration) during the life of the animal. The warped curvilineal course of this suture in many trilobites, and the fact that the opposing edges of the hypostoma and doublure (or rostral plate) are cut normal to the surface of the exoskeleton, makes the possibility of any movement rather implausible.

In some trilobites belonging to different families (Olenellidae, Redlichiidae, Paradoxididae, Zacanthoididae, Oryctocephalidae), the hypostomal suture is in a state of complete symphysis, the hypostoma being fused with the rostral plate to form a single "rostral-hypostomal plate" (Fig. 44).

CEPHALIC TYPES DEFINED BY SUTURAL PATTERNS

Rasetti (1952) has attempted to systematize our knowledge concerning ventral cephalic sutures among Cambrian trilobites, distinguishing several types which he designated by the names of the characteristic genus or family portraying them. The classification of cephalic types here offered, modified from Rasetti's, with such additions as seem needed to cover both Cambrian and later trilobites, is based on the whole sutural pattern and takes into consideration the presence or absence of marginal, facial, connective, median, rostral, and hypostomal sutures.

Descriptive List of Trilobite Cephalic Types Defined by Sutural Pattern

Agnostid type. Cephalic sutures lacking; hypostoma absent (Fig. 48*A*). Absence of the hypostoma may be due to chitinous natures of this plate, nonmineralized in the living animal. Agnostida.

Eodiscid type. Like agnostid type, but probably with hypostoma joined to anterior doublure by hypostomal suture. Occurrence of hypostoma known only in *Pagetia* but judging by the close relationship between the Pagetiidae and Eodiscidae, probably the latter possessed a small hypostoma. Eodiscidae.

Olenellid type. Perrostral and hypostomal sutures functional, rostral plate large, crescentic; metaparian sutures may be present (Fig. 48*B*). Some Olenellidae, Daguinaspididae.

Holmiid type. Like olenellid type, but with hypostoma fused to rostral plate forming a single "rostral-hypostomal plate" (Fig. 48*D*). Some Olenellidae.

Paedeumiid type. Like olenellid type, but without hypostomal suture, hypostoma being connected with rostral plate by a narrow *(tr.)* stalk (Fig. 48*C*). *Paedeumias.*

Ptychopariid type. Facial, rostral, connective, and hypostomal sutures all functional (Fig. 48*E*). Most Ptychopariidae, Ellipsocephalidae, some Redlichiidae, and Paradoxididae, Ogygopsidae, Catillicephalidae, Proetidae, Otarionidae, Illaenidae, Thysanopeltidae, Styginidae, Phillipsinellidae, Calymenidae, Cheiruridae, Encrinuridae, Pliomeridae. Probably also the Pagetiidae, since it is likely that *Pagetia* had an anterior marginal (rostral) suture connecting the anterior sections of the facial sutures, and a wide rostral plate to which the hypostoma was connected by a functional hypostomal suture.

Dimeropygid type. Like ptychopariid type, but without hypostomal suture, hypostoma being connected with rostral plate by a narrow *(tr.)* stalk, which seems to be a backwardly directed prolongation of the rostral plate (Fig. 48*F*). *Dimeropyge.*

Corynexochid type. Like ptychopariid type, but with hypostomal suture in a state of complete symphysis, hypostoma being fused with rostral plate forming a single "rostral-hypostomal plate" (Fig. 48*G*). Some Redlichiidae, some Paradoxididae, Gigantopygidae, Corynechoxidae, Dolichometopidae, Dorypygidae, Zacanthoididae, *Hemirhodon, ?Hysterolenus.*

Oryctocephalid type. Like corynexochid type, but with connective sutures nonfunctional in ecdysis, though usually fairly well marked. Oryctocephalidae.

Homalonotid type. Facial, rostral, connective, and hypostomal sutures all functional; rostral suture dorsal-intramarginal; connective sutures partly dorsal and partly ventral, converging backward on cephalic doublure; rostral plate subtriangular, partly dorsal in position (Fig. 48*H*). Homalonotidae.

Bathynotid type. Facial sutures functional, marginal anteriorly; paired ventral sutures diverge from mid-point of cephalic margin toward inner edge of doublure, separating adaxial extremities of librigenal doublures from the hypostoma; rostral plate apparently absent, but probably fused with so-called hypostoma forming a "rostral-hypostomal plate" (paired ventral sutures being then regarded as true connective sutures); rostral suture absent (Fig. 48*I*). *Bathynotus.*

Asaphid type. Facial, median, and hypostomal sutures functional; rostral plate and suture absent; hypostoma connected with anterior doublures of librigenae (Fig. 48*J*). Asaphidae, *Theodenisia lata, T. spinosa, Stenopilus, Leiocoryphe gemma, Dikelocephalus raaschi, Housia, ?Proceratopyge.*

Nileid type. Facial, transverse ("rostral"), and hypostomal sutures functional; connective and median sutures absent (doublures of librigenae confluent anteriorly); rostral plate absent; hypostoma connected with anterior doublures of librigenae (Fig. 48*K*). Nileidae, Raphiophoridae, most Conocoryphidae, *Dikelocephalus retrorsus, D. subplanus, Levisella, Hungaia, Lauzonella, Loganellus, Leiocoryphe transversa, Rasettia.*

Olenid type. Like the nileid type, but with hypostoma separated from anterior cephalic doublure, supported only by ventral membrane. Olenidae.

Phacopid type. Like the nileid type, but with facial sutures (including transverse anterior suture, which may be dorsal-intramarginal) nonfunctional in ecdysis (Fig. 48*L*). Phacopidae, Dalmanitidae.

Trinucleid type. Marginal to submarginal sutures functional, becoming definitely dorsal across base of genal angles; hypostomal suture functional; facial sutures absent (Fig. 48*M*). Trinucleidae, Dionididae, Alsataspididae, Harpididae. (Characters of the marginal flange and method of numbering pits on the flange are illustrated in Figure 84.)

Harpid type. With functional wholly marginal suture all around cephalon and prolongations; hypostomal suture functional; facial and rostral sutures absent (Fig. 48*N*). Harpidae. (Characters of the harpid cephalon and nomenclature applied to parts are illustrated in Figure 85.)

It is believed that the ptychopariid type should be regarded as the primitive basic structural pattern of the whole class Trilobita. All other types can be considered as being secondarily derived from the ptychopariid by migration and regression of the dorsal and ventral sutures. For instance, it is abundantly clear that the fusion of the hypostoma with the rostral plate originated the corynexochid type independently in several Lower, Middle, and Upper Cambrian families and even in some Ordovician genera. The asaphid type appeared independently in some genera belonging to the Cambrian families Catillicephalidae (*Theodenisia*), Plethopeltidae (*Leiocoryphe, Stenopilus*), Dikelocephalidae (*Dikelocephalus*), and Housiidae (*Housia*), as well as in the Ordovician Asaphidae. The nileid type characterized by functional facial and hypostomal sutures and absence of connective and median sutures, appeared independently in the

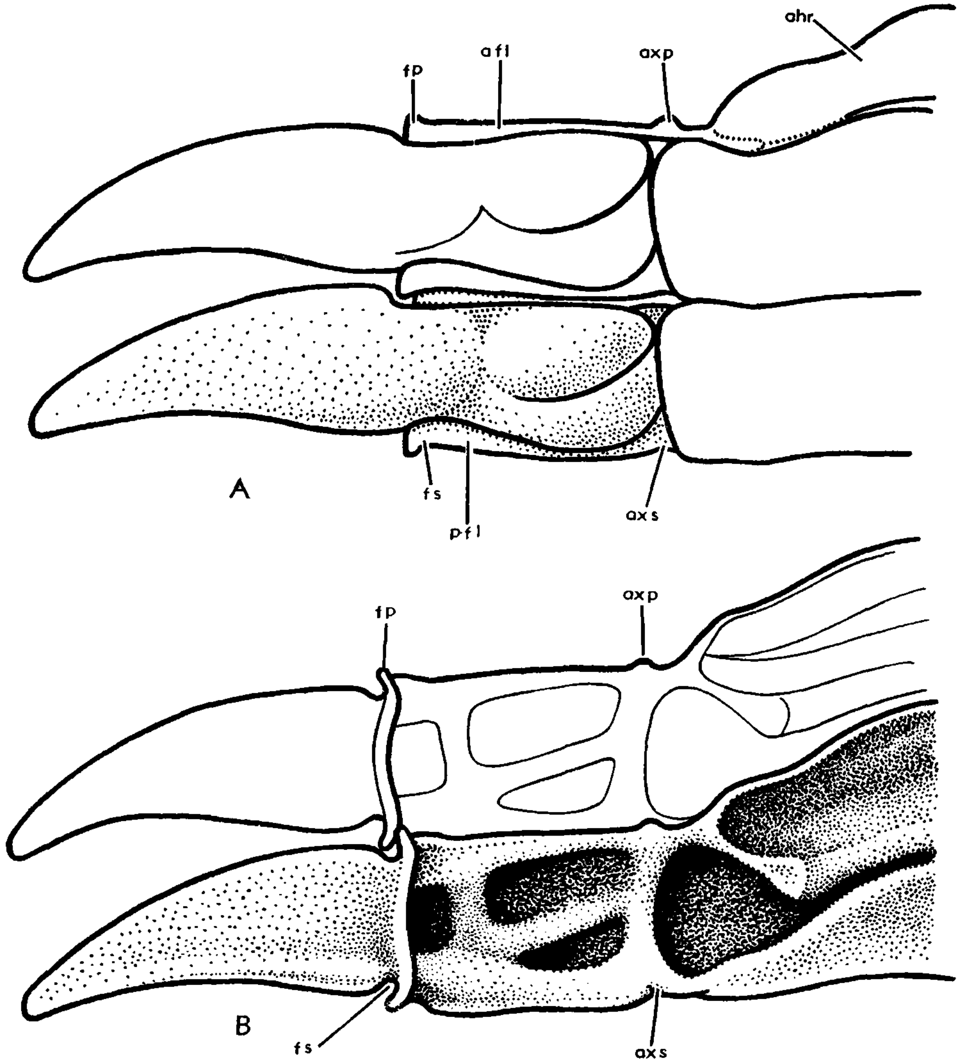


FIG. 49. Articulation of thoracic segments in *Ceraurinella typa* COOPER, M.Ord., USA(Virginia), ×8 (after 71).——*A*. Left half of 2 articulated thoracic segments, dorsal view.——*B*. Same, ventral (interior) view.——*C*. Left half of a thoracic segment, anterior view.——*D*. Same, posterior view.——*E*. Lateral view of 2 articulated thoracic segments. (Explanation: *afl*, anterior flange; *ahr*, articulating half-ring; *ap*, apodeme; *ax*, axial furrow; *axp*, axial process; *axs*, axial socket; *fp*, fulcral process; *fs*, fulcral socket; *im*, internal margin of flange; *pfl*, posterior flange.)

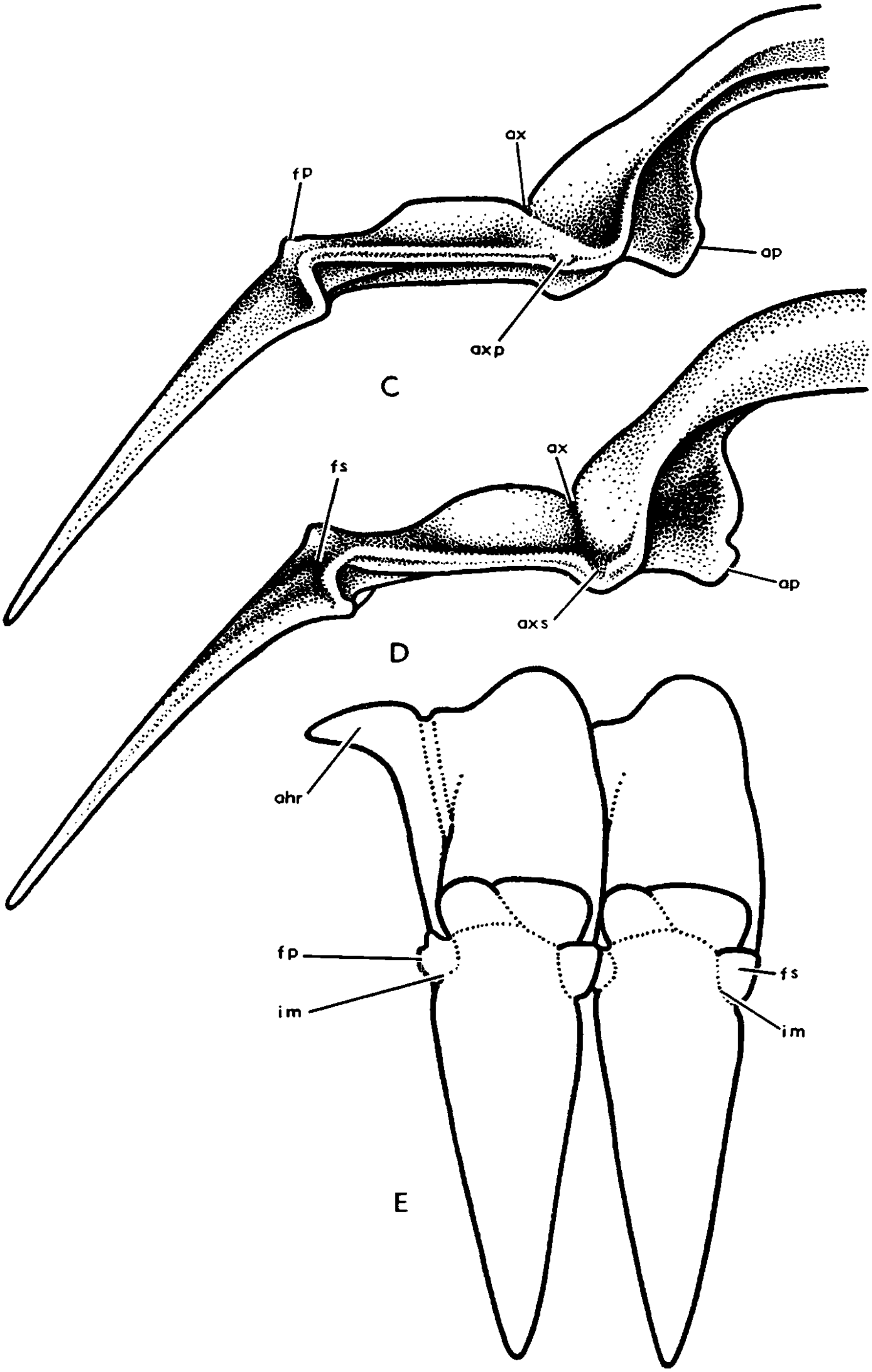


FIG. 49 *(Continued from facing page)*

Cambrian Hungaiidae *(Hungaia),* Lecanopygidae *(Rasettia),* and Loganellidae *(Lauzonella, Loganellus),* and in the Ordovician Nileidae. The outward migration of the facial sutures, *pari passu* with the outward migration, reduction, and final disappearance of the eyes, gave origin to the dorsal-intramarginal and submarginal sutures of many Conocoryphidae during Middle Cambrian time. The same pattern appeared independently in the Raphiophoridae during the Ordovician and even in such Upper Devonian genera as the phacopid *Ductina.* In this genus, however, the marginal suture was nonfunctional in ecdysis, betraying its derivation from the phacopid type.

THORACIC REGION

As in the case of the cephalon, distinction should be made between the thoracic region and the thorax. The **thoracic region** is here defined as comprising the ensemble of metameric somites interposed between the cephalon and the pygidium. Naturally, in practically every fossil trilobite, all that remains of the thoracic region is its dorsal exoskeletal covering or **thorax** proper, which in the living animal was formed of successive tergites articulating and movable upon each other.

The thorax is usually parallel-sided, slightly tapering backward, or somewhat spindle-shaped in dorsal outline. The number of thoracic segments ranges from 2 (Agnostida) to more than 40 (Olenellidae, Menomoniidae). Some families, and even taxa of suprafamilial rank, are characterized by a fixed number of thoracic segments. All the members of the suborder Agnostina have 2 segments, those of the family Eodiscidae have 3, and those of the family Asaphidae have 8. Generally, however, the number of thoracic segments is variable within a family and even within a single genus.

The thoracic tergites are formed of a median part, the **axial ring,** and paired lateral extensions, or **pleurae.** All successive axial rings together form the **axial region** or axis of the thorax, and all of the lateral pleurae taken together form the paired **pleural regions,** separated from the axis by longitudinal **axial furrows.** In a large majority of trilobites, the thoracic segments are fundamentally alike, differing only in a gradual decrease in size from the anterior to posterior segments (Fig. 28*B,C*). In most Olenellidae, however, 2 sharply different thoracic sections can be distinguished: an anterior part, or **prothorax,** comparable to the whole thorax of other trilobites, and a posterior part, or **opisthothorax,** characterized by very small and short *(tr.)* pleurae (Fig. 28*A*).

AXIAL RINGS

The axial portion of each thoracic somite has a mineralized dorsal covering **(mesotergite)** and a corresponding noncalcified softer sternite, which, by its very nature, is seldom if ever preserved.

The mesotergite consists of 2 parts of dissimilar size, the **axial ring** proper and the **articulating half-ring.** The name "ring" is an obvious misnomer, as the tergites are clearly not annular, but nothing would be gained by trying to uproot this well-entrenched term. The axial ring proper, forming the bulk of the mesotergite, is a comparatively narrow *(sag.)* and wide *(tr.)* band that is more or less convex transversely. It is always visible, whether the specimen has been preserved in an outstretched or enrolled attitude. The articulating half-ring is a crescentic extension of the anterior part of the mesotergite, separated from the axial ring proper by a transverse furrow. In outstretched specimens it is covered by the posterior part of the preceding ring, but it is plainly visible in enrolled individuals. The posterior border of each ring has a narrow ventral doublure which was connected to the anterior border of the succeeding articulating half-ring by a soft articulating membrane (Fig. 49). The transverse furrow separating the ring from its articulating half-ring may show paired invaginations of the dorsal integument projecting downward (ventrally). These are the **apodemes,** regarded as places of attachment of ventral appendage muscles (Fig. 49*C,D*).

The axial rings of different genera and species may show considerable differences as regard presence or absence of granules, mesial tubercles, or spines. In some genera, one or more of the axial rings may bear a **macrospine** which may project farther back than the posterior margin of the pygidium (Fig. 28*A*). In some species, paired tubercles are developed close to the axial furrows.

PLEURAE

The pleurae are comparatively narrow *(exsag.)* and long *(tr.)* lateral extensions of the thoracic tergites. They may be more or less flat, stretching horizontally outward *(Dionide)*, uniformly arched outward-downward *(Nileus)*, or strongly bent downward at their distal extremities *(Placoparia, Calymene)*. The distal extremity of the pleurae is reflected ventrally into a doublure, which may be narrow *(Calymene)* or wide *(Placoparia)*. In some specimens *(Ceratocephala)* it is projected downward in a secondary narrow fold. A thin membrane, attached to the adaxial margin of the doublure, covered the ventral side of the pleurae, leaving a thin body cavity between the calcified dorsal exoskeleton and the soft ventral integument.

In most trilobites the pleurae had a more or less marked geniculation or **fulcrum** located somewhere between their adaxial and abaxial ends. The adaxial (proximal) part, extending between the axial furrow and the fulcrum, articulated with the contiguous pleurae, whereas the abaxial (distal) part was free. Different articulating mechanisms between contiguous pleurae were developed in different trilobite stocks. In the most primitive Lower and Middle Cambrian forms, such as the Olenellidae, Redlichiidae, and Paradoxididae, no special devices were present, articulation being achieved by simple overlap of a narrow posterior strip of

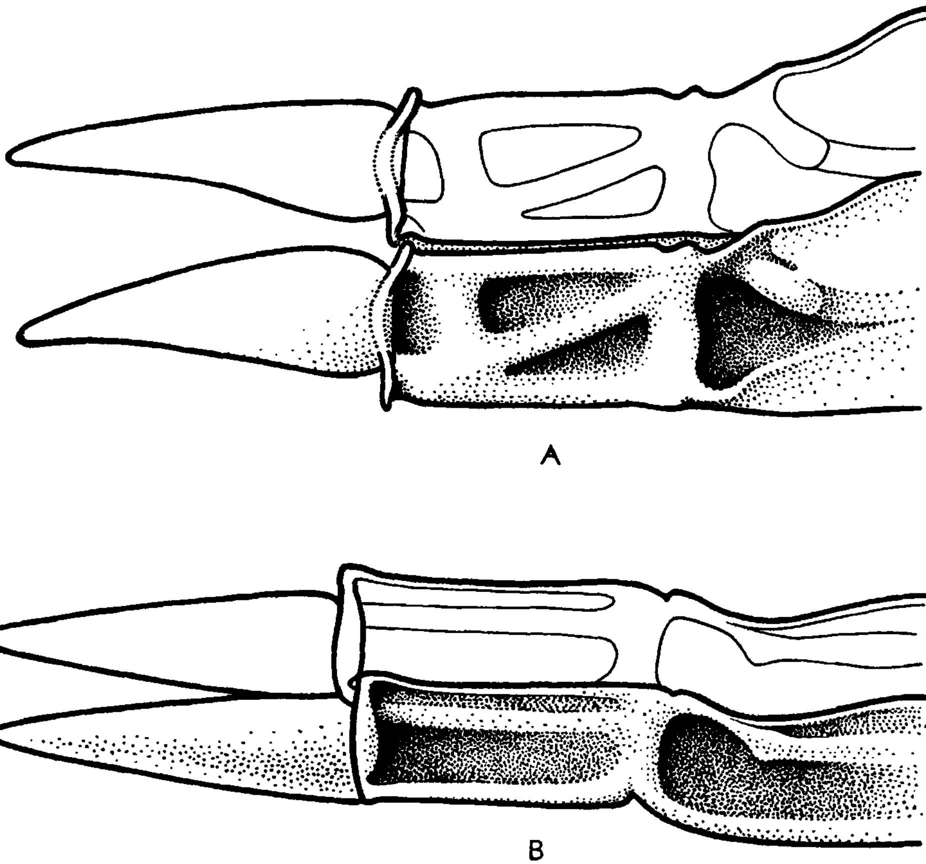


Fig. 50. Articulation of thoracic segments. Interior (ventral) view of left half of 2 articulated segments. ——*A. Ceraurus aculeatus* Eichwald, M.Ord., Estonia, ×3.3 (after 34).——*B. Rossaspis superciliosa* (Ross) Harrington, L.Ord., USA(Utah), ×18.3 (after 88, 1952).

one pleura over the anterior border of its neighbor immediately behind. Different articulating devices appeared in Late Cambrian and Ordovician trilobites, reaching a high degree of efficiency in the Cheiruridae and Pliomeridae. In some genera belonging to these families articulation was accomplished by a narrow raised band separated from the main body of the pleura by a fine submarginal furrow, the posterior edge of a pleura fitting into the submarginal furrow of the one immediately behind (Figs. 49, 50). The mechanism was complemented with bosses and corresponding sockets located along the margins of the contiguous pleurae. In certain trilobites, particularly the Asaphidae and Illaenidae, the doublure of the pleurae bears elongated crests or rounded bosses which represent special devices to prevent overgliding of the free extremities of the overlapping pleurae during enrollment (see panderian protuberances, p. O105).

Typically, each pleura is obliquely crossed by a **pleural furrow**, starting at the axial furrow opposite the anterior extremity of an axial ring and running outward-backward toward the distal extremity of the pleura. The pleural furrow marks off an anterior and a posterior pleural band. This type of furrowed pleura (*"plèvre à sillon"* in Barrande's terminology) characterizes almost all Cambrian trilobites and many later families, such as the Asaphidae, Proetidae, and Phacopidae. In many Ordovician and later trilobites, however, this primitive type suffered different important modifications. In some forms (Illaenidae, Homalonotidae, some Nileidae) the pleurae became smooth by the disappearance of the pleural furrows. In others, the 2 principal pleural bands fused into a single band by disappearance of the pleural furrow, while auxiliary bands were developed along the anterior and posterior edges of the pleurae. This type of banded pleura (*"pleura à bourrelet"* of Barrande) characterizes many Cheiruridae and Pliomeridae (Fig. 51).

The distal extremities of the pleurae may be rounded, truncate, or prolonged into spines of varying length. In some Odontopleuridae each of the pleural bands ends in a free spine and, in some species, auxiliary spines may be developed also. In many trilobites belonging to very different families, such as *Paedeumias* and *Olenellus* (Olenellidae), *Bathynotus* (Bathynotidae), *Albertella* (Zacanthoididae), *Anoria* (Dolichometopidae), *Shumardia* (Shumardiidae), *Promegalaspides* (Asaphidae), and *Hypodicranotus* (Remopleurididae), one pair of pleurae is considerably more developed than the rest, and the corresponding spines are far larger than the others. These **macro-**

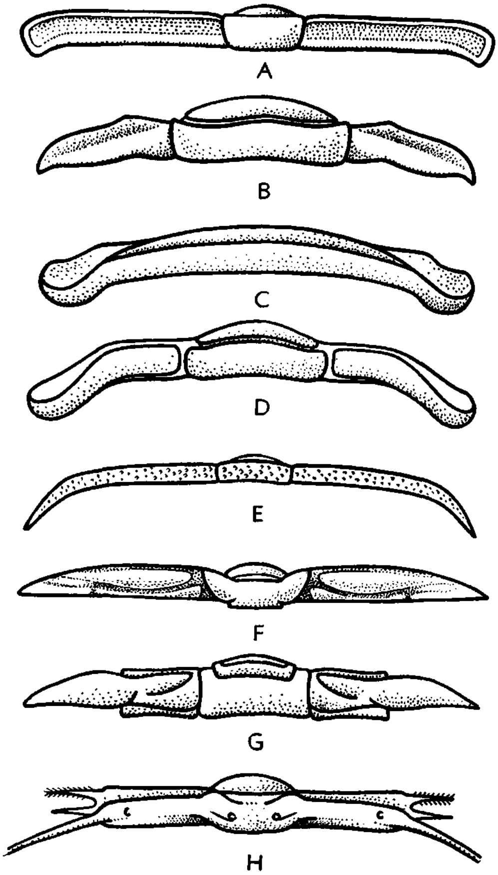


Fig. 51. Different types of thoracic segments.——*A. Hapalopleura clavata* Harrington & Leanza, L. Ord., S.Am.(Arg.), ×10.6 (after 19).——*B. Peltura scarabaeoides* (Wahlenberg) Milne Edwards, U.Cam., Swed., ×2.33 (after 97, 1923).——*C. Trimerus delphinocephalus* Green, M.Sil., USA(N.Y.), ×0.8 (after 17).——*D. Pliomera fischeri* (Eichwald) Angelin, M.Ord., Estonia, ×2.8 (after 34).——*E. Nieszkowskia capitalis* Öpik, Ord., Estonia, ×0.3 (after 34).——*F. Dichelepyge pascuali* Harrington & Leanza, L.Ord., E.Am.(Arg.), ×8.3 (after 19).——*G. Ceraurus aculeatus* Eichwald, Ord. Estonia, ×2.4 (after 34).——*H. Miraspis mira* (Barrande) Richter & Richter, M.Sil., Bohemia, ×3.75 (after 99, 1956).

pleurae were probably related to internal sexual organs.

In most trilobites having well-marked pleural fulcra, as the Asaphidae, Nileidae, Proetidae, and Phacopidae, the anterolateral extremity of the pleurae bears a subtriangular **articulating facet,** consisting of a smooth flat surface slanting forward-downward. This facet, also developed on the anterolateral angles of the pygidium, facilitated the gliding of the free extremities of the pleurae over one another. Articulating facets are absent in spiny or very long pleurae, as well as in those having auxiliary bands.

PYGIDIAL REGION

As for the cephalon and thorax, distinction should be made between pygidial region and pygidium proper. The **pygidial region** consists of several fused posterior somites, whereas the **pygidium** proper is formed of their exoskeletal coverings (tergites) fused dorsally into a single rigid plate. Exceptionally, as in some Olenellidae, the pygidium is formed of a single tergite. In all other trilobites it is formed of a variable number of segments, up to more than 30 in some Dionididae. Actually, however, the single-segmented pygidium of *Olenellus* and allied forms is not homologous to the pygidia of other trilobites. The typical olenellid pygidium is a true telson or caudal piece, the pygidia of other trilobites being the equivalent of the ensemble of opisthothorax plus "pygidium" of the Olenellidae. The reduction and "caudalization" of the opisthothorax was already achieved by some Olenellidae, as is plainly shown in the subfamily Holmiinae.

The relative size of the pygidium compared with the cephalon has taxonomic importance. A trilobite is said to be **micropygous, macropygous,** or **isopygous** according to whether the pygidium is smaller, larger, or subequal in size as compared to the cephalon.

Typically, the pygidium of trilobites is semielliptical in outline, but important departures from this basic shape are numerous and sharply marked (Fig. 52). Its convexity, both transverse and longitudinal, is also variable in different genera, for pygidia range from almost flat in some Dionididae to highly inflated and globose in such genera as *Pemphigaspis* and *Leiagnostus.*

The pygidium of most trilobites, being formed by the fusion of several tergites fundamentally like those of the thorax, also show an axial and paired pleural region (Fig. 53).

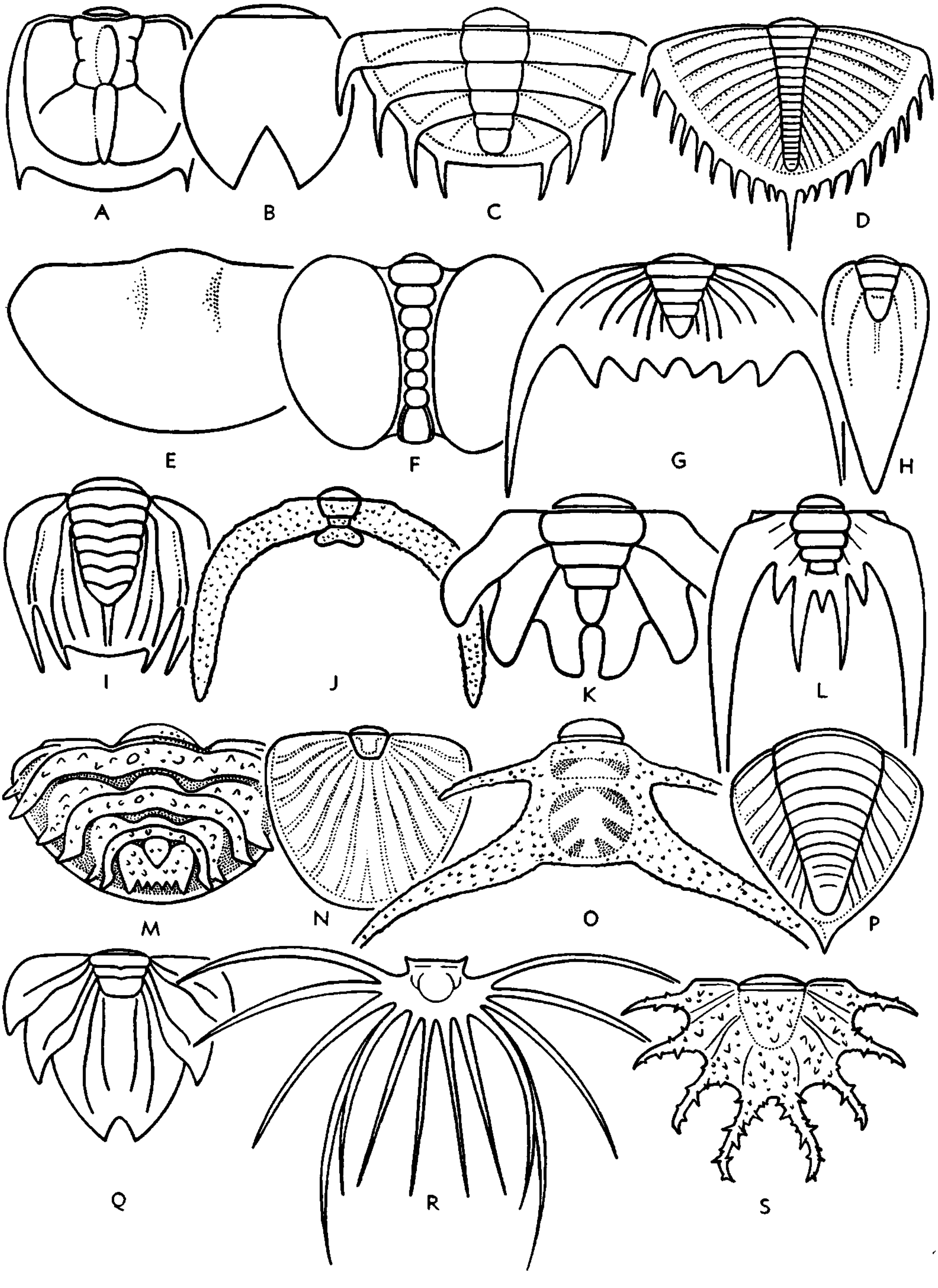
AXIS

The axial region or axis of the pygidium is formed of a succession of **axial rings** separated by transverse ring furrows. The segmentation varies from well marked to obsolete, the latter giving a smooth appearance to the axis. In many pygidia, particularly large ones, segmentation is well marked on the anterior part of the axis but progressively obsolete toward the rear, so that often it is impossible to determine the true number of fused segments. The axis may end with an unsegmented **terminal piece** that is more or less sharply marked off from the well-segmented part. A **postaxial ridge** may extend from the rear end of the axis toward the posterior margin of the pygidium (Fig. 53).

PLEURAL REGIONS

The axis is separated from the pleural regions on either side by **axial furrows.** The pleural regions, extending from these furrows to the margins of the pygidium, are usually more or less convex. In many pygidia they display well-marked segmentation, resulting from the fusion of several pleurae similar to those of the thorax. Typically, the pleural regions are crossed obliquely by 2 different sets of furrows. The most conspicuous and well defined are usually true **pleural furrows,** corresponding to the furrows of the thoracic pleurae. The 2nd set consists of **interpleural furrows,** typically finer and less impressed, representing the line of fusion of 2 successive pleurae. Both sets of furrows usually curve outward-backward across the pleural regions, but the pleural furrows, starting at the axial furrows opposite the anterolateral extremities of the axial rings, have an oblique direction with respect to that of the interpleural furrows (Fig. 53). In some trilobites there are as many pleural segments as axial rings, but in many genera, especially those characterized by large pygidia, the correspondence between axial rings and pleural segments is lost from front to back, the number of axial rings being greater than that of pleural segments.

In many trilobites, the fusion of the pygidial pleurae is complete and interpleural furrows disappear. Then, only the pleural furrows remain, marking off smooth **ribs**



that result from complete fusion of the posterior band of a pleura with the anterior band of one immediately behind it (Fig. 53). In some species, however, the reverse is true, the pleural furrows becoming obsolete and only the interpleural furrows remaining, marking off true pleurae. Lastly, in the so-called "smooth trilobites," both the pleural and interpleural furrows disappear, the pleural regions losing all or nearly all vestiges of their segmentation. In extremely modified pygidia even the axial furrows disappear, giving rise to a uniformly convex, smooth plate (Fig. 27).

The pleural and interpleural furrows may reach the margin of the pygidium or end at some distance from it. In many trilobites, a smooth convex or concave **border,** more or less well defined by a border furrow, is present around the lateral and posterior margins. The term **pleural field** is then applied to that part of the pleural regions extending between the axis and the border (Fig. 53).

The pygidium is reflected ventrally into a **doublure.** Though no absolute correspondence exists, it seems that, generally speaking, the doublure is wide if the pygidial axis is narrow. No ventral sternites are known in the pygidium. It is probable that the so-called "anal plate" described by BEECHER and RAYMOND from a few specimens of *Triarthrus eatoni* with ventral appendages preserved, is nothing more than the tips of the last, tiny pairs of biramous appendages protruding from beneath the posterior pygidial margin.

Many pygidia bear **marginal spines,** which are actually projections of the dorsal integument and doublure. These may be paired lateral spines, or mesial spines projecting from the posterior margin. In most fossils, the lateral spines are direct continuations of the pygidial pleurae. Whereas in some genera *(Ctenopyge, Coronura, Pliomera, Cromus)* each pleura ends in a free spine, in others *(Hartshillina, Vanuxemella, Housia, Marjumia,* some Olenidae) only a fraction of the pleurae are spinose, part of the pygidial margin being entire. In a few trilobites, such as *Ceratopyge,* the lateral spines spring from the posterior band of one pleura fused with the whole pleura next behind it, whereas in many others belonging to the families Yinitidae, Crepicephalidae, Dikelocephalidae, Dikelocephalinidae, Taihungshaniidae as well as in some Zacanthoididae, the spines spring from 2 or more fused pleurae, correspondence between the spines and pleural segmentation being usually very obscure or lost entirely. In a few genera (e.g., *Thysanopyge*) the correspondence between spines and pleural segments, plainly seen in young holaspid specimens, is lost after successive molts, the large individuals having irregularly distributed spines that commonly do not coincide in number from one margin to the other.

The mesial spine carried by many trilobites may be either a true **posterior spine,** springing from the border and doublure and disconnected from the axis *(Thysanopyge, Kayseraspis, Anchiopsis, Eocyphinium),* or a **terminal axial spine** that forms a posterior projection of the pygidial axis *(Symphysurina, Xenostegium).*

(See facing page)

FIG. 52. Different shapes and segmentation of pygidia.——*A. Machairagnostus tmetus* HARRINGTON & LEANZA, L.Ord., S.Am.(Arg.), ×12.3 (after 19).——*B. Wanneria walcottana* (WANNER) WALCOTT, L. Cam., USA(Pa.), ×5.3 (after 64).——*C. Parabolina heres* BRØGGER, U.Cam., Swed., ×8 (after 97, 1923). ——*D. Thysanopyge argentina* KAYSER, L.Ord., S.Am.(Arg.), ×0.45 (after 19).——*E. Illaenus crassicauda* (WAHLENBERG) DALMAN, Ord., Swed., ×2.6 (after 79, 1954).——*F. Pemphigaspis bullata* HALL, U.Cam., USA(Minnesota), ×6 (after 82, 1951).——*G. Pseudokainella keideli* HARRINGTON, L.Ord., S.Am. (Arg.), ×14 (after 19).——*H. Macropyge chermi* STUBBLEFIELD, L.Ord., Eng., ×4.3 (after 93, 1927). ——*I. Kainella billingsi* (WALCOTT) WALCOTT, U.Cam., Can.(B.C.), ×0.85 after 96, 1925).——*J. Holia secristi* WHITTINGTON & EVITT, M.Ord., USA(Virginia), ×12.2 (after 71).——*K. Sphaerexochus pulcher* WHITTINGTON & EVITT, M.Ord., USA(Virginia), ×7 (after 71).——*L. Ceraurus aculeatus* EICHWALD, M. Ord., Estonia, ×2 (after 34).——*M. Dimeropyge virginiensis* WHITTINGTON & EVITT, M.Ord., USA(Virginia), ×27 (after 71).——*N. Scutellum brevifrons* (BARRANDE), U.Sil., Bohemia, ×0.65 (after 2).——*O. Deiphon forbesi* BARRANDE, L.Sil., Bohemia, ×11.3 (after 2).——*P. Trimerus delphinocephalus* GREEN, U.Sil., Eng., ×0.65 (after 89, 1865).——*Q. Dicranopeltis scabra* (BEYRICH), Ord. Bohemia, ×0.81 (after 2).——*R. Ancyropyge romingeri* (HALL & CLARKE) CLARKE, M.Dev., USA(Michigan), ×1.33 (after 17). ——*S. Terataspis grandis* HALL, M.Dev., USA(N.Y.), ×0.15 (after 91, 1944).

VENTRAL APPENDAGES

Ventral appendages of trilobites are very rarely preserved. Although EICHWALD, as far back as 1825, and later BILLINGS in 1870, had correctly described and interpreted fragmentary appendages, they failed to convince the majority of specialists as to trustworthiness of their studies. It was not until 1876, when WALCOTT first published his observations on trilobite biramous appendages, that these structures came to be recognized as such.

Ventral appendages of some 19 species of trilobites have been described up to the present, but only in 5 species are all the appendages known. The following list tabulates all such species, with citation of age, locality, mode of preservation, papers dealing with the description of the appendages, and kind of appendages known.

Trilobite Species and Ventral Appendages Studied

Olenellidae

Olenellus getzi DUNBAR, *L.Cam.* (Kinzers Formation), Rohrerstown, Pa., USA. Single specimen preserved in shale. DUNBAR, 1925. .... Antennae

Dorypygidae

Olenoides serratus (ROMINGER) KOBAYASHI [=*?Nathorstia transitans* WALCOTT], *M.Cam.* (Burgess Shale, Stephen Formation), Burgess Pass, B.C., Canada. Several complete specimens preserved in shale. RAYMOND regarded type specimen of *N. transitans* as a "recently molted *O. serratus,* still in the 'soft-shelled' condition." WALCOTT, 1912, 1918, 1921; RAYMOND, 1920; STØRMER, 1939, 1951 .... All appendages

Kootenia dawsoni (WALCOTT) WALCOTT, *M. Cam.* (Burgess Shale, Stephen Formation), Burgess Pass, B.C., Canada. Single specimen preserved in shale. WALCOTT, 1918. ....Limbs

Alokistocaridae

Elrathina cordillerae (ROMINGER) RESSER, *M. Cam.* (Burgess Shale, Stephen Formation). Burgess Pass, B.C., Canada. Single incomplete specimen preserved in shale. WALCOTT, 1918. Fragmentary limbs

Ehmaniella burgessensis RASETTI [=*Ptychoparia permulta* WALCOTT *(partim)*]. *M.Cam.* (Burgess Shale, Stephen Formation), Burgess Pass, B.C., Canada. Single specimen preserved in shale. WALCOTT, 1918. ....Antennae

Olenidae

Westergaardia lata (MATTHEW) HENNINGSMOEN, *U.Cam.* (Acerocare Zone), Sandby, Skåne, Sweden. Single cephalon preserved in black limestone. WESTERGÅRD, 1909, 1922. .... Antennae

Triarthrus eatoni (HALL) RUEDEMANN [=*T. becki* AUCTT. (*non* GREEN), *M.Ord.* (Utica Shale), Holland Patent, Rome, N.Y., USA. Several complete pyritized specimens in black shale. BEECHER, 1895; WALCOTT, 1918, 1921; RAYMOND, 1920; STØRMER, 1939. .... All appendages

Asaphidae

Isotelus arenicola RAYMOND, *L.Ord.* (Aylmer Formation), Britannia, Ont., Canada. Single ventral impression in sandstone. RAYMOND, 1910, 1930. ....Fragmentary limbs

Isotelus gigas DEKAY, *M.Ord.* (Trenton Limestone), Trenton Falls, N.Y., USA. Single specimen preserved in limestone. WALCOTT, 1881; RAYMOND, 1920. ....Fragmentary limbs

Isotelus maximus LOCKE, *M.Ord.* (Richmond Group), Oxford, Ohio, USA. Single fragmentary specimen preserved in limestone. MICKLEBOROUGH, 1883; WALCOTT, 1918; RAYMOND, 1920. ....Fragmentary limbs

Isotelus latus RAYMOND, *M.Ord.* (Trenton Limestone), Ottawa, Ont., Canada. Single fragmentary specimen preserved in limestone. BILLINGS, 1870; RAYMOND, 1920. .... Fragmentary limbs

Asaphus cornutus PANDER, *M.Ord.* Baltic region of Russia. Single specimen preserved in limestone. HUPÉ, 1949. ....?Limb

Trinucleidae

Cryptolithus tessellatus GREEN, *M.Ord.* (Utica Shale), Holland Patent, Rome, N.Y., USA. Thirteen pyritized specimens preserved in black shale. BEECHER, 1895; RAYMOND, 1920; WALCOTT, 1921; STØRMER, 1939. ....All appendages

Cheiruridae

Ceraurus pleurexanthemus GREEN, *M.Ord.* (Trenton Limestone), Trenton Falls, N.Y., USA. Several complete specimens preserved in limestone. WALCOTT, 1881, 1918, 1921; RAYMOND, 1920; STØRMER, 1939, 1951. ....Limbs

Calymenidae

Flexicalymene senaria (CONRAD) SHIRLEY, *M.Ord.* (Trenton Limestone), Trenton Falls, N.Y., USA. Several complete specimens preserved in limestone. WALCOTT, 1918, 1921; RAYMOND, 1920; STØRMER, 1939. ....Limbs

Odontopleuridae

"*Acidaspis trentonensis* HALL" (identification of specimen somewhat doubtful), *M.Ord.* (Utica Shale), Holland Patent, Rome, N.Y., USA. Single specimen preserved in black shale. RAYMOND, 1920. ....Fragmentary limbs

Phacopidae

Phacops sp., *L.Dev.* (Hunsrück Shale), Bundenbach, Germany. Four complete specimens, partly pyritized and partly silicified, preserved in black shale. Broili, 1929, 1930; Størmer, 1939. ....All appendages

Dalmanitidae

Asteropyge sp., *L.Dev.* (Hunsrück Shale), Bundenbach, Germany. Single complete specimen, partly pyritized and partly silicified, preserved in black shale. Broili, 1930. ....All appendages

Incertae Sedis

Gen. et sp. indet., *L.Ord.* (Shumardia Limestone, Levis Formation), Levis, Quebec, Canada. Single detached appendage. Clark, 1922 ..?Limb

Ventral appendages have been preserved under exceptional circumstances. In some fossils, such as specimens from the famous Middle Cambrian Burgess Shale of British Columbia obtained by Walcott, they appear as extremely fine impressions coated with a very thin silvery film. In others, as in specimens from the Middle Ordovician Utica Shale of New York and Lower Devonian Hunsrück Shale of Germany, the appendages are partly pyritized; these sediments are very fine-grained mudstones. Excellent specimens are also found in limestones, such as Middle Ordovician remains collected in the Trenton Limestone of New York and eastern Canada; the exceptional preservation of soft parts is due to entombment of enrolled or partially enrolled individuals in an extremely fine mud.

Generally, elaborate and time-consuming techniques are necessary to uncover the appendages and to prepare them for study. Enrolled or partially enrolled trilobites preserved in limestone can best be investigated by means of serial sections. Interpretation of the true structure of appendages is, at best, a difficult matter, subject to considerable divergence of opinion among specialists. The fundamental papers on the subject are by Walcott (1918, 1921), Raymond (1920), and Størmer (1939, 1951). Størmer's interpretations, which show considerable departure from the views of previous authors, will be followed here in the main.

Though a sweeping generalization based on the evidence furnished by only 19 species belonging to 15 genera is somewhat risky, we can accept with a certain degree of confidence the conclusion that trilobites possessed a pair of multijointed uniramous antennae succeeded by a variable number of nondifferentiated biramous appendages, 4 pairs of which were cephalic. Antenniform cerci have been discovered in a single species.

ANTENNAE

These appendages are known in 8 species of trilobites, ranging in age from Early

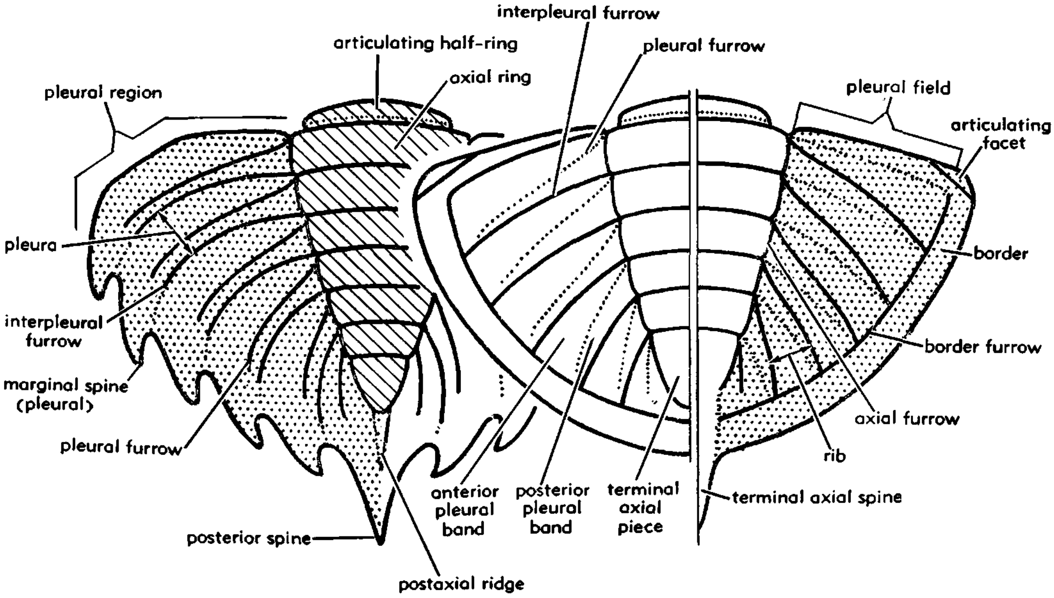


Fig. 53. Pygidial nomenclature.

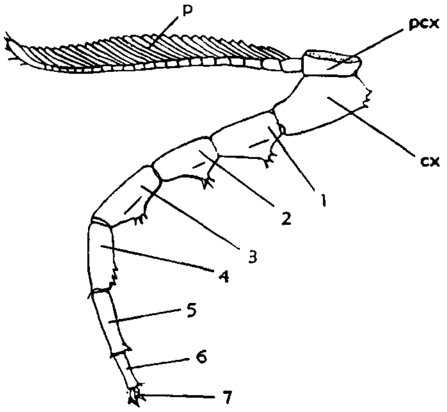


FIG. 54. General plan and terminology of the trilobite biramous appendage (after 56). (Explanation: *cx,* coxa; *p,* pre-epipodite; *pcx,* precoxa; *1,* trochanter; *2,* prefemur; *3,* femur; *4,* patella; *5,* tibia; *6,* tarsus; *7,* pretarsus; *1-7,* telopodite.)

Cambrian to Early Devonian. The antennae are, in all observed examples, multijointed and uniramous. They were attached to the ventral membrane close to the lateral margins of the hypostoma and, in some genera *(Cryptolithus),* directly below the dorsal fossulae or "anterior pits."

The 1st (basal) joint of the antennae is usually somewhat larger than the remainder. It is succeeded by a variable number of shorter segments, which become smaller toward the distal tip of the appendage. In *Cryptolithus,* where the joints are elongated in shape, only 15 or 20 are counted. In other trilobites, where the joints are shorter than their width or about as long as wide, their number is considerably greater: 30 in *Phacops,* 35 to 40 in *Asteropyge,* 40 in *Ceraurus,* and between 40 and 50 in *Triarthrus* and *Olenoides.* In the last-named genus, the joints carry short bristles.

The length of the antennae varies from genus to genus. In *Westergaardia* they are slightly shorter than the cephalon, in *Phacops* as long as the cephalon, and slightly longer in *Olenellus.* In *Ehmaniella* they are about 1.5 times the length of the cephalon, and in *Triarthrus* about twice this length. In *Olenoides* their length approximately equals that of the cephalon plus thorax, and in *Asteropyge* it is about equal to ⅔ of the total length of the dorsal exoskeleton.

In *Olenellus, Westergaardia,* and *Ehmaniella,* the antennae seem to have been rather stiff and nearly straight, directed forward and slightly outward, diverging at different angles. In *Olenoides, Triarthrus, Ceraurus, Phacops,* and *Asteropyge,* they were evidently very flexible. In *Olenoides, Triarthrus,* and *Ceraurus,* they were directed forward and S-shaped. In *Phacops* and *Asteropyge,* they seem to have been gently curved and directed outward and slightly backward. In *Cryptolithus,* they were also slightly curved but directed almost straight backward, passing below the adaxial parts of the biramous appendages and stretching as far back as the level of the anterior border of the pygidium.

BIRAMOUS APPENDAGES

The paired biramous appendages of trilobites, which apparently served the triple purpose of ambulatory, natatory, and respiratory organs, were nondifferentiated among themselves other than by location and size. The evidence available shows that, in any given genus, all the appendages were very similar in structure and shape, the only differences noted between successive pairs being a general increase in size from the 1st to the 3rd cephalic pair, and then a general decrease to the last pygidial pair.

Most authorities are agreed that 4 pairs of appendages were cephalic and postoral in position, the remainder being thoracic and pygidial, a pair of biramous appendages being attached to each postcephalic somite (with the exception of the last pygidial segment, which seems to have been apodous or in some genera to have carried caudal rami). The appendages were attached to the thickened ventral integument along the anterior half of each sternite at a place located about midway between the sagittal line and the axial furrow, directly below the ventral tips of the apodemes (when present).

The biramous appendages of all species in which they have been preserved, show that invariably they were built on the same general plan (Fig. 54). The appendages consist of 2 branches: (a) a principal "walking leg" or **telopodite,** and (b) a secondary "gill-bearing branch" or **pre-epipodite.** The appendage was attached to the ventral integument by means of a basal segment, the **precoxa,** succeeded by a considerably larger podite called the **coxa** (or coxopodite). The ensemble of precoxa and coxa is usually termed **protopodite.** Contrary to previous assertions, Størmer has shown that the inner outgrowth (endite) of the coxa (basiendite), is feebly developed and cannot be regarded as a gnathobase.

The principal branch of the appendage, the telopodite, springs from the coxa. It is formed of 7 successive articulating podites called trochanter, prefemur, femur, patella, tibia, tarsus, and pretarsus. All joints, except the distal pretarsus, are similar in structure, being subcylindrical in shape with somewhat flattened sides. The ventral side of the trochanter, prefemur, and femur (*Triarthrus,* Fig. 55*A,B*), and in some genera (*Cryptolithus,* Fig. 55*C,D*) also of the patella, was produced into subtriangular endites bearing spines or bristles. In some species, spines or bristles are found also on the flattened sides and on the distal margins of the segments. The tibia and tarsus are usually more tubular in shape and more slender than other limb segments, the tarsus being considerably smaller than the tibia. The distal joint, or pretarsus, consists of a small basal plate (equivalent to the pseudonychium of some Recent Arachnida) bearing a tripartite claw formed of 3 diverging spines, the mesial spines being longer than the others (Fig. 57*C,D*). The telopodite had no well-marked knee, the articulations between successive podites being of subequal importance.

The pre-epipodite, or gill branch, sprang from the precoxa and, in the living animal, it occupied a dorsal position with respect to the telopodite. It was usually shorter than the telopodite and, except in *Triarthrus,* it did not extend beyond the pleural extremities. The pre-epipodite, especially characteristic of the trilobite limb, was essentially formed of an elongated shaft bearing a fringe of bladelike filaments. Certain differences are evident when the pre-epipodites of different genera are compared, even if they can all be reduced to a common basic type. In *Cryptolithus, Triarthrus, Phacops,* and *Asteropyge,* the shaft is narrow, rodlike, and divided into numerous (15 to 20) subsegments. The bladelike filaments are directly attached to the shaft, but the distal spoon-shaped portion of the shaft bears no filaments, being provided, instead, with thin bristles or setae. In *Olenoides* and *Kootenia*

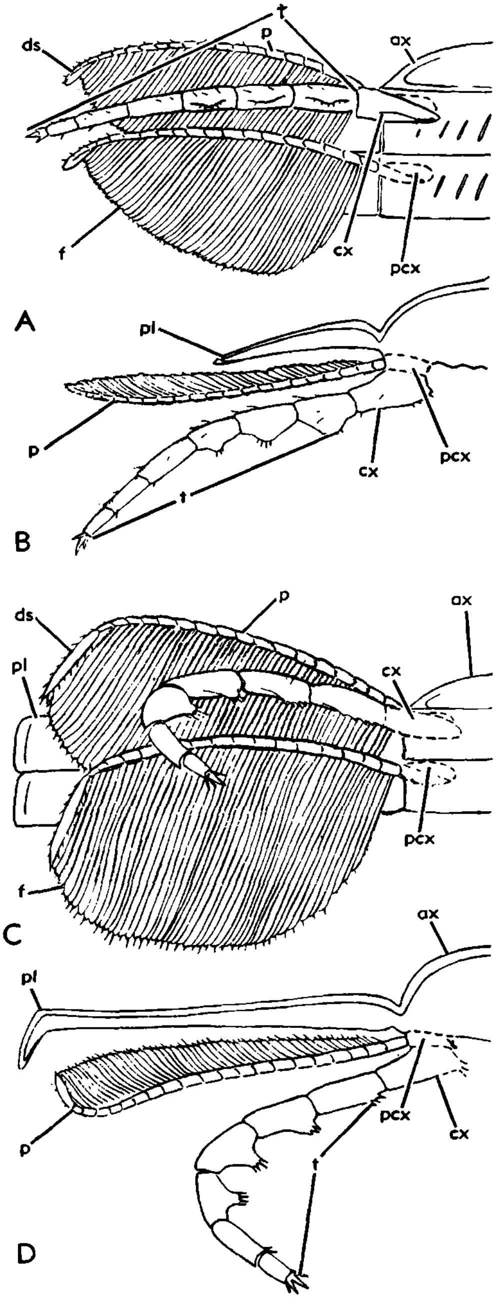


Fig. 55. Diramous appendages of trilobites; reconstructions of the appendages of 2 thoracic segments (after 56).——*A,B. Triathrus eatoni* (Hall) Ruedemann, M.Ord., USA(N.Y.); *A,* ventral view; *B,* anterior view, ×5.——*C,D. Cryptolithus tesselatus* Green, M.Ord., USA(N.Y.); *C,* ventral view; *D,* anterior view, ×14. (Explanation: *ax,* axis; *cx,* coxa; *ds,* distal segment of pre-epipodite; *f,* filaments; *p,* pre-epipodite; *pcx,* precoxa; *pl,* pleura; *t,* telopodite.)

(Fig. 56*B-D*), the rodlike shaft forms the anterior ridge of a rather broad paddle-shaped or spatulate lobe bearing faint traces of transverse segmentation, the filaments being attached to the posterior border of the lobe. A distal, subtriangular segment is clearly defined from the main part of the spatulate lobe, but contrary to what hap-

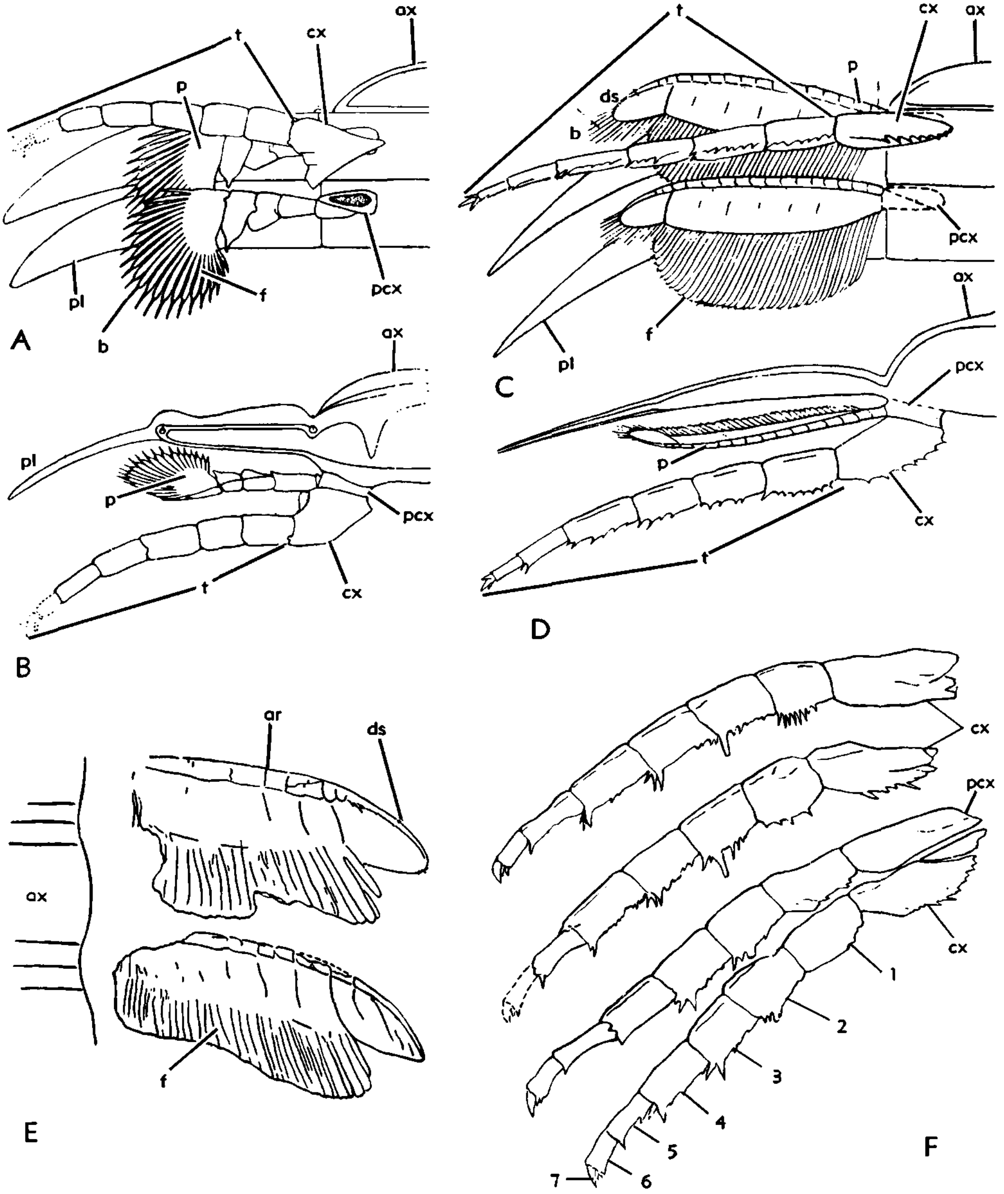


FIG. 56. Biramous appendages of trilobites.——*A-D*. Reconstructions of the appendages of 2 thoracic segments; *A,B, Ceraurus pleurexanthemus* GREEN, M.Ord., USA(N.Y.) (after 24, from 56); *A*, ventral view; *B*, anterior view, ×6.35; *C,D, Olenoides serratus* (ROMINGER) KOBAYASHI, M.Cam., Can.(B.C.) (after 56); *C*, ventral view;*D*, anterior view, ×2.——*E*. Pre-epipodites of *Kootenia dawsoni* (WALCOTT) WALCOTT, M.Cam., Can.(B.C.), ×5 (after 56).——*F*. Telopodites of *Olenoides serratus* (ROMINGER) KOBAYASHI, M.Cam., Can.(B.C.), ×3.3 (after 56). (Explanation: *ar*, anterior ridge of pre-epipodite; *ax*, axis; *b*, bristles; *cx*, coxa; *ds*, distal segment of pre-epipodite; *f*, filaments; *p*, pre-epipodite; *pcx*, precoxa; *pl*, pleura; *t*, telopodite; *1-7*, segments of telopodite.)

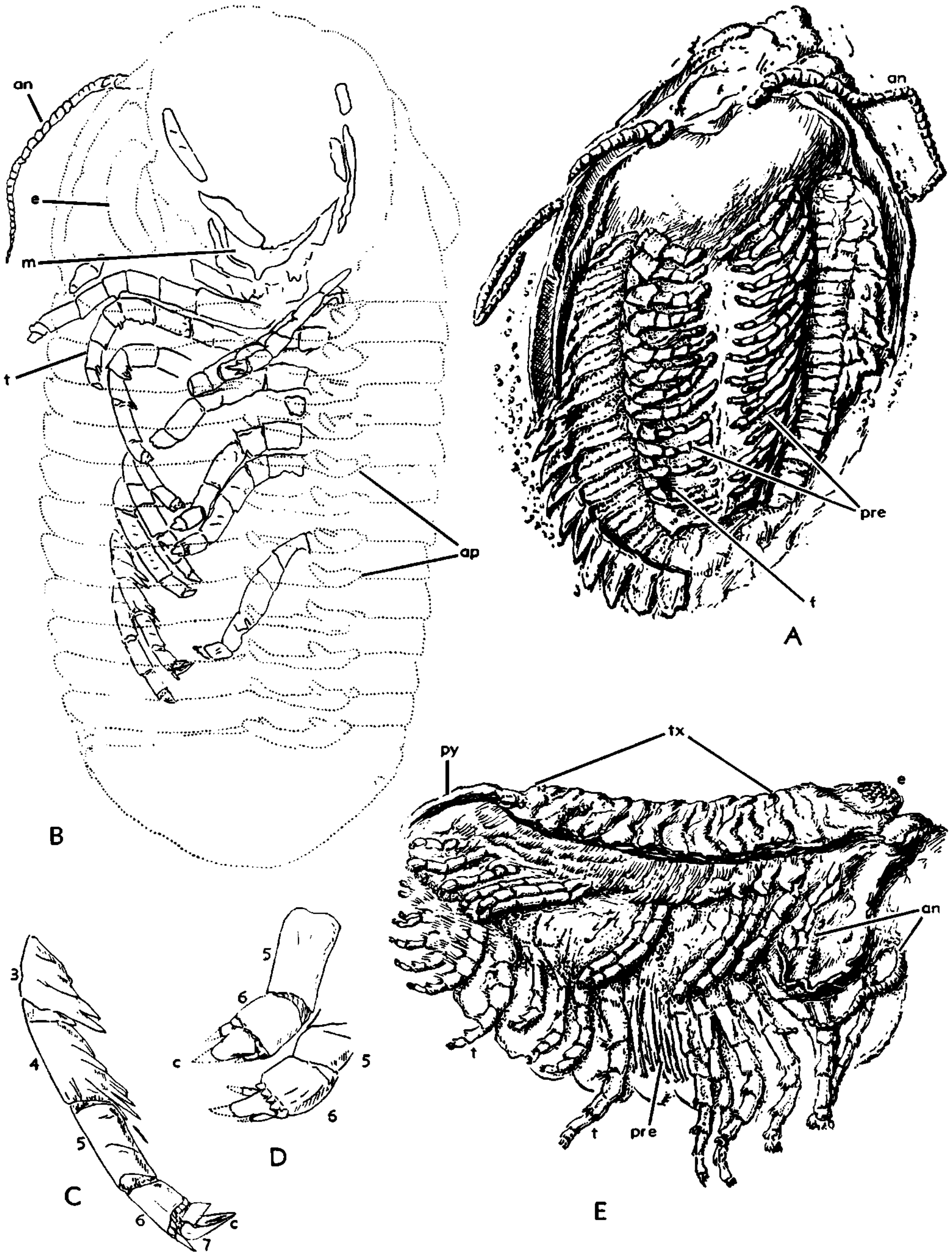


Fig. 57. Ventral appendages of trilobites.——*A. Asteropyge* sp., L.Dev., Ger., ×2; ventral view of specimen lacking cephalic biramous appendages (after 72).——*B-E. Phacops* sp., L.Dev., Ger.; *B,* ventral view of specimen retaining several telopodites, right antenna, and metastoma, ×1.33; *C-E,* enlargment of fragmentary telopodites, showing distal claw, ×3.7 (after 55); *F,* lateral view of specimen showing biramous appendages and antennae, ×0.75 (after 72). (Explanation: *an,* antenna; *ap,* apodeme; *c,* claw; *e,* eye; *f,* filaments; *m,* metastoma *p,* pre-epipodite; *py,* pygidium; *t,* telopodite; *tx,* thorax; *3-7,* segments of telopodite.)

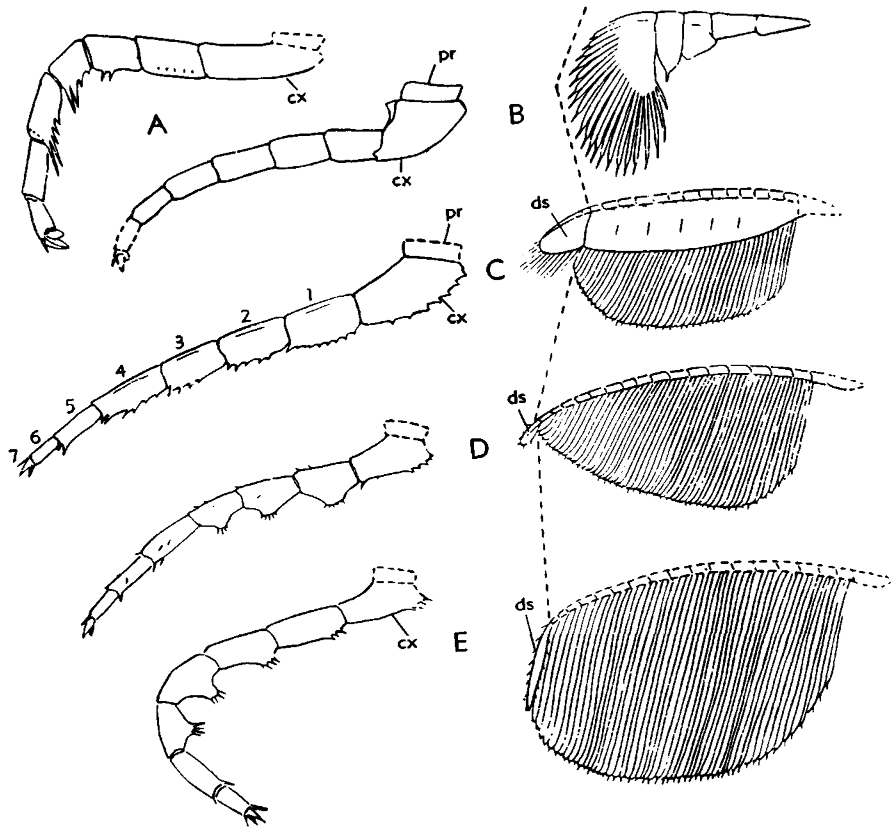


FIG. 58. Structural uniformity of trilobite biramous appendages; left side, telopodites; right side, pre-epipodites (after 56).——*A. Phacops* (Devonian).——*B. Ceraurus* (Ordovician).——*C. Olenoides* (Cambrian).——*D. Triarthrus* (Ordovician).——*E. Cryptolithus* (Ordovician). (Explanation: *cx*, coxa; *ds*, distal segment of pre-epipodite; *pcx*, precoxa; *1-7*, segments of telopodite.)

pens in *Cryptolithus* and *Triarthrus,* this distal part also bears filaments, albeit much shorter than those carried by the main part of the lobe. Lastly, the pre-epipodite of *Ceraurus* (Fig. 56*A,B*) consists of 5 joints increasing in size abaxially, the distal joint bearing filaments attached to its outer and posterior margins. The joints may be homologized with the broad faintly jointed lobe of *Olenoides* and *Kootenia.* The rodlike shaft is apparently reduced to a faint anterior ridge, barely marked in the the 3 distal segments of *Ceraurus.* In this genus there is no structure equivalent to the distal spoon-shaped or subtriangular joints of *Triarthrus* and *Olenoides* (Fig. 58).

The bladelike filaments, regarded as breathing organs or external gills, are very similar in all genera (Fig. 59). They are thin ribbon-like structures bearing a short cylindrical bristle at their blunt distal extremity. They were attached to the shaft or lobe so as to resemble the teeth of a comb, with their broad sides facing each other. The fringe of gill blades was usually directed backward, the anterior edge of one pre-epipodite overlapping the posterior edge of its neighbor immediately in front. In *Ceraurus* and *Cryptolithus,* however, it seems that the fringe could have been turned forward.

FUNCTION OF LIMBS

Fundamentally, the telopodites clearly are walking limbs, by means of which trilobites were capable of crawling over the sea bottom and along sea weeds or floating objects. The abundance of *Cruziana* markings in lower Paleozoic rocks and their almost total absence in post-Permian sedimentites suggests, as already pointed out by WALCOTT and RICHTER, that they mainly represent trails left by trilobites. The structure of the strong distal claw of *Phacops* indicates that, at least in some genera, the telopodites may also have been used for digging in the soft bottom. Isolated *Cruziana* trails commonly end in a subcircular depression, suggesting that the animal responsible for the marking dug down into the soft sediment.

Several authors have suggested that the telopodites were both walking and swimming organs, the endites of the successive podites acting as paddles. This is extremely unlikely, however, since it is difficult to admit that such primitive Arthropoda could have been capable of co-ordinating the movements of the same organs for such different purposes as walking and swimming. In walking, the arthropod legs move one after the other in such a way that when one of the rear legs is being moved backward for "pushing" the body forward, one of the anterior legs is being moved forward without touching the substrate. In swimming, all legs move backward or forward synchronously, the back stroke being a sudden flip that propels the body forward. It is unbelievable that primitive Arthropoda could have had the highly developed nervous system necessary to co-ordinate at will the movements of the same appendages in these 2 very different manners. If the telopodites were used in swimming, which is very unlikely, they must have moved just as in walking, the result being a very inefficient "walking in water."

The pre-epipodites, unlike the telopodites, were probably swimming and breathing organs. Their swimming function has been suggested by several authors, although opposed by others, but it must be owned that their shape strongly indicates a swimming adaptation. The flat expanse of the spatulate lobe of *Olenoides* and *Kootenia,* and the paddle-shaped pre-epipodite of *Ceraurus,* suggest an oarlike function. These peculiar shapes indicate that, admitting a respiratory function of the fringe of bladelike filaments, the pre-epipodites must have had some other use than serving simply as supporters for the gills. Actually, the "gill blades" themselves may have aided effectively in swimming, since, during the "back stroke," they could have overlapped each other like the shutters of a closed Venetian blind, thus greatly increasing the "useful swimming surface" of the pre-epipodite. During forward movement of the limb, the blades may have rotated 90° or thereabout, presenting the appearance of an open Venetian blind, which would offer minimum resistance to the water passing between the blades. The distal spoon-shaped or subtriangular segment of *Triarthrus* and *Olenoides* may have served the purpose of a flipper or horizontal rudder to control oblique upward or downward swimming. In short, it is believed that the pre-epipodites could have acted as effective swimming organs with synchronized backward and forward movements. If this was so, the telopodites were probably not used at all in swimming. They may have been bent inward and backward and left idle in that position, leaving ample room for free movement of the pre-epipodites.

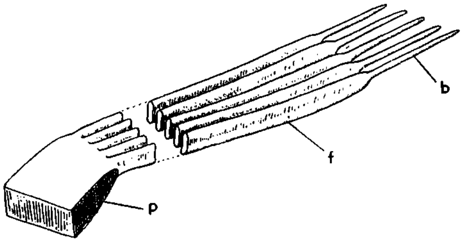


FIG. 59. Diagrammatic reconstruction of the filaments (gill blades) of *Ceraurus pleurexanthemus* GREEN, M.Ord., USA(N.Y.), greatly enlarged (after 56). (Explanation: *b,* bristle; *f,* filaments; *p,* 5th segment of pre-epipodite.)

The breathing function of the bladelike filaments has been accepted by most authors and, in truth, their structure and disposition strongly suggest that they acted as external branchia. ERIKSON (1934) and STØRMER (1939) have suggested that a "sucking chamber" could have been formed between the pleurae and the overlapping pre-epipodites, water being forced into the chamber by a downward movement of the pre-epipodites and expelled through the gill blades by an upward movement. The distal segments of the pre-epipodites could have acted as valves or opercula, rhythmically opening and closing the lateral borders of the chamber and alternately permitting the influx and preventing outflow of water. This suggestion, though ingenious, seems rather farfetched and evidently it cannot be applied to *Ceraurus.* The same results—maintaining circulation of aerated water around the gill blades—could have been achieved in a far simpler way by a gentle "fanning" of the pre-epipodites. If the pre-epipodites were used for swimming in the manner suggested, their movement would have bathed the gills with a continuous supply of aerated water.

ANTENNIFORM CERCI

In *Olenoides serratus,* the terminal (18th) pair of ventral appendages consists of multijointed uniramous cerci, very similar to the cephalic antennae (Fig. 60). Excellently preserved specimens show that the antenniform cerci are somewhat shorter than the antennae and evidently they were considerably stiffer. They were attached by

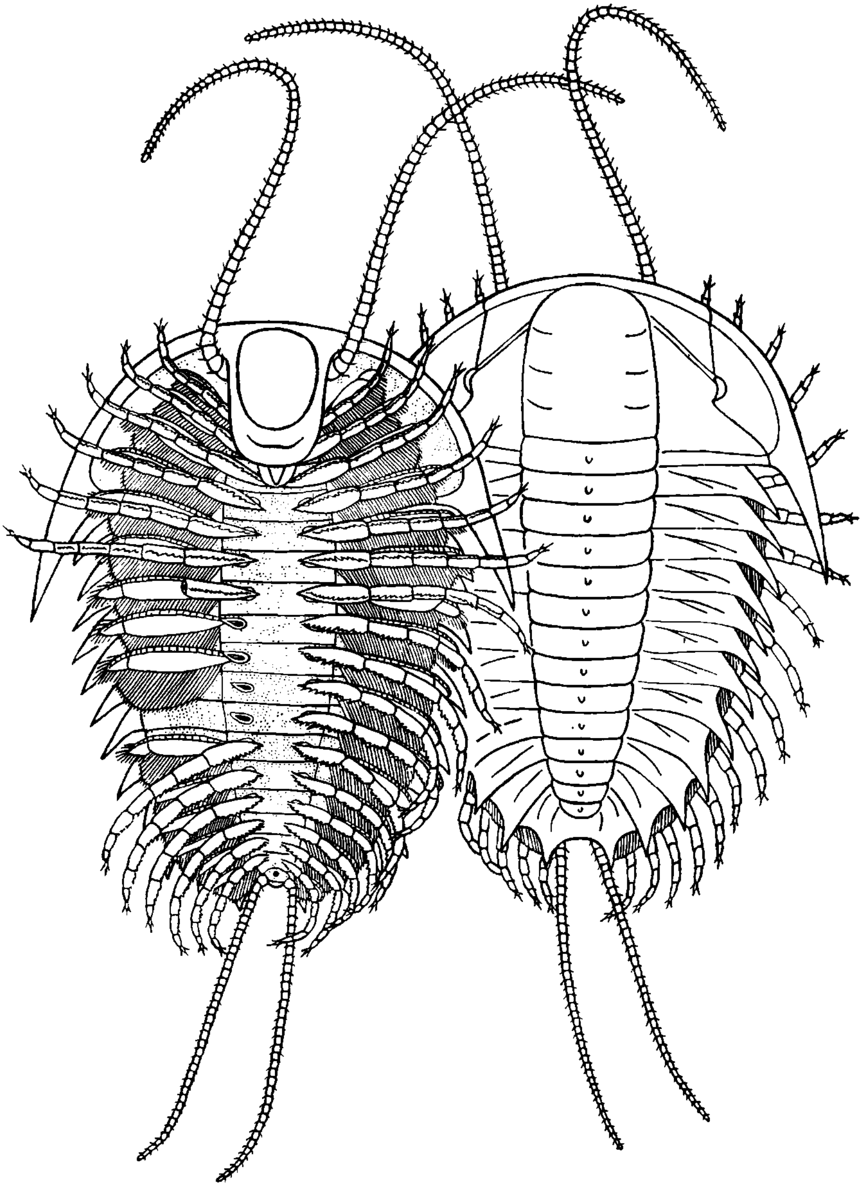


FIG. 60. Reconstruction of *Olenoides serratus* (ROMINGER) KOBAYASHI, M.Cam., Can.(B.C.), ×1 (after 60).

joints to the ventral integument of the last pygidial segment. No trace of antenniform cerci has been found in other trilobites, and it is likely that they were absent in *Triarthrus, Ceraurus* (Fig. 61), *Phacops,* and other genera in which the ventral appendages are known.

MICROSTRUCTURE OF EXOSKELETON

The exoskeleton of trilobites consists of a thin integument that is directly comparable to the chitinous cuticle of other Arthropoda. Parts of the integument, notably that forming the dorsal covering of the body but also certain areas of the ventral side, were mineralized and hard. In these parts, the inner layers of the cuticle were impregnated by calcareous salts (carbonate, phosphate) as in many living Crustacea. According to SCHULZE (1937), P_2O_5 may form as much as 30 per cent of the exoskeletal substance. This mineralization gave a high rigidity to the test, rendering it easily fossilizable.

Thickness of the mineralized exoskeleton is variable and not directly related to size of the trilobites. In specimens of *Tretaspis* averaging 17 to 18 mm. in length, thickness of the cephalic exoskeleton is about 0.2 mm. (STØRMER, 1930). Pygidia of *Scutellum flabelliferum* 10 to 20 mm. in length are

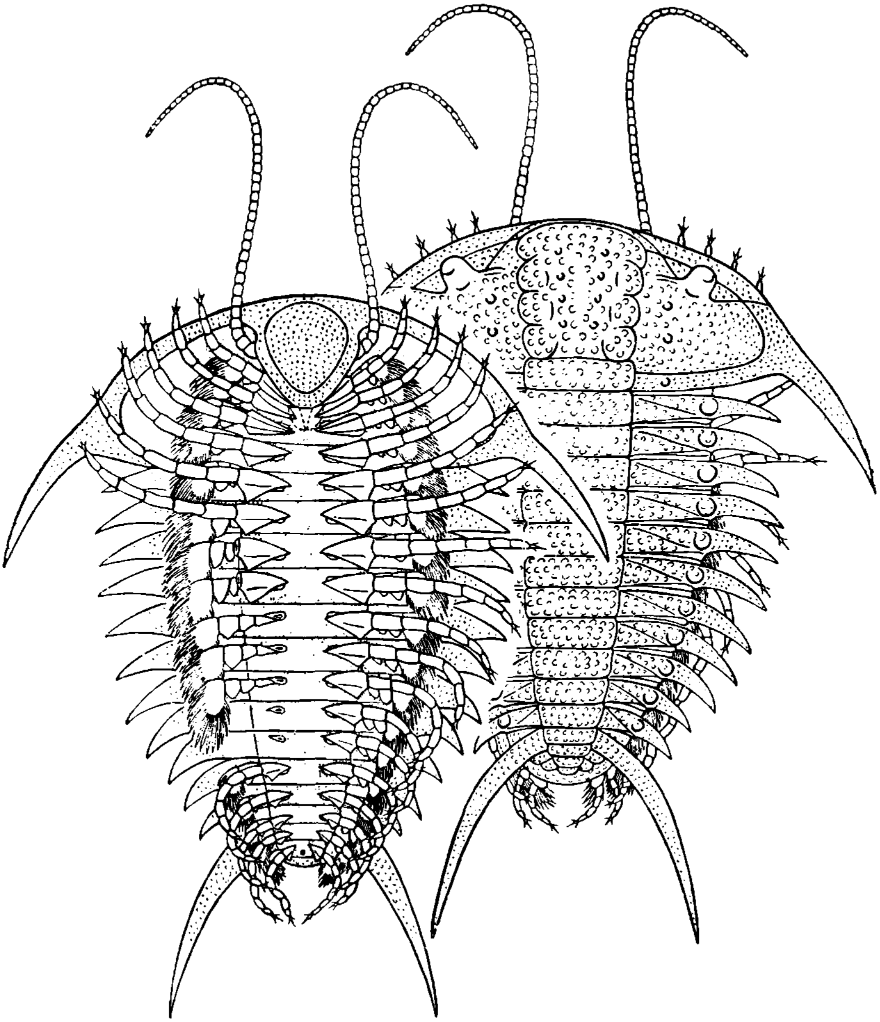


FIG. 61. Reconstruction of *Ceraurus pleurexanthemus* GREEN, M.Ord., USA(N.Y.), ×2.15 (after 60).

about 0.07 mm. thick, where cephala of *Phacops sobolevi* about 15 mm. long are approximately 0.33 mm. thick (KIELAN, 1954). Most Olenellidae have a very thin exoskeleton but specimens of *Agraulos* only 4 mm. long may have exoskeletons as much as 0.5 mm. thick[1] (HUPÉ, 1953). It seems probable that in some olenellids the dorsal integument of the opisthothoracic segments was mineralized only weakly or not at all, and accordingly, the opisthothorax of such forms is never preserved. Lack of mineralization also could explain apparent absence of the hypostoma among Agnostida.

The microscopic constitution of the mineralized integument has been described in only a few species, notably *Trinucleus bronni, T. bucculentus, Tretaspis kiaeri, T. seticornis, Scutellum (Scutellum) flabelliferum,* and *Phacops (Phacops) sobolevi* (STØRMER, 1930; KIELAN, 1954). Sections of well-preserved specimens (Fig. 62) show that the integument is formed of 3 layers: (1) a thin apparently pigmented outer layer, (2) a median principal layer, and (3) a thin nonpigmented inner layer. In addition, some thin sections of *T. seticornis* show what seems to be a very thin outermost layer that is indicated in sections by a dark line (Fig. 67*C*). The principal layer makes up about 0.7 to slightly more than 0.8 of the whole

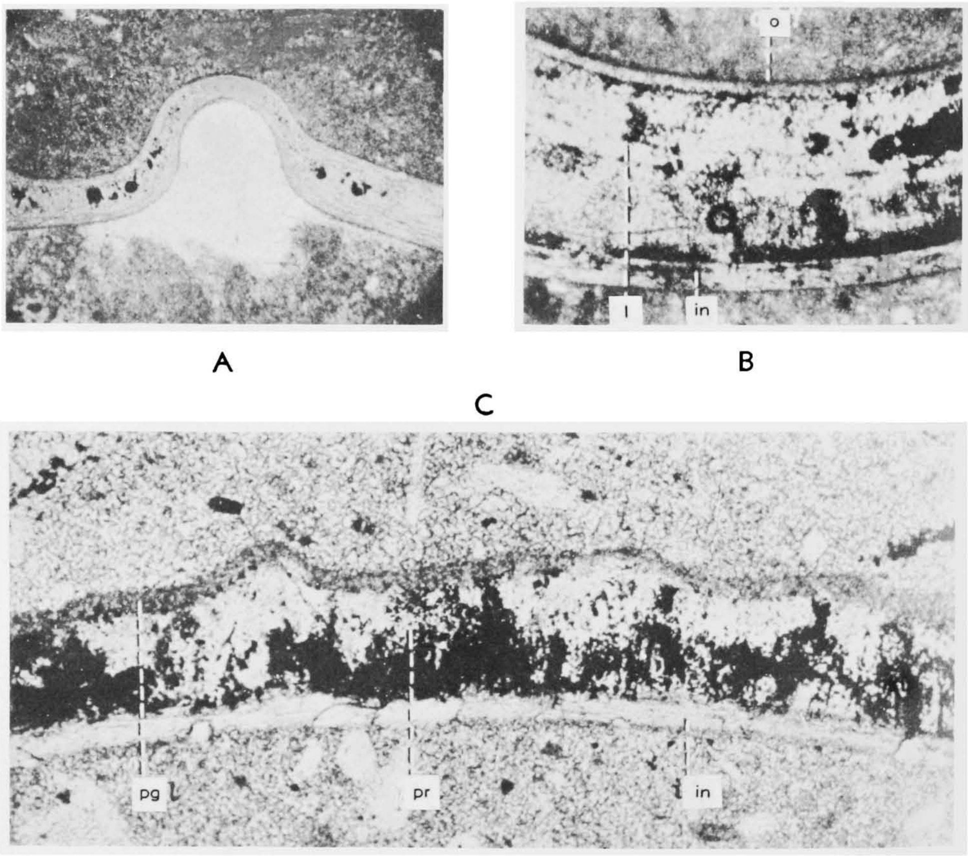


FIG. 62. Microstructure of the dorsal exoskeleton indicated by thin sections of parts of the cephalon of *Tretaspis seticornis* (HISINGER) STØRMER, Ord., Norway (after 55).——*A*, Transverse section across lateral eye tubercle, ×38.——*B*, Cross-section of glabellar region, ×150.——*C*, Transverse section across axial furrow, ×100. (Explanation: *o*, possible traces of outermost layer; *pg*, pigmented layer; *pr*, principal layer; *in*, inner layer; *l*, laminations of the integument.)

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[1] Some authors (such as RAW, 1937) have claimed that some trilobite exoskeletons have been thickened secondarily during fossilization.—C.J.S.

thickness. In *Trinucleus* and *Tretaspis* the inner layer, in many specimens not sharply defined from the principal layer, is slightly thicker than the outer layer, whereas in *Scutellum* the reverse is true. The layers show distinct lamination, which, however, is most conspicuous in the median or principal layer. In addition, all layers are traversed by very fine straight canaliculi directed normally to the lamination, the canaliculi being most abundant and closely crowded together in the principal layer. This microscopic constitution is closely comparable to that of the dorsal integument of living Arthropoda. Taken together, the 3 main layers seem to correspond to the modern arthropod endocuticle; the pigmented (outer) and principal (median) layers of trilobite exoskeletons respectively represent the outer and inner zones of the pre-exuvial layers of living Arthropoda, and the inner layer (trilobites) corresponds to the deep postexuvial zone of the dorsal integument (modern arthropods). The doubtful outermost layer seen in *Tretaspis seticornis* may represent the thin epicuticle of other Arthropoda. It is worth while to mention that sections of the granulose pygidial integument of *Scutellum flabelliferum* show that the exoskeleton becomes very thin at the granules, where it is formed exclusively of the outer pigmented layer (Fig. 63).

SENSORY ORGANS

With the exception of the antennae and antenniform cerci, the only well-known sensory organs of trilobites are the paired dorsal eyes. Less understood are the hypostomal maculae, the median glabellar tubercle, and the possible integumentary organs connected with perforations of the exoskeleton in certain species. The antennae and antenniform cerci have already been described in dealing with the ventral appendages (p. O76).

EYES

Normally, the dorsal side of the cephalon of trilobites bears a pair of laterally placed eyes, the visual surfaces of which are carried by the librigenae if facial sutures are present. The eyes vary in size from very small, as in some Harpidae, to extremely large, as in most Cyclopygidae. Excepting a very few genera, such as *Cyclopyge, Ellipsotaphrus,* and *Symphysops* (Fig. 64,2), in which the visual surfaces are confluent anteriorly, all trilobites have separate eyes.

The visual surface of the eye is usually crescentic or reniform in dorsal outline, whereas in transverse section it is convex outward-upward. In many trilobites a narrow raised area of the librigena, called **eye platform,** forms a sort of socle at the base of the visual surface. Adaxially, the visual surface is separated from the palpebral lobe of the fixigena by the facial suture. In a few

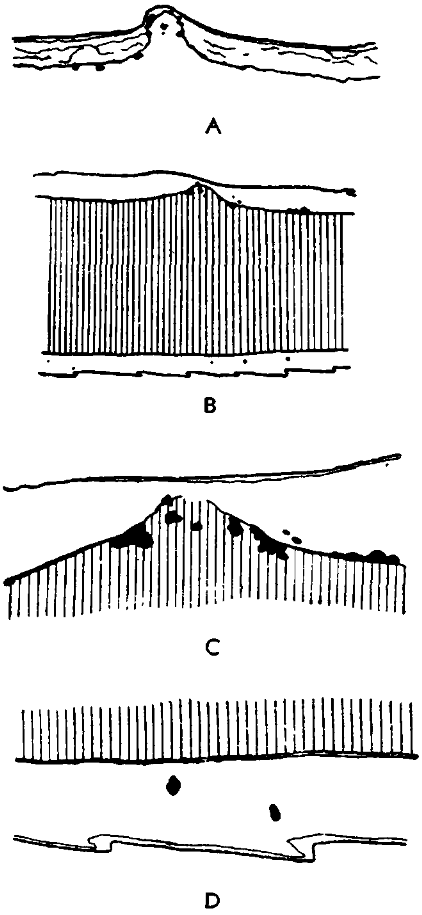

Fig. 63. Microstructure of the dorsal exoskeleton indicated by thin sections of parts of the pygidium of *Scutellum (Scutellum) flabelliferum* (Goldfuss) Richter & Richter, M.Dev., Poland (after 29).——*A,* Section across axis, cutting a tubercle, ×35.——*B,* Longitudinal section along rib, cutting doublure (ruled area corresponds to matrix), ×35.——*C,* Part of the upper (dorsal) integument of *B,* ×140.——*D,* Part of the lower integument (doublure) of *B,* ×140.

trilobites, the eye platform and the palpebral lobe rise almost vertically from the genal surface, forming a sort of stalk or peduncle that carries the visual surface on the abaxial side of its extremity (Fig. 400).

Several authors have described in detail the eyes of different trilobites. The most important contributions are those of CLARKE (1889), LINDSTRÖM (1901), RICHTER & RICHTER (1926), BRINK (1951), and BECKMANN (1951).

Since CLARKE's (1889) early studies and LINDSTRÖM's (1901) classical investigations, it has been generally accepted that 2 types of eyes are present among trilobites. These are holochroal (compound) and schizochroal (aggregate) eyes.

HOLOCHROAL EYES

The holochroal (CLARKE) or compound (LINDSTRÖM) eyes are characterized by the presence of many small lenses packed closely together in direct contact with one another. The ensemble of all the lenses is covered by a very thin pellucid cornea, which grades laterally into the mineralized integument of the cephalon. The cornea, therefore, is a single continuous membrane that covers the whole eye. The so-called "eye facets" are nothing more than the outline of the in-

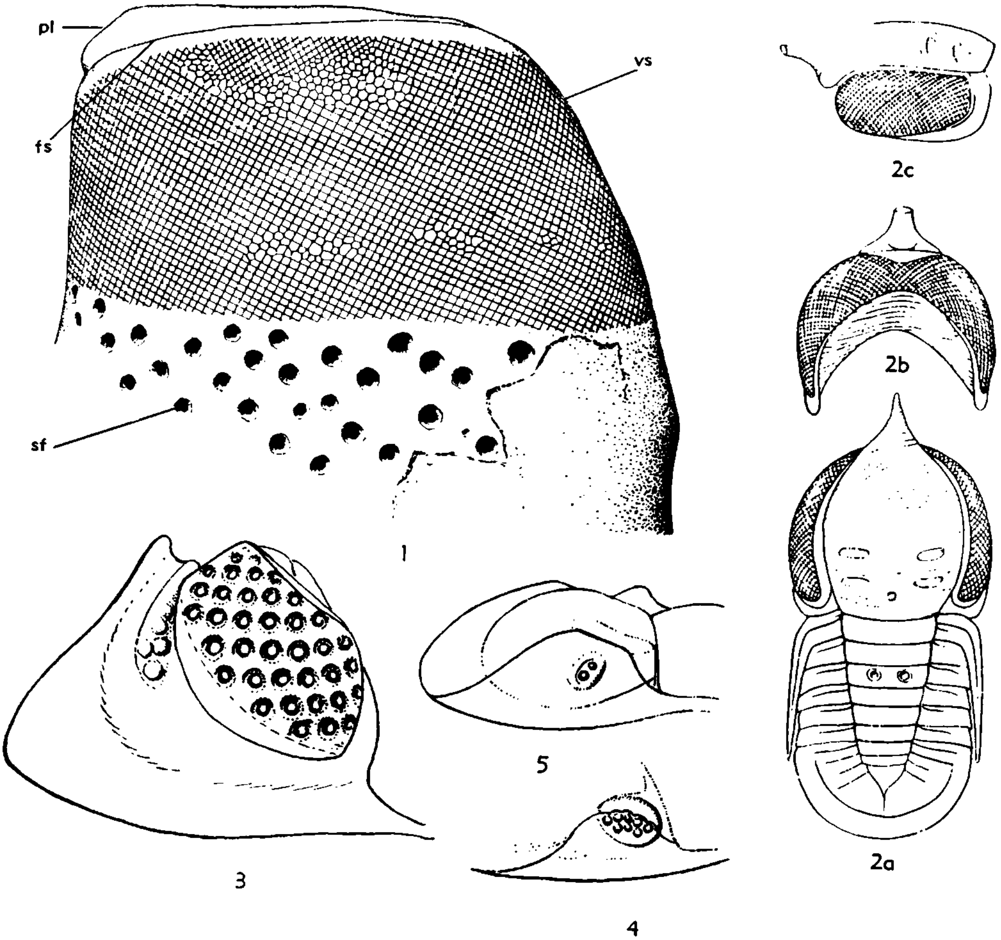

FIG. 64. Eyes of trilobites.——*1.* Holochroal eye of *Asaphus cornutus* PANDER, Ord., Russia, ×25 (after 24). (Explanation: *fs,* facial suture; *sf,* sensorial fossette; *pl,* palpebral lobe; *vs,* visual surface.)——*2.* Confluent eyes of *Symphysops subarmatus* (REED) RAYMOND, U.Ord., G.Brit., ×1.2; *2a,* dorsal view of carapace; *2b,* ventral view of cephalon; *2c,* lateral view of cephalon (after 26).——*3.* Right eye of *Phacops latifrons* (BRONN), M.Dev., Ger., ×2.5 (after 45).——*4.* Right eye of *Cryphops cryptophthalmus* (EMMRICH), U.Dev., Ger., ×7 (after 45).——*5.* Left eye of *Nephranops incisus incisus* (ROEMER), U.Dev., Ger., ×2 (after 45).

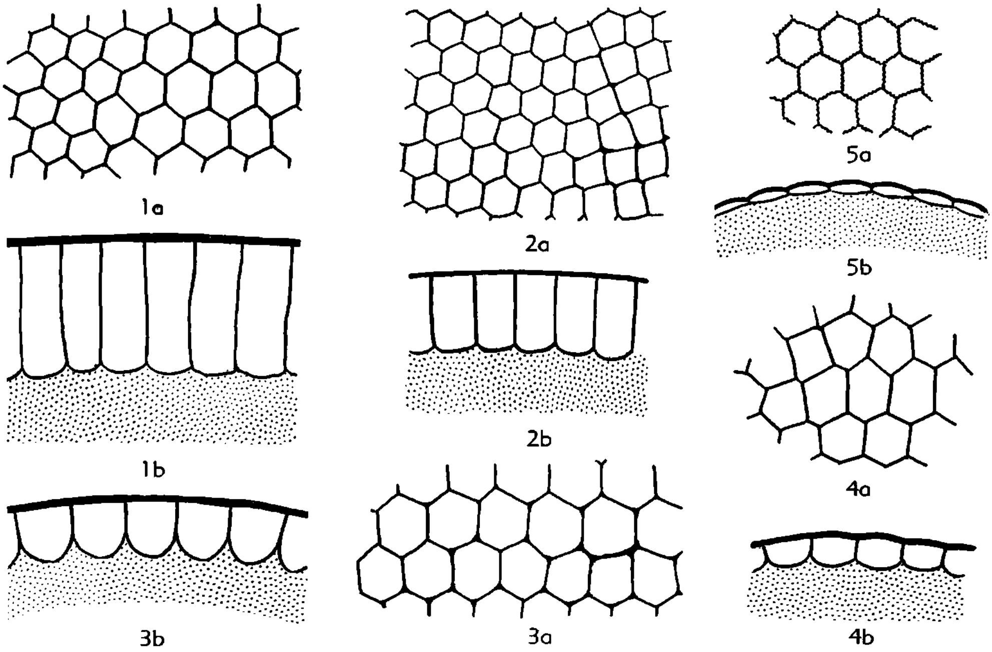

FIG. 65. Holochroal trilobite eyes (after 31).——*1. Illaenus chiron* HOLM, Ord., Swed.; *1a,b,* transv. and long secs. of several eye lenses, ×60.——*2. Dysplanus centrotus* (DALMAN), Ord., Swed.; *2a,b,* transv. and long. secs., ×60.——*3. Cyrtometopus clavifrons* (DALMAN), Ord., Swed.; *3a,b,* transv. and long. secs., ×60; *4. Sphaerophthalmus alatus* (BOECK) ANGELIN, U.Cam., Swed.; *4a,b,* transv. and long. secs., ×100.

dividual lenses beneath the transparent cornea. The number of lenses in a single eye ranges from a hundred in some species of *Peltura,* and more than 15,000 in some *Remopleurides.* The lenses are usually hexagonal in outline and arranged with great economy of space, but rhomboidal and even quadrate outlines are by no means rare. Lenses with quadrate outline seem to be the rule in eyes with a very large visual surface (Fig. 64,*1,2*), but they may occur side by side with hexagonal lenses in eyes of moderate or small size.

LINDSTRÖM recognized 2 subtypes of holochroal eyes: (1) with prismatic planoconvex lenses, and (2) with thin biconvex lenses. The eyes of *Asaphus fallax* and of *Illaenus chiron* (Fig. 65,*1*) illustrate the 1st subtype. Here the lenses are hexagonal prisms that, as seen in sections normal to the visual surface of the eye, are between 2 and 3 times as long as wide. In LINDSTRÖM's words, the lenses "are columnar prisms, like the pillars of basalt," having a plane outer surface and a convex inner extremity. In *Dysplanus centrotus* (Fig. 65,*2*) the prisms are considerably shorter than in *Asaphus fallax,* whereas in some species of *Acidaspis* they are just a little longer than their width.

The 2nd subtype is illustrated by *Cyrtometopus clavifrons* and *Sphaerophthalmus alatus* (Fig. 65,*3,4*). Here the lenses are truly "lenticular" in cross section, being thin and biconvex. Probably this is the most primitive subtype of holochroal eye, and it seems that transitions exist between this and all other types. The eyes of *Peltura scarabaeoides* appear to be intermediate between the "biconvex" and the "planoconvex" subtypes, and those of some Cheiruridae seem to provide a link between the holocroal and the schizochroal types.

SCHIZOCHROAL EYES

The schizochroal (CLARKE) or aggregate (LINDSTRÖM) eyes are especially characteristic of the phacopid trilobites, but as WHITTINGTON & EVITT (1953) have shown, they also occur in some Cheiruridae, notably in the genera *Holia, Acanthoparypha,* and *Sphaerexochus.* The eye consists of biconvex lenses, larger and less numerous than those of the holochroal type, each lens having its own corneal covering. The individual lenses, which are circular in outline in the phacopids but hexagonal in the cheirurids, are separated from each other by thick sclerotic walls that project into the interior of the

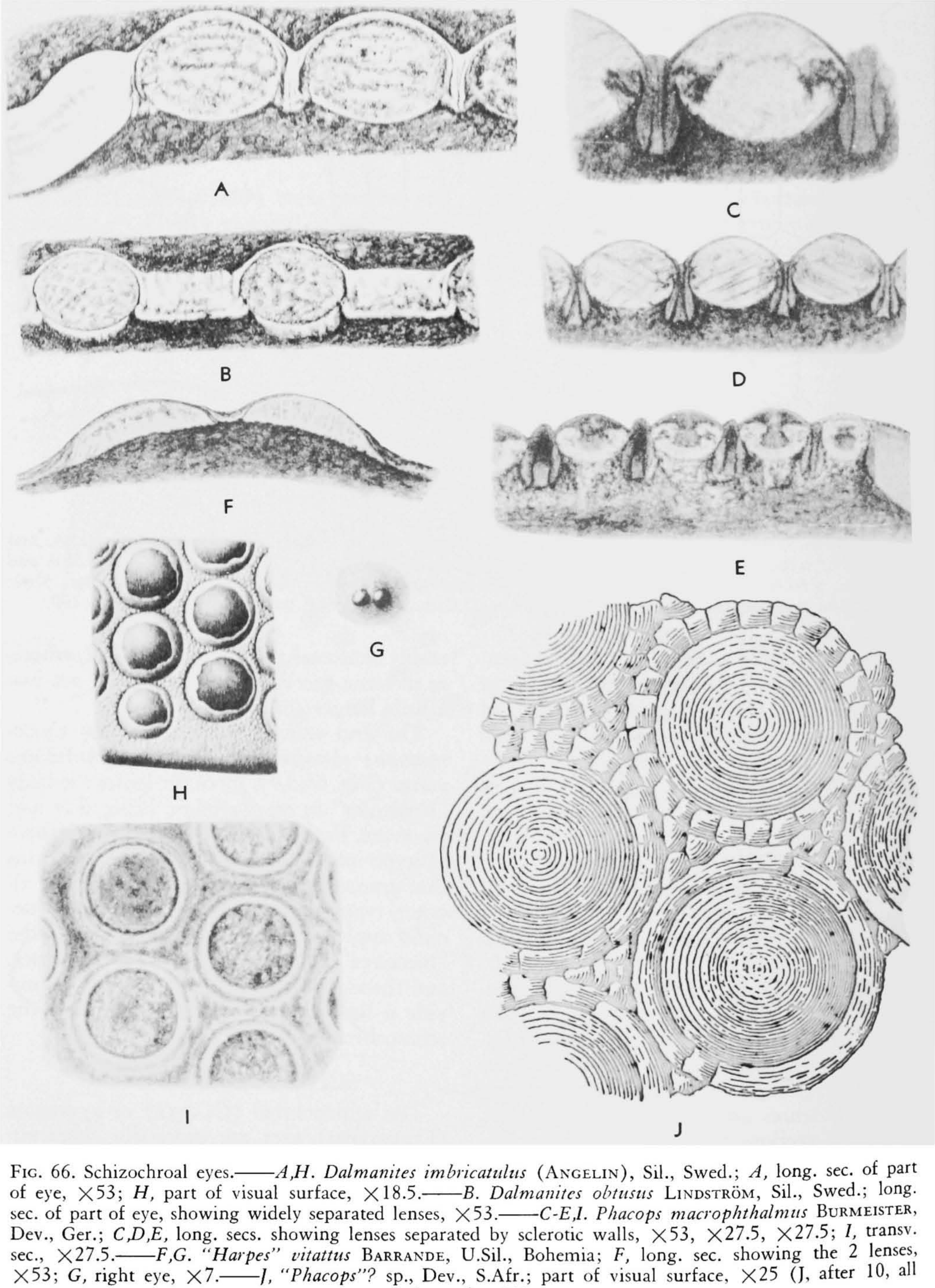

FIG. 66. Schizochroal eyes.——*A,H. Dalmanites imbricatulus* (ANGELIN), Sil., Swed.; *A,* long. sec. of part of eye, ×53; *H,* part of visual surface, ×18.5.——*B. Dalmanites obtusus* LINDSTRÖM, Sil., Swed.; long. sec. of part of eye, showing widely separated lenses, ×53.——*C-E,I. Phacops macrophthalmus* BURMEISTER, Dev., Ger.; *C,D,E,* long. secs. showing lenses separated by sclerotic walls, ×53, ×27.5, ×27.5; *I,* transv. sec., ×27.5.——*F,G. "Harpes" vitattus* BARRANDE, U.Sil., Bohemia; *F,* long. sec. showing the 2 lenses, ×53; *G,* right eye, ×7.——*J, "Phacops"?* sp., Dev., S.Afr.; part of visual surface, ×25 (J, after 10, all others after 31).

aggregate eye. The cornea itself is a very thin pellucid membrane of uniform thickness, convex outward like a tiny watch glass. Around each of the individual lenses the cornea grades down into the sclera forming the walls. The actual lenses, lodged in the pits between the sclerotic walls and the corneal covering, were evidently structures separate from the cornea. In beautiful silicified specimens of *Holia, Acanthoparypha,* and *Sphaerexochus* from Ordovician rocks of Virginia (Whittington & Evitt, 1953) the lenses are never preserved, all that remains of the eyes being the convex corneas and the sclerotic walls delimiting the pits where the lenses were located. In some trilobites, the individual lenses are set considerably apart and the intervening integument is directly comparable to that forming the bulk of the cephalon. The surface of the areas between the individual lenses may bear a reticulate sculpture (Fig. 66).

The number of lenses forming the aggregate eye ranges in different genera from 2 to 300 or 400. Wide variation in the number of lenses may occur even within a single species, different specimens of *Ormathops atava* bearing any number of lenses from 15 to 300, inclusive. The reduction of the eyes in some stocks of phacopid trilobites may lead to a marked decrease in the number of lenses and even, in extremely modified forms as *Ductina ductifrons,* to their complete disappearance. A most unusual condition characterizes one observed individual of the progressive phacopid *Nephranops incissus.* In this specimen the visual surface, separated from the nonfunctional facial suture, carries 2 lenses. However, this is true only for the right side of the cephalon; the left side is blind. Other specimens have no eyes.

The lateral eyes of the Harpidae are clearly also of schizochroal type (Fig. 66*F,G*), but in members of this family the lenses of each eye invariably have been reduced to only 2. Probably also the lateral eyes of some Trinucleidae *(Tretaspis),* consisting of a single biconvex lens, are best interpreted as extremely simplified schizochroal eyes.

BLINDNESS

We have no means of knowing whether some trilobites provided with eyes were blind, a condition that could have been caused by simple sclerosis of the cornea, but we know positively that many lacked eyes and were, therefore, blind. For the purposes of paleontology, "blindness" is used in the sense of being eyeless.

Though Lindström (1901) believed blindness to have been a primitive condition of trilobites and the appearance of eyes a secondary character acquired in Late Cambrian time, it is now generally accepted (Raymond, 1917; Richter, 1921; Raw, 1925; Hupé, 1953) that the reverse is true, blindness being of secondary origin.

This is clearly indicated by the fact that sporadic blindness appeared at different times in the midst of families characterized by normal eyes and, conversely, by the fact that in many eyeless families, some genera retained ocular protuberances, palpebral lobes, and other such features suggestive of a derivation from eye-bearing ancestors. The first case is illustrated by *Porterfieldia* (Olenidae); *Placoparia* (Pliomeridae); *Areia* (Cheiruridae); *Dindymene* (Encrinuridae); *Typhloproetus, Drevermannia, Pteroparia* (Proetidae); and *Dianops, Trimerocephalus, Ductina* (Phacopidae). Examples of the 2nd are *Aulacodiscus* (Eodiscidae), *Couloumania* (Conocoryphidae), and *Shumardops* (Shumardiidae). *Reedolithus* and *Tretaspis* are the only genera among blind Trinucleidae possessing lateral eyes, these eyes being characterized by a single small biconvex lens.

The overwhelming majority of Lower Cambrian trilobites, such as the olenellids, redlichiids, and ellipsocephalids, had well-developed eyes, the early conocoryphids *Atops* and *Pseudatops* being counted among the few exceptions. However, all of the small eodiscid and agnostid trilobites were blind. During Middle Cambrian time eyeless trilobites became more abundant. In addition to the Agnostida and Eodiscidae, all the Conocoryphidae were blind, as well as most Corynexochidae. Most authorities (other than Poulsen) agree that the blind Conocoryphidae are derived from an early ptychopariid stock possessing normal eyes.

Blindness was rather exceptional among Late Cambrian trilobites, the plethopeltid *Leiocoryphe* being one of the few examples, but in Ordovician time it was fairly widespread. Whole Ordovician families are characterized by lack of eyes, as for example the

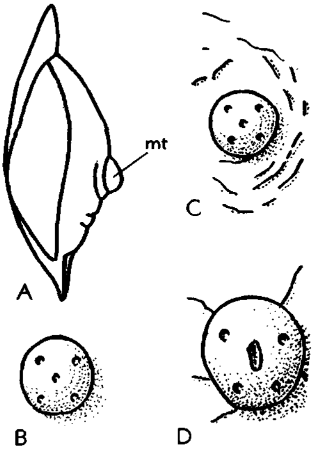

FIG. 67. Median glabellar tubercle of *Tretaspis seticornis* (HISINGER) STØRMER, Ord., Norway (after 55). *A*, Lateral view of meraspid cephalon (stage II) showing median tubercle *(mt)*, ×36; *B*, dorsal view of median tubercle of same cephalon, ×80; *C,D*, dorsal views of median tubercle of 2 holaspid cephala, ×50.

Raphiophoridae, Dionididae, Alsataspididae, and Shumardiidae, while sporadic blindness appeared in some genera belonging to eye-bearing families, such as the Olenidae, Pliomeridae, Cheiruridae, and Encrinuridae.

In Silurian times blindness was again the exception (disregarding, of course, the Raphiophoridae which continued the Ordovician tradition), but in Devonian time eyeless genera appeared sporadically in the midst of families with normal eyes, such as the Proetidae and Phacopidae. The last Late Paleozoic trilobites had normal holochroal eyes.

The tendency towards development of blind forms seems to have been a persistent trend among trilobites since the very beginning of the class. Why this tendency materialized in certain stocks and not in others is yet unknown. In all probability the appearance of blind forms had no connection with environmental conditions. Some of the blind Devonian phacopids like *Ductina* and *Trimerocephalus* were, in all likelihood, vagrant benthic forms, while the blind Ordovician olenid *Porterfieldia* was probably a pelagic epiplanktonic animal.

MEDIAN SENSORY ORGAN

A median tubercle or pustule is present on the glabella of many trilobites. Its location is rather variable from species to species. In some it is found close to the occipital furrow, whereas in others it is located at the level of the median lateral glabellar furrows or farther forward. In many trilobites the tubercle is absent.

The median tubercle has been variously interpreted as representing the beginning of the alimentary canal (BEYRICH, 1846), as a "dorsal organ" similar to that of the living *Apus* (BERNARD, 1894), as a median eye or ocellus (M'COY, 1865; OEHLERT, 1895; BEECHER, 1895; RUEDEMANN, 1916; STØRMER, 1930), or as a "sensorial complex" similar to that existing among living syncarid crustaceans (HANSTRØM, 1926; STØRMER, 1949; HUPÉ, 1953). As RAYMOND (1920) remarked, however, it seems likely that the mesial glabellar tubercle is not homologous in all trilobites.

At least in the Trinucleidae the median tubercle seems to have been some sort of sensory organ. STØRMER'S (1930) investigations on the tubercle of *Tretaspis seticornis* have shown that it consists of an almost semispherical pustule bearing 5 tiny pits on its outer surface (Fig. 67). One pit, usually a little larger than the others, occupies a central position, the remaining 4 being evenly disposed around it. According to STØRMER, the median tubercle is highly developed in the larval stages of *T. seticornis*, being larger than the lateral eyes. In holaspid specimens the lateral eyes are larger than the median tubercle. In 1930 STØRMER concluded that "the median tubercle must be regarded as a true median eye," but in 1949 he was inclined to accept HANSTRØM'S (1934) view that it represents a "sensorial complex" comparable to that of Recent syncarids. Similar tubercles are known also in the trinucleid genera *Reedolithus*, *Trinucleus*, and *Cryptolithus*.

MACULAE

Maculae are absent in the hypostomata of many trilobites, whereas in others they consist of a pair of smooth rounded or elongate protuberances visible on the lateral or posterolateral areas of the median body (Fig. 68). In a few species the outer surface of the maculae is reticulate or bears closely set, regularly arranged tubercles resembling the lenses of the dorsal eyes.

Usually only a small portion of the macular surface is reticulate or faceted, the remainder being smooth.

The significance of the maculae and of their reticulate or faceted surface, is still a matter of subjective interpretation. LINDSTRÖM (1901), HANSTRØM (1926), and HUPÉ (1953) regard the maculae as true ventral eyes, whereas other paleontologists such as RAYMOND (1920), STØRMER (1949), and WHITTINGTON & EVITT (1953) prefer to regard them as places of muscle attachment.

The probability that the maculae represent places of muscle attachment seems rather small. This is indicated by several features: (1) the mineralized integument of the maculae is much thinner than that of the remainder of the hypostoma, as pointed out by LINDSTRÖM and amply verified by WHITTINGTON & EVITT (1953) on silicified material: (2) the places of muscle attachment in the cephala of trilobites lacking apodemes invariably have a smooth surface, differing markedly in this respect from maculae with a reticulate or faceted surface; and (3) in some species of trilobites having the hypostoma firmly welded to the rostral plate (as *Holmia kjerulfi, Redlichia noetlingi, Paradoxides davidis, Fieldaspis furcata*) smooth maculae are well developed. In the last-named trilobites it is evident that, if the maculae represent places of muscle attachment, the muscles would function as for movements of the hypostoma alone. They may have been expansor muscles of the stomach, attached to the ventral wall of the subglabellar proventriculum, but it seems strange that such powerful muscles (judging by the size of the maculae) should have been needed to produce slight expansion of the soft-tissued stomach.

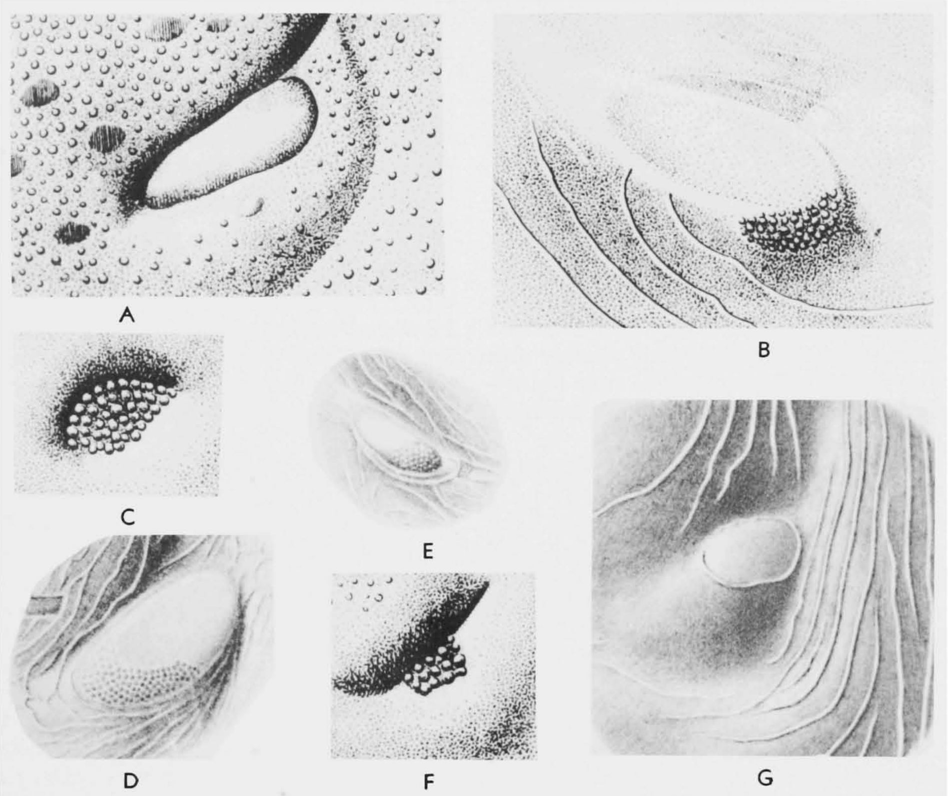

FIG. 68. Hypostomal maculae.——*A, Cheirurus* sp., Ord., Swed.; left macula, ×10.5.——*B, Scutellum platyactin* (ANGELIN), Sil., Swed.; right macula, ×10.5.——*C,F, Lichas* sp., ?Ord., Swed.; *C,* wax impression of internal side of right macula, ×10.5; *F,* internal side of another right macula, ×10.5.——*D, Scutellum* sp., Sil., Swed.; right macula, ×10.5.——*E, Scutellum polyactin* (ANGELIN), Sil., Swed.; right macula, ×17.5.——*G, Asaphus raniceps* DALMAN, Ord., Swed.; left macula, ×10.5 (all after 31).

The available evidence seems to favor the view that the maculae had a visual function. This is especially true for the reticulate and faceted maculae present in such genera as *Scutellum, Lichas,* and *Illaenus.* The smooth maculae seem best regarded as "degenerate" ventral eyes that have lost their lenses. Sections normal to the surface of the maculae show that in those of "reticulate" type the macula consists of numerous prismatic bodies very similar to the prismatic lenses of the dorsal holochroal eyes. According to LINDSTRÖM this is true of the maculae observed in several asaphids and in some species of *Illaenus.* The "faceted" maculae show an aggregate of "globular" lenses resembling biconvex lenses of the dorsal eyes. These are especially well developed in some species of *Scutellum* and *Lichas* (Fig. 68*B-F*).

The presence of ventral eyes in some trilobites would certainly not constitute a unique feature among the Arthropoda, as similar organs are known among the Chelicerata and Myriapoda (HANSTRØM, 1926).

INTEGUMENTARY SENSORY ORGANS

Trilobites possessed a variety of integumentary sensory organs which, in the main, seem to have had a tactile function. Three principal categories may be distinguished: (1) stiff setae or bristles carried by the ventral appendages and possibly also by the ventral membrane; (2) tiny funnel-shaped fossettes carried by some trilobites on the eye platform; and (3) perforated tubercles of the exoskeleton.

In all species in which the ventral appendages are known, bristles are carried by the telopodites, pre-epipodites, and antennae. In the telopodites, the bristles are usually located on the ventral face of the endites. In the pre-epipodites, they are carried both by the distal segment and by the bladelike filaments, the free extremity of which ends in a single stiff bristle. In the antennae, they seem to spring from the base of each segment. It seems likely that bristles were also carried by the ventral membrane (HUPÉ, 1949).

Sensorial fossettes, excavated on the surface of the eye platform, are known in some trilobites. According to HUPÉ (1953), the fossettes of *Asaphus cornutus* are irregularly distributed, funnel-shaped pits connected with the interior of the cephalic region by very fine tubelike canaliculi.

Perforated tubercles have been observed in some Calymenidae, Odontopleuridae, Dimeropygidae, and Cheiruridae (SHIRLEY, 1936; WHITTINGTON, 1941; WHITTINGTON & EVITT, 1953). They are plainly visible in silicified specimens, and it is evident that they are an original feature and not due to a particular state of preservation. The perforations are located either at the tip of the tubercle or slightly behind it. Seemingly, they represent passageways for tactile setae. However, we cannot altogether discard the possibility that some of these perforations represent the external opening of cutaneous or subcutaneous glands.

INTERNAL ANATOMY

MUSCULAR SYSTEM

No actual remains of muscles have been found in trilobites but judging from the structure and location of certain areas of the exoskeleton regarded as places of muscle attachment, it is possible to draw some tentative conclusions as to distribution and function of the more important muscles. This is facilitated by a comparison with conditions in living Arthropoda, especially Arachnida and Crustacea.

Areas regarded as places of muscle attachment belong mainly in 2 categories: (1) apodemes and (2) so-called "dark markings." The **apodemes** are invaginations of the dorsal exoskeleton extending inward as more or less conspicuous processes. A corresponding pit or depression is usually developed on the dorsal surface of the carapace. The **dark markings** are areas of darker tone which may be slightly pyritized, observed on the internal (ventral) surface of the carapace. They are usually plainly visible only when the specimens are immersed in alcohol.

CEPHALIC MUSCLES

Judging by what is known in recent Arthropoda, it is evident that the basal joint of the biramous appendages of trilobites must have been connected with the ventral surface of the carapace by means of more or less powerful muscles that controlled movements of the appendage. The assumption that all trilobites had 4 pairs of cephalic biramous appendages and a pair of antennae, leads to the inevitable conclusion that 4 pairs of muscle scars or areas of

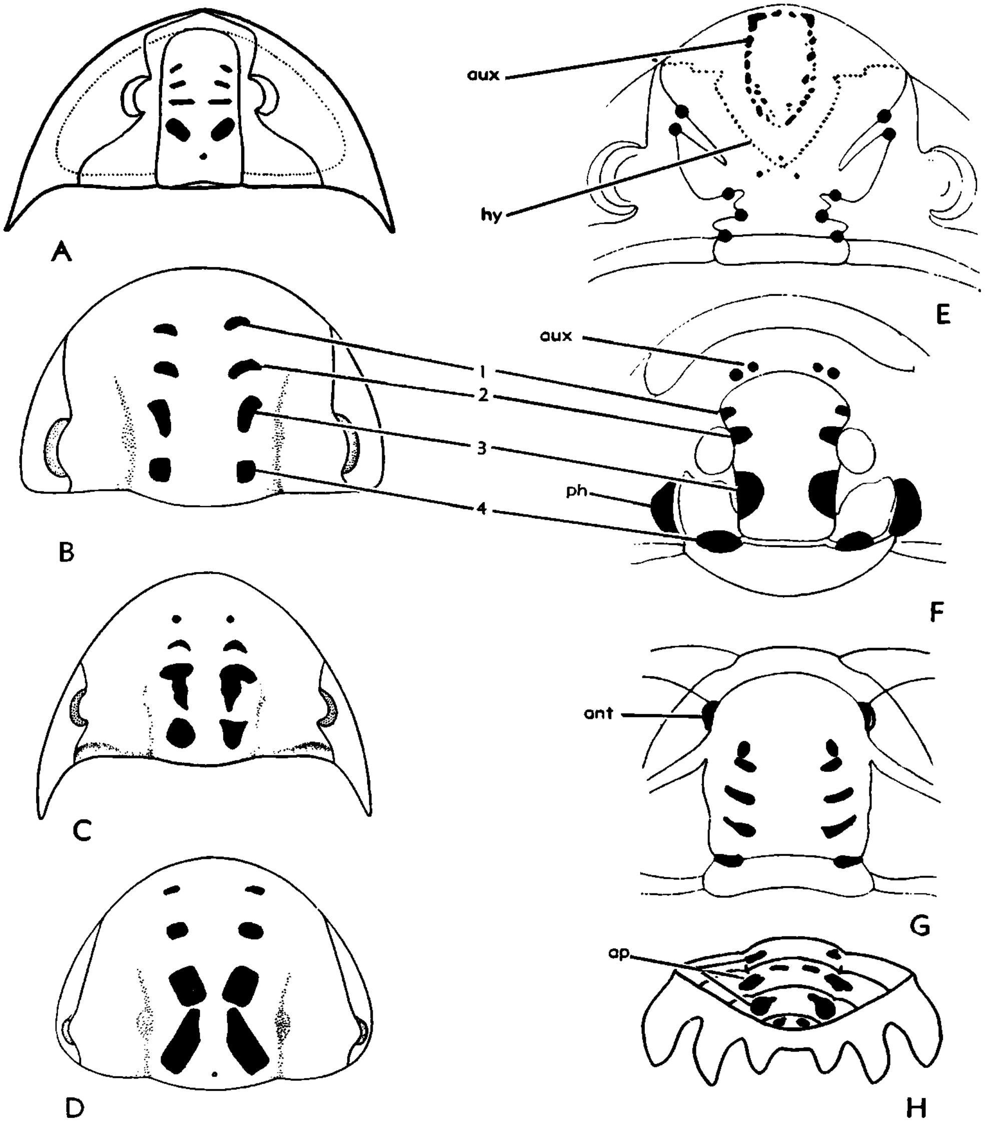

Fig. 69. Areas of muscle attachment.——*A*, Cephalon of *Notopeltis orthometopus* (Harrington) Harrington & Leanza, L.Ord., Arg., ×2.5 (after 19).——*B*, Cephalon of *Illaenus dalmani* Volborth, Ord. Russia, ×1.2 (after 79, 1954).——*C*, Cephalon of *Dysplanus centrotus* (Dalman) Burmeister, L.Ord., Swed., ×1.2 (after 79, 1954).——*D*, Cephalon of *Stenopareia oviformis* (Warburg) Jaanusson, M.Ord., Swed., ×1.8 (after 79, 1954).——*E*, Cephalic axial region of *Chasmops odini* (Eichwald), M.Ord., Estonia, ×2 (after 9).——*F*, Cephalic axial region of *Pharostoma nieszkowski* Schmidt, Ord., Estonia, ×5.75 (after 24).——*G*, Cephalic axial region of *Cybele grewingki* Schmidt, Ord., Estonia, ×1.25 (after 24).——*H*, Ventral view of pygidium of *Reraspis plautini* (Schmidt) Öpik, M.Ord., Estonia, ×3.95 (after 34). (Explanation: *ant*, antennary muscle scar; *app*, appendage muscle scars; *aux*, auxiliary impressions; *hy*, outline of the hypostoma; *ph*, pharostomian scar; *1-4*, principal muscle scars of cephalic axis, regarded as places of attachment of ventral appendage muscles.)

muscle attachment must exist on the ventral surface of the cephalon in connection with the 4 pairs of biramous appendages, and that an additional pair of scars must also be present, corresponding to the places of attachment of the antennary muscles.

In many trilobites, and especially in those possessing well-marked lateral glabellar furrows, the appendage muscles were almost certainly attached to apodemes projecting obliquely downward from infoldings of the integument represented by the glabellar furrows. These apodemes were usually located about midway between the sagittal line and the axial furrows or somewhat nearer to the axial furrows than to the mid-cephalic line. They are especially conspicuous in many Cheiruridae, and can be plainly seen in silicified specimens of *Ceraurinella*. In all probability, 2 bundles of antagonistic muscles (adductor-abductor) were attached to each apodeme.

In many other trilobites, particularly in those having a more or less smooth glabella, such as many Illaenidae, Raphiophoridae, Asaphidae, and Nileidae, no apodemes were developed, the appendage muscles being attached directly to certain areas of the ventral surface of the cephalon. These areas, which are also known in some Olenidae, Encrinuridae, Calymenidae, and Dalmanitidae, appear as paired "dark markings." They have been described and figured by many authors, including BARRANDE (1852), VOLBORTH (1863), HOLM (1886), MOBERG (1902), RAYMOND & NARRAWAY (1908), NOVÁK (1918), BORN (1919), RICHTER & RICHTER (1926), ÖPIK (1929, 1937), REED (1935), LAMONT (1939), WHITTARD (1939), SINCLAIR (1947), STØRMER (1949), WHITTINGTON (1950), HUPÉ (1953), JAANUSSON (1957), and HENNINGSMOEN (1957).

The dark markings are best known in the Illaenidae, where they are usually represented by 4 pairs on the internal surface of the axial region (Fig. 69*B*). HUPÉ (1953) has interpreted the anterior pair as the places of attachment of the antennary muscles, and the 3rd *(2p)* pair as representing the "fused" places of attachment of the muscles of the 2nd and 3rd pairs of biramous appendages. This interpretation may be correct, especially in such forms as *Stenopareia oviformis* (Fig. 69*D*), which has the anterior pair of markings located far forward on the cephalon. Also, the 3rd pair of markings is usually considerably larger than the others. However, it seems likely that at least in some Illaenidae *(Platillaenus)* the places of atachment of the antennary muscles were the small apodemes found immediately below the fossulae or "anterior pits."

The significance of the fossulae, and of the corresponding "fossular apodemes," is still doubtful. WHITTINGTON (1941) discussed these structures at some length, reaching the sound conclusion that they are not homologous in all trilobites and that they probably served different functions in different genera. In some cases, as *Ceraurus, Ceraurinella,* and *Flexicalymene,* the "fossular apodemes" seem to have acted as places of attachment of the antennary muscles and likewise as supports for anterior wings of the hypostoma. In these genera, the "fossular apodemes" bear a tiny pit on the anterior face near their ventral extremity, which has been interpreted by WHITTINGTON as a socket for the articulation of the anterior wing process of the hypostoma (Fig. 40). However, it seems very likely that the posterior face of the apodemes was the place of attachment of the antennary muscles, because in these genera the basal section of the antennae runs forward along the lateral notches of the hypostoma between the anterior wings and the lateral shoulders. In other genera, such as *Platillaenus* and *Cryptolithus,* it seems hardly possible that the fossular apodemes had any relation with the hypostoma.

In addition to the apodemes and axial-region dark markings, other paired impressions have been observed in the cephalon of a few species. The **auxiliary impressions** of BARRANDE are small, usually rounded dark spots, distributed in a few pairs on the preglabellar field *(Pharostoma),* along the axial furrows *(Chasmops),* or along the anterior and posterior areas of the glabella *(Dalmanites, Proetus)* (Fig. 69*E,F*). These markings were regarded by BORN (1919) and RAYMOND (1920) as the places of attachment of hypostomal muscles, but as RICHTER (1933) and SCHULZE (1937) have pointed out, it seems more likely that they represent points of attachment of expansor (dilator) muscles of the esophagus and stomach. The **pharostomian scars** of ÖPIK, consisting of a pair of large impressions found in *Pharo-*

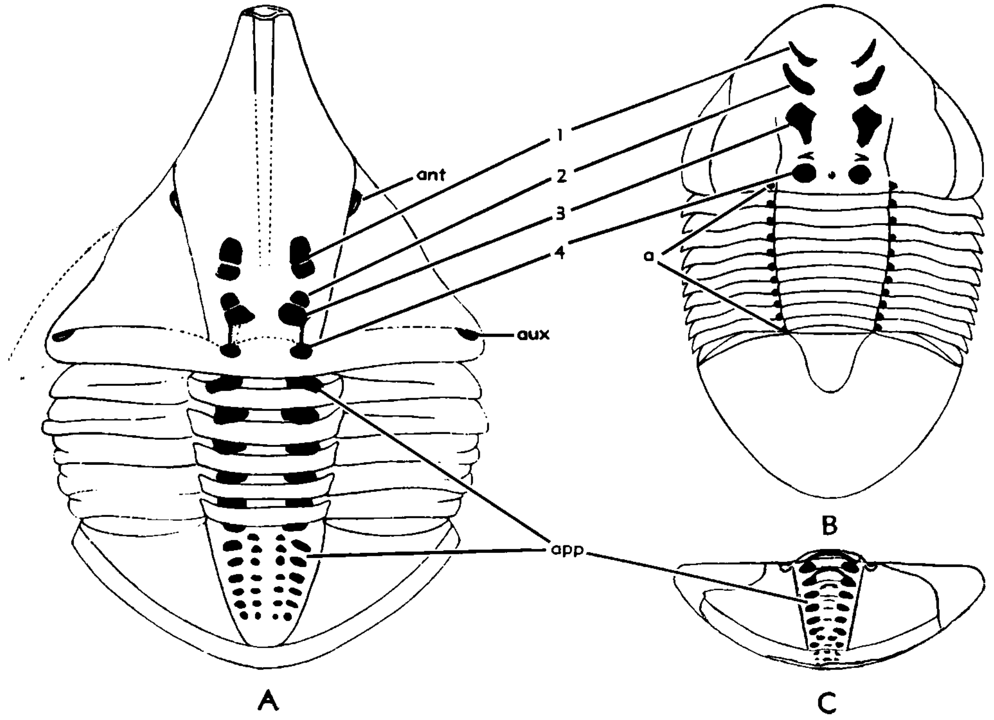

FIG. 70. Areas of muscle attachment.——*A*. Exoskeleton of *Lonchodomas rostratus* (SARS), L.Ord., Norway, ×5 (after 24).——*B*. Exoskeleton of *Ectillaenus katzeri* (BARRANDE) JAANUSSON, M.Ord., Bohemia, ×0.8 (after 24).——*C*. Pygidium of *Tretaspis kiaeri* STØRMER, U.Ord., Norway, ×1.5 (after 55). (Explanation: *a*, axial furrow apodemes, ?places of attachment of dorsoventral muscles; *ant*, antennary muscle scars; *app*, places of attachment of the thoracic and pygidial appendage muscles; *aux*, auxiliary impressions, ?places of attachment of dorsoventral muscles; *1-4*, principal cephalic axis muscle scars, regarded as places of attachment of the cephalic appendage muscles.)

stoma (Fig. 69*F*) along the axial furrows at the level of the preoccipital glabellar lobes, are probably related to dorsoventral muscles. This seems to apply also to the small pits found in *Lonchodomas* and *Ampyx* near the distal extremities of the posterior border furrows (Fig. 70*A*).

THORACIC AND PYGIDIAL MUSCLES

In both the thorax and pygidium the most conspicuous places of muscle attachment correspond to the insertions of the appendage muscles. The respective apodemes, if present, are downward projections of the infolded integument forming the ring furrows that separate the axial rings proper from the articulating half-rings. They are located along the anterolateral portions of each individual ring, nearer to the axial furrows than the sagittal line of the body. Axial ring apodemes are conspicuous in *Ceraurus, Ceraurinella,* and *Cryptolithus,* but are feebly developed in *Flexicalymene* and absent in many Asaphidae, Illaenidae, Raphiophoridae, and other trilobites. In their place, dark markings are found along the anterolateral portions of each ring (Fig. 70). In the pygidium there seem to be as many pairs of markings as original segments and appendages, but the markings are usually split into double pairs, probably representing the separate insertions of 2 bundles of antagonistic muscles (Fig. 70*A, C*).

In some Asaphidae *(Kayseraspis, Hoekaspis, Megalaspidella)* and Illaenidae *(Ectillaenus)* (Fig. 70*B*) a distinct pit is found on the axial furrow close to the posterior border of each thoracic pleura, and a similar pit is found close to the posterior margin of the cephalon. These probably correspond to smaller apodemes, which are best regarded

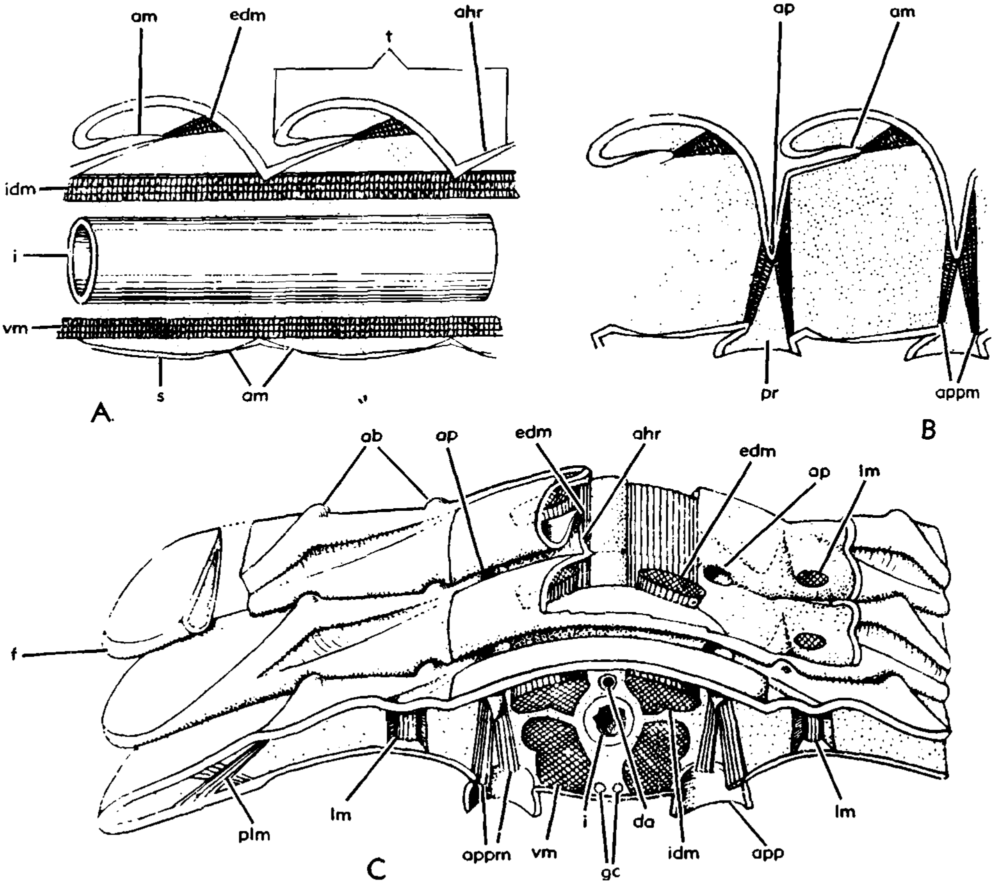

FIG. 71. Internal anatomy of the thoracic region of trilobites, according to HUPÉ (1953).——*A*, Sagittal section of the thorax, showing 2 segments.——*B*, Exsagittal section of the thorax, passing through the apodemes and the underlying basal segments of the ventral appendages.——*C*, Schematic reconstruction of the internal anatomy of 3 thoracic segments; one segment shown in transverse section and dorsal integument of the right side of 2 segments supposed to have been removed. (Explanation: *ab*, articulating boss on pleura; *atr*, articulating half-ring; *am*, articulating membrane; *ap*, apodeme; *app*, appendage muscle; *da*, dorsal vessel of circulatory system; *edm*, external dorsal muscle; *f*, pleural facet; *gc*, ganglion chain of nervous system; *i*, intestine; *idm*, internal dorsal muscle; *lm*, lateral muscles; *plm*, pleural muscles, hypothetical; *pr*, precoxa; *s*, sternite; *t*, tergite; *vm*, ventral muscles.)

as places of attachment of dorsoventral muscles (compressors of the body).

Extensor muscles, in all likelihood, were well developed in most trilobites, particularly in those capable of enrollment. The principal extensors (internal dorsal muscles) were probably attached to the ventral side of the ring furrows on both sides of the sagittal line, whereas the auxiliary extensors (external dorsal muscles) probably extended from the anterior margin of one articulating half-ring to the anterior part of the axial ring immediately in front (Figs. 50, 71). Clearly, the trilobites must have had ventral muscles, particularly flexors of the body (internal ventral muscles) attached to the intersegmental folds of the ventral membrane, but, of course, nothing remains of such muscles or of their places of attachment (Fig. 71*A*,*C*).

DIGESTIVE SYSTEM

Very little is known about the digestive system of trilobites and even the position of the mouth is not known with certainty. It is generally assumed that the oral opening was located immediately behind the hypostoma and in front of the metastoma, somewhere in the posterior part of the ventral side of the cephalic region. In truth, this is very likely, but in no specimen have actual traces of the mouth opening been detected. In all probability this is due to the fact that the mouth was bounded by soft tissue that decayed rapidly after the death of the animal.

The accepted location of the mouth near the rear part of the ventral cephalic region suggests one of 2 possibilities: (1) the digestive tract extended directly backward from the mouth, with practically no cephalic section; and (2) the tract began with a short esophagus directed forward-upward, leading to a stomach or proventriculum lodged beneath the glabella and continued backward in a long and narrow intestine, ending near the posterior extremity of the pygidial region. The second possibility seems the more likely and it has been generally accepted by most paleontologists who have studied this problem.

Structures regarded as representing traces of the actual digestive tract have been described in a few specimens, but in most of them these structures are of more than doubtful significance. VOLBORTH (1863) described and figured an enrolled specimen of *"Illaenus"* sp. from the Ordovician of Russia showing a narrow, multisegmented raised band running sinuously along the sagittal line of the thorax. The structure was interpreted as a camerate heart by both VOLBORTH (1863) and RAYMOND (1920), but as a metamerized intestine by HUPÉ (1953). In all likelihood, however, the structure is alien to the trilobite and it may represent a crinoid arm accidentally preserved in an unusual manner. From VOLBORTH's figure it is evident that the number of segments in the so-called "heart" or "intestine" is considerably greater than the number of somites in the trilobite. Moreover, just before it disappears on reaching the cephalic region, the "heart" or "intestine" clearly bifurcates in a manner suggesting the bifurcation of a crinoid arm.

The "alimentary canals" seen by WALCOTT (1881, 1921) and RAYMOND (1920) in some sections of enrolled specimens of *Ceraurus* and *Flexicalymene,* have been reinterpreted by STØRMER (1939) as appearances due to the differential mud-filling of the body cavity of the trilobites shortly after entombment of the enrolled individuals.

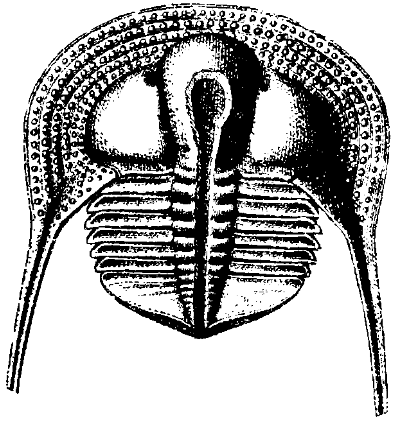

FIG. 72. Digestive system of trilobites. *Onnia ornata* (STERNBERG) WHITTINGTON, U.Ord., Bohemia, ×2 (after 2, illustrated as *Trinucleus goldfussi* BARRANDE); specimen showing hollow axial tube regarded as representing the digestive tract.

Skania fragilis, from the Middle Cambrian Burgess Shale of British Columbia, shows unquestionable traces of a long digestive tube, but this species, regarded by HUPÉ (1953) as "probably a larval form," is evidently not a trilobite. The type specimen, illustrated by WALCOTT (1931), is 2 cm. long and does not resemble any known trilobite meraspis.

The only described structure that may be regarded as representing true remains of a digestive tract is that figured by BARRANDE (1852) in 2 specimens of *Onnia ornata* (STERNBERG) WHITTINGTON from the Ordovician of Bohemia (originally described by BARRANDE as *Trinucleus goldfussi* BARRANDE) (Fig. 72). In both specimens, the structure consists of a pyriform excavation in the glabellar region followed by a narrow sagittal canal ending at the posterior extremity of the pygidial axis. The anterior pyriform expansion has been regarded as representing the stomach or proventriculum, located below the glabella, whereas the sagittal canal has been interpreted as representing a hollow intestinal tube. Judging by BARRANDE's figures this interpretation seems plausible enough, and it agrees with the usual assumption that the stomach pouch of trilobites was located below the glabella.

Contrary to RAYMOND's (1920) opinion, however, it seems that no close correspondence could exist between size of glabella and size of stomach. In most, if not all, trilobites, the stomach probably occupied only a fraction of the space below the glabella, and it seems certain that in all species it was much narrower than the glabella. This is pointed out by the location of the "dark markings" and apodemes regarded as places of attachment of the cephalic appendage muscles. It must be evident that in most Illaenidae (Fig. 70*B*) very little space was left for the stomach (or any other organs, for that matter) between the appendage muscles. The same is true for many Cheiruridae with well-developed apodemes.

GENAL CAECA

Many trilobites belonging to diverse families, such as Olenidae, Ptychopariidae, Conocoryphidae, Olenellidae, Remopleurididae, Loganopeltidae, Harpidae, Harpididae, Trinucleidae, and Dionididae, show radiating cephalic "nervures" (usually bifurcating and in cases anastomosing) that Raymond (1920) proposed to call "genal caeca." The "nervures" are raised lines that usually radiate outward toward the periphery of the

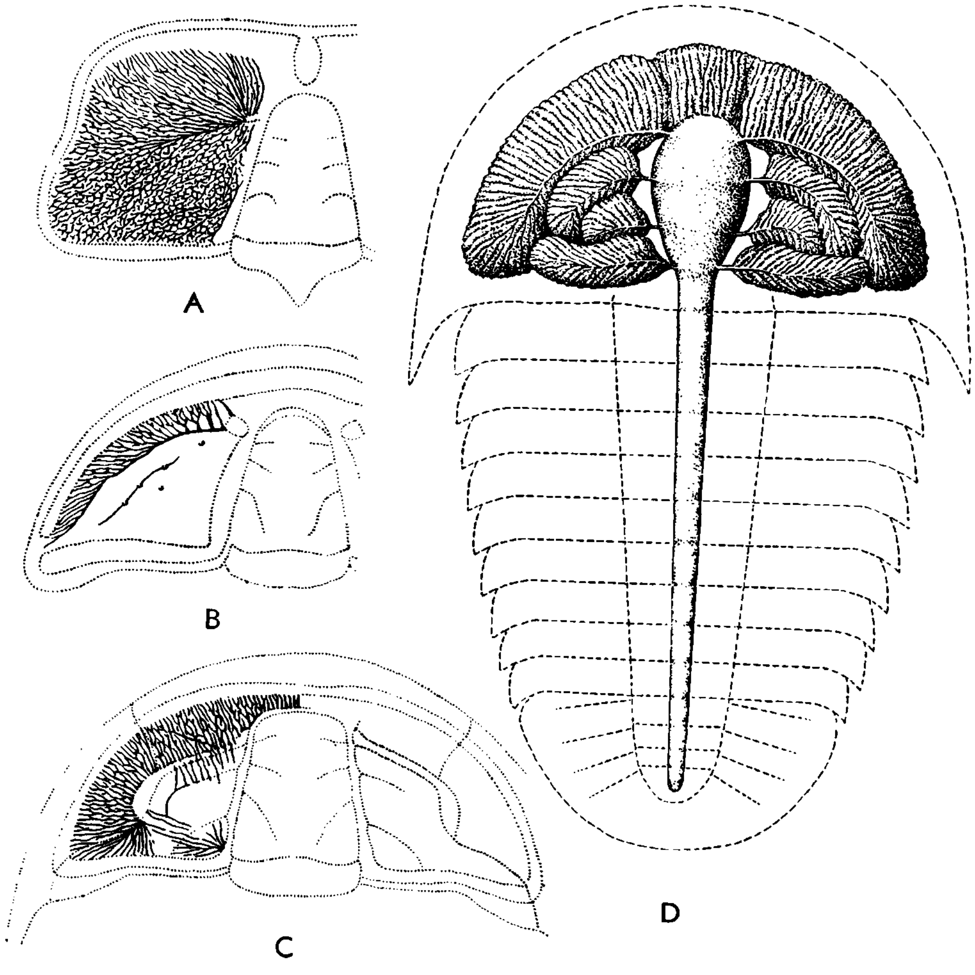

Fig. 73. Genal caeca of trilobites and schematic reconstruction of the digestive system.——*A-C,* Camera lucida drawing of genal caeca; *A, Elyx laticeps* (Angelin), M.Cam., Swed.; *B, Conocoryphe sulzeri* (Schlotheim), M.Cam., Bohemia; *C, Ptychoparia striata* (Emmrich), M.Cam., Bohemia.——*D,* Schematic reconstruction of the digestive system of trilobite, showing stomach and genal diverticules in the cephalic region, and intestine in the thoracic and pygidial regions (all after 24).

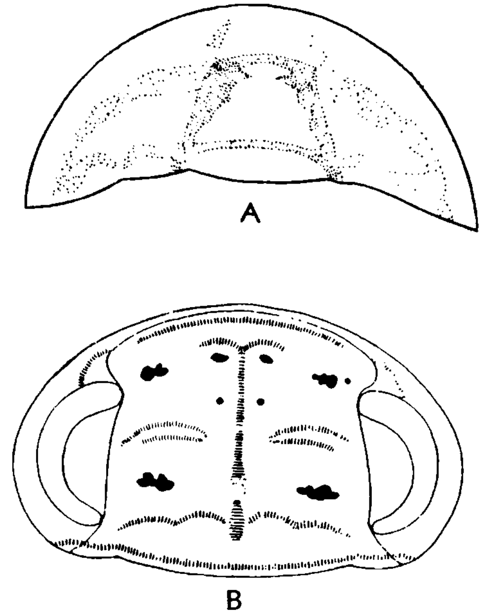

FIG. 74. Cephalc impressions.——*A*. Cephalic impressions of a specimen of *Asaphus cornutus* PANDER, Ord., ×1, regarded by HUPÉ as possible impressions left by blood vessels.——*B*. Cephalic impressions of a specimen of *Nileus armadillo* DALMAN, Ord., Swed., ×2, showing sagittal marking regarded as impression of the ligament suspensor of the heart, and paired muscle scars (after 24).

cephalon, transecting the librigenae, preglabellar area, or fixigenae. They never occur in the glabella or occipital ring (Fig. 73). Usually they are far better impressed on the internal (ventral) face of the cephalon. They probably represent impressions left in the integument by glandular diverticles of the digestive tube. Such organs, obviously in close correlation with the proventriculum or stomach, are beautifully preserved in several Trilobitomorpha found in the Middle Cambrian Burgess Shale of British Columbia, suggesting that they also occurred in trilobites. Fig. 73*D* is a theoretical reconstruction (according to HUPÉ, 1953) of a generalized trilobite showing the probable position of the digestive tract and cephalic glandular diverticles.

CIRCULATORY, NERVOUS, AND RESPIRATORY SYSTEMS

Nothing is known with certainty about the circulatory and nervous systems of trilobites. HUPÉ (1949) described what he regarded as doubtful traces of a circulatory system in a single cephalon of *Asaphus cornutus* from the Ordovician of Rusisa (Fig. 74). Two sets of "communicating canals filled by calcite," one set infraglabellar in position and the other infragenal, were tentatively regarded as representing traces of collateral and hepatic arteries respectively. The structures, however, seem of very doubtful significance. Equally doubtful is the meaning of a median cephalic impression seen in a specimen of *Nileus armadillo* described by MOBERG (1902) and in some cranidia as *Bellefontia chamberlaini* illustrated by ROSS (1951). These impressions have been regarded (HUPÉ, 1953) as the place of attachment of a ligament suspensory of the heart or some other large cephalic vessel.

The respiratory system of trilobites was essentially external, represented by the bladelike filaments borne by the pre-epipodites, which functioned as external branchia (p. O79). RICHTER's suggestion that the ventral membrane may have aided in respiration, probably by osmotic exchange, is beyond the possibility of factual confirmation.

REPRODUCTIVE AND EXCRETORY SYSTEMS

Again, nothing is known about the reproductive and excretory systems of trilobites. BARRANDE, in 1872, described and illustrated a specimen of *Barrandia crassa* from the Middle Ordovician of Bohemia bearing a mass of tiny ovoid bodies located below the integument of the frontal glaellar lobe.[1] The bodies were regarded as eggs still in place in ovaries below the cephalic exoskeleton. If it could be proved that the tiny corpuscles are, in fact, ova, this would mean that the ovaries in *Barrandia* (and possibly in other trilobites) were unusually located very far forward in the cephalic region. However, the nature of the ovoid bodies is, to say the least, still a matter for speculation. For all we know, they could be alien to the single specimen in which

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[1] C. J. STUBBLEFIELD notes that in 1852 BARRANDE described as trilobite eggs various spheroidal bodies found associated with trilobite exoskeletons in Silurian and Devonian deposits of Bohemia. These bodies were red or black pellicles classifiable in 3 size groups: (1) 4 to 5 mm. diameter, (2) 2 mm. diameter, and (3) less than 0.7 mm. diameter.—R.C.M.

they have been noticed.[2] Equally uncertain is the possibility, suggested by HUPÉ (1953), that the macropleurae of some trilobites may have a secondary sexual meaning, representing the genital segments bearing the gonopores.

It is worthy of mention that RESSER & ENDO (1937) described 2 specimens of *Fengtienia peculiaris* from the Middle Cambrian of Manchukuo, lying side by side and apparently joined by the tips of the pygidia, have been tentatively regarded as 2 individuals that died *in copulo*. Probably, however, this so-called "copulating attitude" is due to accidental association.

As regards excretory organs it seems likely that trilobites, being primitive Arthropoda, possessed nephridia. In the great majority of species the external openings of these metameric organs probably were located on the ventral membrane of the genal areas and thoracic pleurae, but, as already suggested by SIEGFRIED (1936), it seems likely that in some progressive forms the openings were located on the cephalic and thoracic pleural doublures, where they are represented by the "Pander openings" (p. O106).

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[2] According to C. J. STUBBLEFIELD, similar ovoid objects from Tremadocian strata of England have been referred (GROOM, 1902) to the genus *Tomaculum*, suggested to represent either excreta or eggs. RUD. RICHTER (1940) has favored the view that *Tomaculum* (identified by him and others from Ordovician strata of Germany and France) represents the excrement of organisms not confined to that of trilobites.—R.C.M.

ENROLLMENT

Most trilobites were capable of enrollment, being comparable in this respect to the living Isopoda and to certain insects (some blattids) and myriapods (glomerids). However, it is practically certain that the Olenellidae and other primitive Lower Cambrian micropygous forms lacked ability to enroll the carapace. This suggests that the olenellids were essentially benthic forms and that their vulnerable ventral side was protected by close apposition to the substratum.

MECHANISM OF ENROLLMENT

In the normal outstretched attitude of the trilobite, the thoracic mesotergites overlapped each other in such a way that the articulating half-ring of one segment was concealed under the posterior part of the axial ring immediately in front. In this attitude the distal parts of the pleurae overlapped each other slightly, their extremities being more or less separated and free.

During enrollment, maximum longitudinal displacement occurred both along the sagittal line of the body and along imaginary lines passing through the pleural extremities, whereas displacement was very slight along the proximal parts of the pleurae and practically none along the axial furrows. The abaxial extremities of the rings acted as pivots for the movement and, as a result, the articulating half-rings were uncovered, in contrast to the distal parts of the pleurae, which became strongly imbricated, overlapping each other.

Several modes of enrollment may be distinguished among trilobites and, as far back as 1852, BARRANDE recognized 3 types which he called spheroidal, double, and discoidal.

SPHEROIDAL ENROLLMENT

This is the commonest type, characterizing such families as the Bathyuridae, Asaphidae, Illaenidae, Proetidae, Calymenidae, Cheiruridae, and Phacopidae, and in general most isopygous or macropygous trilobites. In the spheroidal mode, all the thoracic segments have an equal share in enrollment. As the gliding of the thoracic segments began, the articulating half-rings were progressively uncovered and the thoracic axis became increasingly convex longitudinally. At the same time the downward curvature of the distal parts of the pleurae increased and their extremities became more and more imbricated, overlapping each other. Also, the transverse curvature of the cephalon increased slightly by downward bending of the genal regions. When enrollment was complete, the pygidium touched the cephalon and the whole animal attained a subspheroidal shape, the overlapping distal parts of the thoracic pleurae forming a sort of continuous lateral closure. The vulnerable ventral part with its comparatively soft appendages was thus protected by the firmly

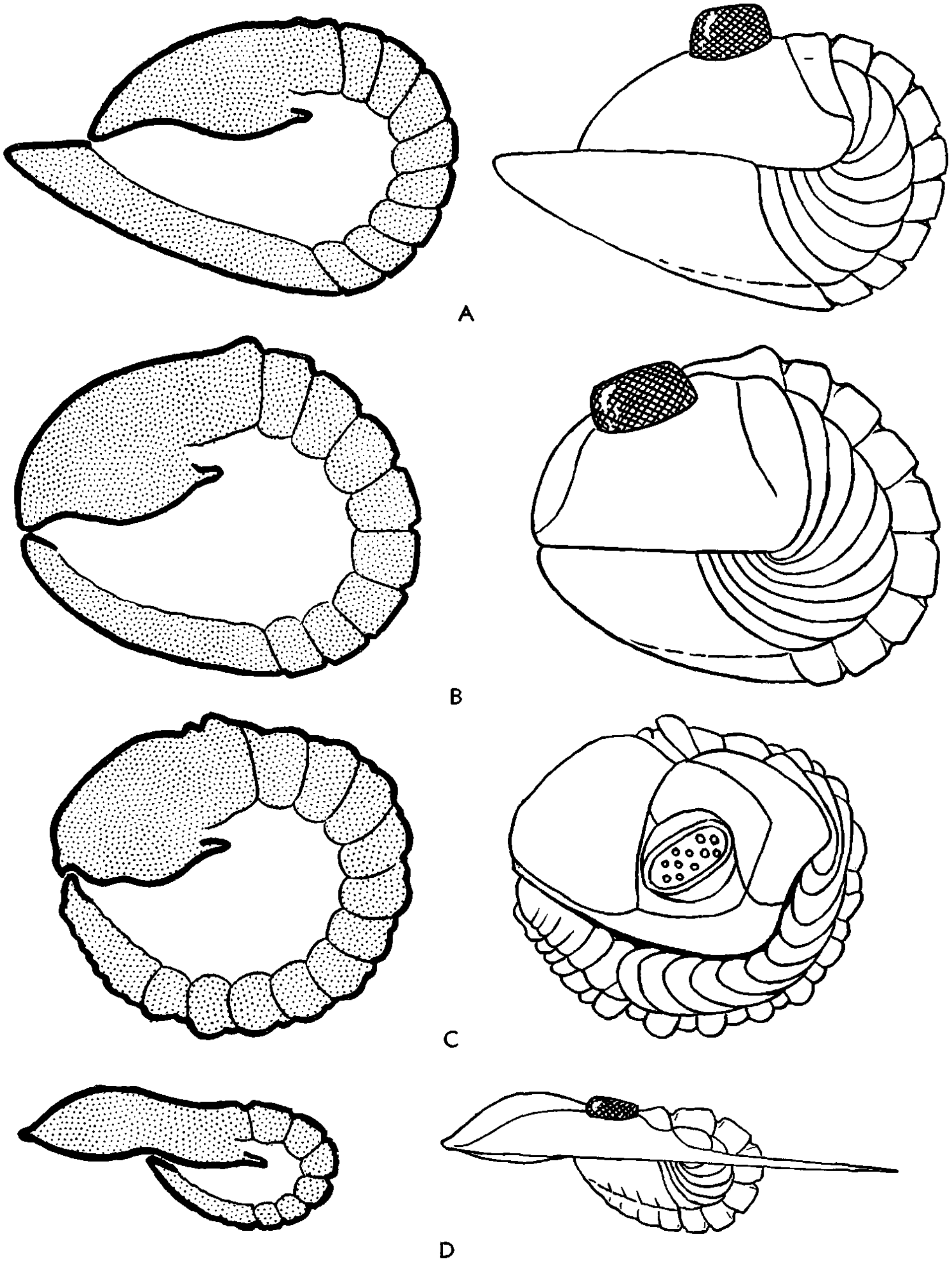

Fig. 75. Types of spheroidal enrollment; right side, lateral view of enrolled specimens; left side, sagittal section of enrolled specimens.——*A*. Pseudomegalaspid type, *Pseudomegalaspis formosa* (Törnquist) Jaanusson, Ord., Swed., ×0.95 (right, after 79, 1953).——*B*. Asaphid type, *Asaphus (Neoasaphus) uplandicus* Wiman, Ord., Swed., ×3.3 (right, after 79, 1953).——*C*. Phacopid type *Eocryphops kayseri* (Hermann), M.Dev., Ger., ×5.5 (right, after 87, 1931).——*D*. Phillipsinellid type, *Phillipsinella parabola* (Barrande) Novák, U.Ord., Scot., ×2 (right, from Whittington's 1950 data).

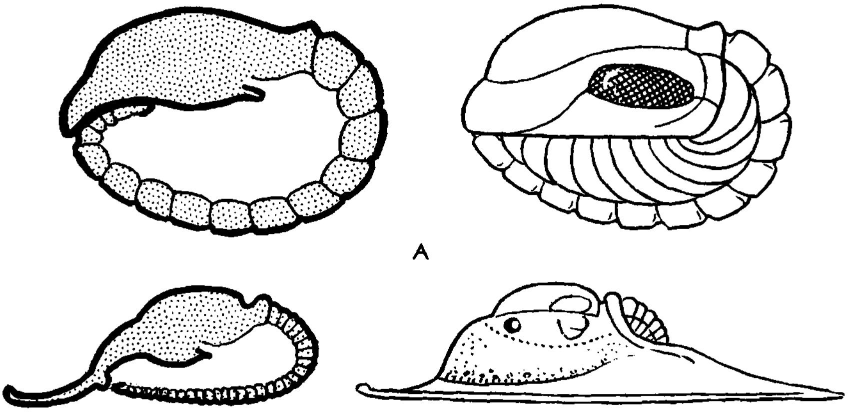

FIG. 76. Double and discoidal enrollment; right side, lateral view of enrolled specimens; left side, sagittal section of enrolled specimens.——Double enrollment (above), *Ellipsocephalus polytomus* LINNARSSON, M. Cam., Swed., ×8.25 (data from 68).——Discoidal enrollment (below), *Harpes macrocephalus* GOLDFUSS, M.Dev., Ger., ×1.25 (right side, after 86, 1921).

closed "box" formed by the enrolled carapace.

Depending, however, on the manner in which the pygidium comes in contact with the cephalon, 4 types of spheroidal enrollment can be distinguished. (1) In the **pseudomegalaspid type** (Fig. 75*A*), the anterior margin of the cephalon fits against the inner edge of the pygidial doublure, while the lateral margins of the cephalon come in contact with the pygidial doublure close to the lateral margins of the pygidium. The pygidium, therefore, protrudes beyond the cephalon for a distance equal to the width of its doublure. (2) In the **asaphid type** (Fig. 75*B*), the anterior margin of the cephalon comes in contact with the posterior margin of the pygidium, the cephalic and pygidial doublures facing each other. (3) In the **phacopid type** (Fig. 75*C*), the posterior margin of the pygidium fits into a furrow on the cephalic doublure, which runs parallel and close to the cephalic margin. (4) Lastly, in the **phillipsinellid type** (Fig. 75*D*), the posterior margin of the pygidium comes in contact with the hypostomal suture, in such a manner that the rostral plate is not covered by the pygidium. The cephalon, therefore, protrudes well beyond the posterior border of the pygidium.

DOUBLE ENROLLMENT

In this mode, characteristic of some primitive micropygous Cambrian trilobites such as *Ellipsocephalus* and *Bailiella,* the posterior thoracic segments bend together with the small pygidium under the thorax, and then the main part of the thorax rolls up according to the spheroidal mode. As a result the dorsal side of the pygidium and last few thoracic segments come in contact with the cephalic doublure, the anterior cephalic margin touching one of the rear thoracic rings (Fig. 76*A*).

DISCOIDAL ENROLLMENT

In this mode, characteristic of certain progressive micropygous and isopygous forms (Harpidae, Trinucleidae, Hapalopleuridae), the thorax folds together in halves like a closing book. The flexion of the thorax is differential, being maximum in a comparatively short anterior stretch that acts as a sort of hinge, whereas it is very slight or none at all along the posterior segments. In this mode of enrollment, the posterior margin of the pygidium may come in contact (1) with the anterior margin of the cephalon **(hapalopleurid type)**, (2) with the girder **(harpid type**, Fig. 76*B*), or (3) with the inner edge of the lower lamella **(cryptolithid type)**. Apparently in no trilobite was the hypostoma uncovered during complete enrollment.

ANATOMIC FEATURES RELATED TO ENROLLMENT

Progressive trilobites developed special structures connected with enrollment. In the main these are devices for providing a

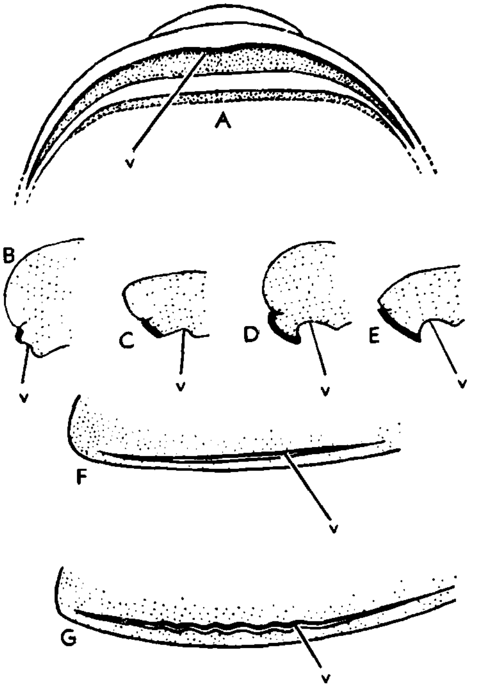

Fig. 77. Vincular furrows.——*A.* Anterior cephalic doublure of *Nephranops miserrimus* (Drevermann), U.Dev., Ger., ×4, showing wide vincular furrow (after 47). *B-E.* Sagittal sections along anterior part of cephalon showing vincular furrow *(v); B, Phacops; C, Trimerocephalus; D, Nephranops; E, Dianops* (after 47).——*F,G.* Lateral vincular furrows; *F,* lateral cephalic doublure of *Phacopidella glockeri* (Barrande), Sil., Bohemia, ×5 (after Hupé, 1953); *G,* lateral cephalic doublure of *Denckmannites micromma* (Roemer), Dev., N.Afr.(Morocco), ×2.5 (after 87, 1943).

firm fastening of the tightly closed "box" formed by the enrolled individual, and devices tending to prevent overgliding of the thoracic pleurae at the completion of enrollment.

VINCULAR FURROWS AND NOTCHES

The name **"vincular furrow"** (from Latin *vinculum,* lock or fastening) is here used as equivalent for Richter & Richter's (1926) *"Verschlussfurche"* and Hupé's (1953) *"sillon de fermiture."* The term "subcranial furrow" used by Delo (1935) to designate these structures is unfortunate because it is both inaccurate and inappropriate; therefore, it is rejected.

The vincular furrow, particularly well developed in the Phacopidae, consists of a more or less deep groove incised on the cephalic doublure, running parallel and close to the cephalic margin. The furrow may be mainly anterior in position, in which case, at the completion of enrollment, the posterior edge of the pygidium fits into the groove as in a tongue-and-groove coupling, providing a very efficient fastening. Anterior vincular furrows are especially well developed in such phacopid genera as *Nephranops* and *Dianops* (Fig. 77*A,D,E*). In some other genera, notably *Phacopidella* and *Denckmannites* (Fig. 77*F,G*), the vincular furrows are found along the lateral cephalic doublures. In this case they acted as grooves for the reception of the thoracic pleural extremities. In *Denckmannites* the furrow is sinuous, providing a close fit for the overlapping pleural extremities.

In some Asaphidae, notably *Asaphus expansus* from the Ordovician of Estonia (Fig. 78), a **vincular notch** is developed along each posterolateral angle of the cephalon. At completion of enrollment, this notch received not only the distal extremities of the pleurae but also a hooklike process carried by the anterolateral angles of the pygidium. This process engaged against the slight anterior concavity of the notch providing a firm fastening.

A very efficient fastening device was developed in the pliomerid genus *Pliomera.* It consists of a row of denticles along the anterior cephalic border and doublure which, upon completion of enrollment, interlocked with the short free extremities of the pygidial pleurae.

PANDERIAN ORGANS

Panderian organs, originally discovered by Pander (1857) in *Asaphus expansus,* are now known to be present in many Asaphidae, Nileidae, Illaenidae, Proetidae, Bathyuridae, Dimeropygidae, and Phacopidae (Fig. 79).

Actually, the name "panderian organs" is applied to 2 different exoskeletal structures which, though apparently related anatomically, may have had, and probably did have, quite dissimilar functions. One of these structures, which (Hupé, 1954) should be called "panderian protuberances," consists of rounded elliptical or elongated ridgelike protuberances found in the fixigenal and thoracic pleural doublures.

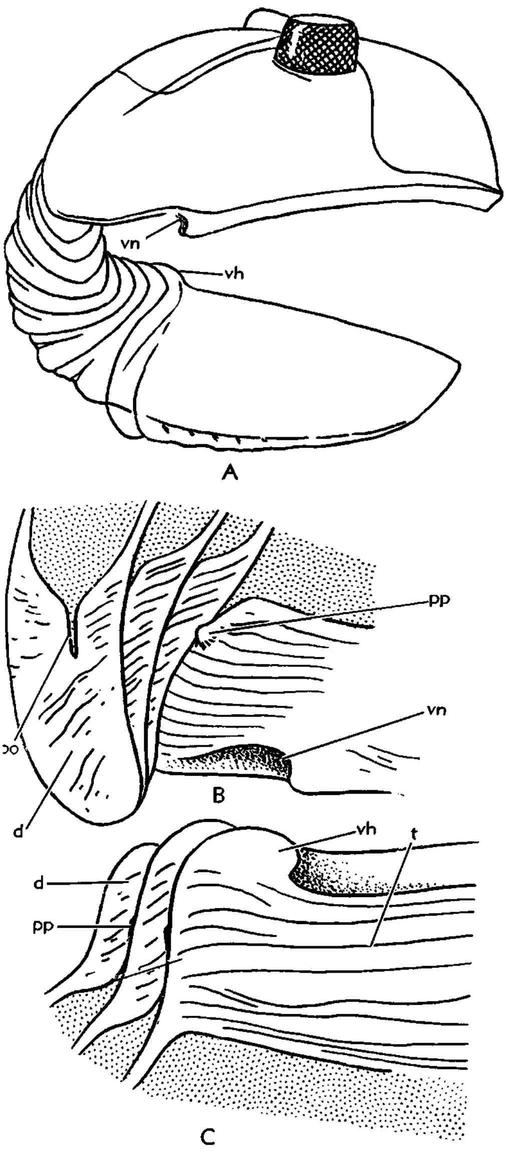

FIG. 78. Vincular notch and hook in *Asaphus expansus* DALMAN, Ord., Estonia (slightly schematic drawing after 52.)——*A*. Specimen not completely enrolled, ×2; the thoracic pleural extremities and the anterolateral angle of the pygidium will fit, at completion of enrollment, into cephalic vincular notch.——*B*. Internal (ventral) view of the posterolateral angle of the cephalon and the anterior 3 overlapping thoracic pleurae, ×4.——*C*. Internal (ventral) view of the anterolateral angle of the pygidium and of the posterior 3 overlapping pleurae, ×4. (Explanation: *d*, doublure; *po*, panderian opening; *pp*, panderian protuberance; *t*, terrace lines; *vn*, vincular notch; *vh*, vincular hook.)

The other structures, which properly should be called "panderian openings," are small rounded or elliptical holes in the exoskeleton, located immediately behind the panderian protuberances. In some trilobites, they appear as notches along the adaxial margin of the pleural doublures, immediately behind the panderian crests.

All authors who have described panderian protuberances agree that they represent "stopping devices" to prevent the overgliding of the onlapping pleurae during enrollment, the anterior border of one pleura abutting against the protuberance of the pleura immediately in front of it when maximum permissible enrollment was reached by the animal.

No agreement exists, however, about the meaning of the panderian openings. Some authors, notably HUPÉ (1945, 1954), actually believe that no such openings existed in the living animal. However, since these openings actually occur in fossil specimens, notably in silicified material of *Isotelus* described by WHITTINGTON (1941), HUPÉ advanced the hypothesis that in this and other trilobites the integument near the panderian protuberances was extremely thin and that it covered a special sensory organ, which he called *"avertisseur panderien,"* which "advertised" the passage of the anterior border of one pleura just before it touched the panderian protuberance of the one immediately in front. He further argued that the integument may have been so thin that, in some individuals, it may have broken away during life of the animal, the traumatism leading to death of the individual. Such an hypothesis seems far-fetched and fails to explain why all the pleurae have openings. If the tiny holes originated accidentally and caused death, it is logical to suppose that only one or at most a few of the pleurae would have been thus perforated, instead of all of them. Moreover, what is known about cicatrization of wounds and regeneration of parts in trilobites suggests that such small wounds, if made, would have healed very rapidly.

All in all, the available evidence seems to be in favor of SIEGFRIED's (1936) suggestion that the panderian openings represent pores leading to some metameric internal organs, such as nephridia. Probably in the great majority of trilobites the pores opened on the ventral membrane of the pleurae and fixigenae, whereas in a few *(Dimeropyge spinifera, Illaenus sarsi)* the pores were located on the ventral membrane directly along the adaxial edge of the doublure ("panderian notches"). In a few species the pores seem to have opened in the doublure itself behind the panderian protuberances, which may have served as protecting bosses or ridges.

OTHER CHARACTERS

COLOR PATTERNS

It is hardly conceivable that living trilobites were colorless, as this would mean that their carapace was translucent. In all probability their exoskeleton was pigmented, but whether it was uniformly or irregularly colored is difficult to judge. Possibly both types of patterns occurred. To the writer's knowledge only 4 instances of color markings on trilobites have been described. These include (1) a pygidium of *Anomocare vittata* from the Middle Cambrian of Alabama (Fig. 80*B*), described by Raymond (1922), with color markings that consist of somewhat irregular fan-shaped bands traversing the pleural regions and continuing across the axis in narrower belts; (2) a pygidium of *Phillipsia? tenuituberculata* from the Mississippian of Missouri (Fig. 80*A*), described by Williams (1930), showing paired rows of rounded pigmented spots on the abaxial part of the rings; (3) a few specimens of *Isotelus maximus* from the Upper Ordovician of Ohio, described by Wells (1940), showing dark areas along the thoracic axial furrows; and (4) a pygidium of *Ditomopyge meridionalis* from the Permian of Western Australia, described by Teichert (1944), showing numerous small rounded spots scattered over the surface of both the pleural regions and the axis.

CICATRIZATION, REGENERATION, PATHOLOGY, AND TERATOLOGY

Trilobites possessed the ability to heal their wounds and to regenerate broken parts. This is clearly shown by different specimens displaying unmistakable evidence of cicatrization of injuries and secondary growth of parts. A notable individual of *Paedeumias robsonensis,* from the Lower Cambrian of British Columbia, illustrated by Burling (1917), has the 4th, 5th, and 6th right prothoracic pleurae damaged, the injuries having healed during the life of the animal (Fig. 81). A pygidium of *Tricrepicephalus paraconus* from the Upper Cambrian of Missouri, described by Lochman (1941), has the left spine broken at the base and a callus, obviously formed during the life of the animal, covering the wound. A pygidium of *T. texanus,* also from the Upper Cambrian of Missouri (Lochman, 1936), has the tip of one of the spines bent abruptly from its normal position. A cephalon of *Illaenus wahlenbergi* from the Middle Ordovician of Estonia, described by Holm (1886), shows an extra facial suture on one side and a duplication of the posterior border. As suggested by Raymond (1916) this seems to have been due to partial retention of the old integument after molting.

Several cases of regeneration of parts also are known. A cephalon of *Ceraurus matranseris,* from the Upper Ordovician of Quebec, described by Sinclair (1947), shows a regenerated spine. The right genal spine was broken near the middle part and the secondary outgrowth differs from the original spine in having a sculpture of concentric striae instead of tubercles. Eye surfaces, being salient unprotected areas, were also easily damaged. Several instances of regeneration of eye lenses are known. In a specimen of *Asaphus cornutus* from the Ordovician of the Baltic region of Russia, described by Hupé (1953), the regenerated parts can be recognized easily. The newly formed facets are either smaller than the original, or polygonal in outline. A similarly damaged eye of *Telephina mobergi,* from the Lower Ordovician of Sweden, was figured by Hadding (1913) and described by Isberg (1917). It is probable that these eye injuries occurred during molting.

Pathological specimens of trilobites are also known. A classical example is a cephalon of *Megistaspis acuticauda* from the Ordovician of the Baltic region illustrated by Schmidt (1906) (Fig. 82*A*) that shows a large tumor on the left side and a corresponding deformation of the anterior sec-

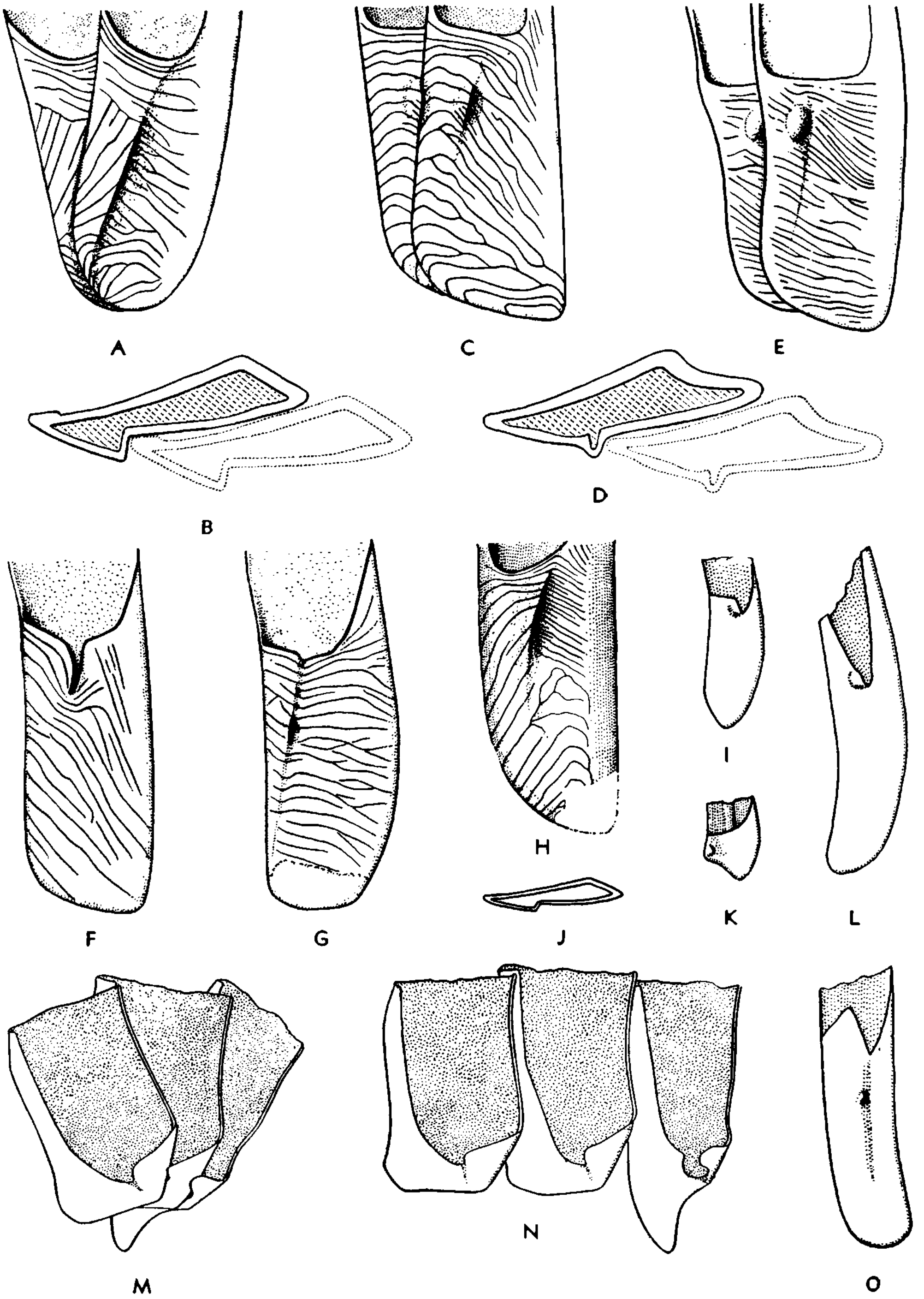

FIG. 79. Panderian protuberances and openings.——*A,B. Symphysurus palpebrosus* (DALMAN), Ord., Swed., *A*, ventral view of 2 thoracic pleurae in enrolled position, ×10; *B*, cross section of same passing through panderian protuberance, ×18 (after 25).——*C,D. Asaphus (Neoasaphus) cornutus* (PANDER), Ord., Russia; *C*, ventral view of 2 thoracic pleurae in enrolled position, ×10; *D*, cross section of same, passing through

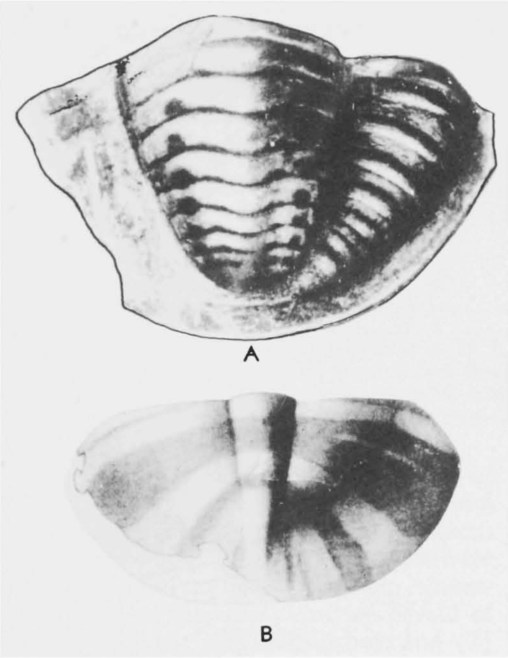

FIG. 80. Color patterns.——*A.* Pygidium of *Phillipsia? tenuituberculata* (J.S. WILLIAMS) HARRINGTON, Miss., USA(Missouri), ×4, showing paired spots on axial rings (after 100, 1930).——*B.* Pygidium of *Anomocare vittata* RAYMOND, M.Cam., USA (Alabama), ×2, showing fan-shaped light and dark bands (after 42).

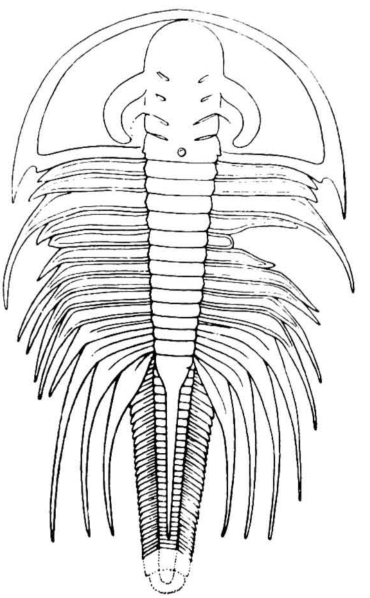

FIG. 81. *Paedeumias robsonensis* BURLING, L.Cam., Can., ×1, specimen showing healed injuries on right side of prothorax (24, after BURLING).

tion of the facial suture.[1] A pygidium of *Nieszkowskia capitalis* from the Ordovician of Estonia, illustrated by ÖPIK (1937), shows strong deformity of the right side affecting both the axis and the pleural region. A pygidium of *Coronura aspectans* from the Devonian of Ohio, illustrated by HALL & CLARKE (1888) (Fig. 82*D*), shows marked deformities in the right pleural region. Notable is the case of the deformities observed in pygidia of *Scutellum flabelliferum* and allied forms, from the Middle Devonian of Germany, described by RICHTER & RICHTER (1934). Here several pathological pygidia were found, suggesting either deformations of parasitic origin or cicatrization of injuries inflicted during molting (Fig. 82*B*). As long ago as 1843 PORTLOCK described and illustrated a deformed pygidium of *Phillipsia ornata* from Lower Carboniferous rocks of Ireland.

Teratological cases are also known among trilobites. In most specimens the malforma-

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[1] Another example from Tremadocian strata of England (STUBBLEFIELD, 1926) is a specimen of *Shumardia pusilla* with normal 4th macropleural spine on the left side but showing on the right side an abnormal 3rd macropleural spine succeeded by the 4th and 5th pleurae fused at about mid-length to form a stout nonmacropleural lateral termination; this is inferred to denote an injury to the right macropleural thoracic spine in a preceding molt.—C.J.S.

(*Continued from facing page*)

panderian protuberances, ×20 (after 25). *E. Pseudomegalaspis formosa* (TÖRNQUIST) JAANUSSON, Ord., Swed.; ventral view of 2 thoracic pleurae in enrolled position, ×4.7 (after 79, 1953).——*F. Asaphus lepidurus* NIESZKOWSKI, Ord., Baltic region; ventral view of thoracic pleura, ×6 (after 25).——*G. Niobe frontalis* (DALMAN), Ord., Swed.; ventral view of thoracic pleura, ×9 (after 25).——*H,I. Nileus armadillo* DALMAN, Ord., Swed.; *H,* ventral view of thoracic pleura, ×10; *I,* cross section of same, passing through panderian protuberance, ×10 (after 25).——*J. Illaenus chudleighensis* HOLM, Ord., Baltic region; ventral view of thoracic pleura, ×3 (after 25).——*K. Acaste downingiae* (MURCHISON), Sil., G.Brit.; ventral view of thoracic pleura, ×9 (after 25).——*L. Illaenus sarsi* JAANUSSON, Ord., Swed.; ventral view of thoracic pleura, ×4 (after 25).——*M,N. Dimeropyge spinifera* WHITTINGTON & EVITT, M.Ord., USA(Virginia); *M,* ventral view of 3 thoracic pleurae in enrolled position, ×30; *N,* same in outstretched position, ×30 (after 71).——*O. Ptychopyge* sp., Ord., ?Swed.; ventral view of thoracic pleura, ×2 (after 25). (Explanation: in Figs. *M,N,* anterior margins of pleurae face to the right but in all others they face to the left.)

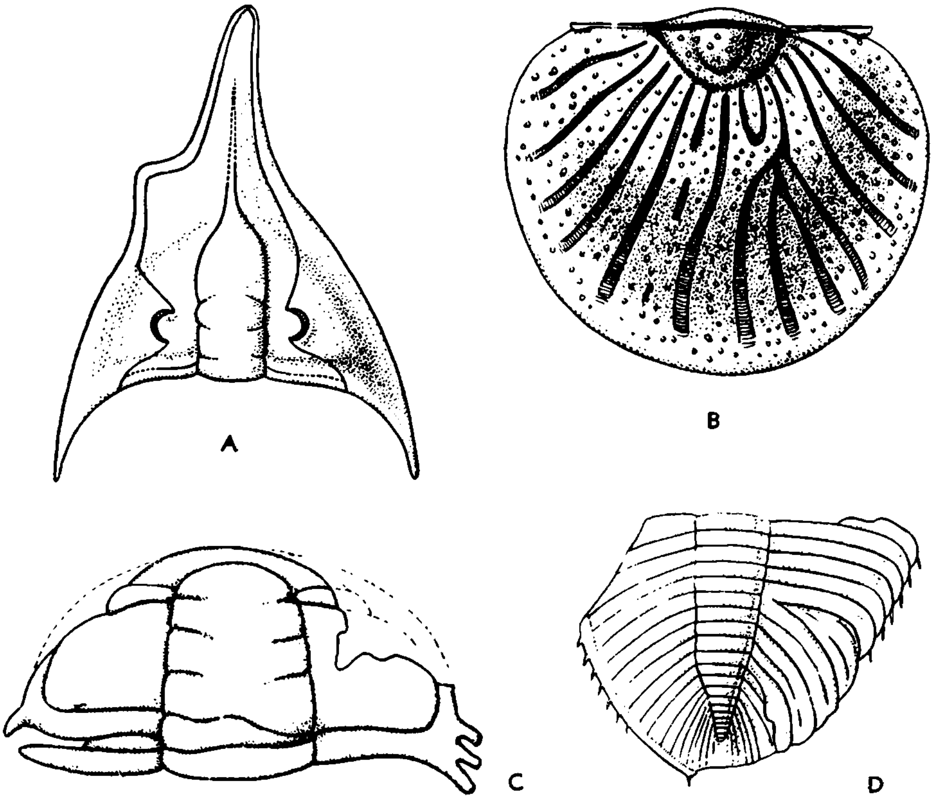

Fig. 82. Pathological and teratological individuals.——*A*. Pathological cephalon of *Megistaspis acuticauda* (Angelin) Jaanusson, Ord., Baltic region, ×0.6, showing tumor on left side and deformation of anterior section of facial suture (after 24).——*B*. Pathological pygidium of *Scutellum (Scutellum) flabelliferum* (Goldfuss), M.Dev., Ger., ×3 (after 24, from 48).——*C*. Teratological specimen of *Rossaspis superciliosa* (Ross) Harrington, L.Ord., USA(Utah), ×1; the 2 anterior thoracic segments of the right side are fused with the cephalon, whereas on the left side the 1st thoracic pleura is abortive (after 24, from 49).——*D*. Pathological pygidium of *Coronura aspectans* (Conrad) Hall & Clark, L.Dev., USA(Ohio), ×1.33 (after 17).

tions consist of abnormal fusion of segments. In an individual of *Paradoxides* from the Middle Cambrian of Sweden described by Westergård (1936) the last thoracic segment is fused with the pygidium, whereas in a specimen of *Bathyuriscus brighamensis* from the Upper Cambrian of Utah figured by Resser (1939), the 1st thoracic segment is fused with the cephalon. An exceptional fossil described by Ross (1951) is a specimen of *Rossaspis superciliosa* from the Lower Ordovician of Utah (Fig. 82*C*). Here the 1st and 2nd right pleurae are fused with the cephalon, whereas they are developed on the left side. However, the 1st left pleura is deformed and abortive.

A special case is that of *"Trinucleus" pongerardi* from the Ordovician of France, described by Rouault (1846) and Oehlert (1895). Oehlert's studies have shown that, in a collection of 2,000 specimens, about 40 per cent are characterized by bifurcated genal spines. The bifurcation may affect only one (right or left) or both spines, and it may occur at the base, the middle, or close to the extremity of the spine. The abundance of teratological individuals may even suggest hybridism and hereditary transmission of malformations.

MOLTING

Trilobites, having a hard unyielding exoskeleton, could grow only by molting or, more precisely, only during the brief periods immediately after they had shed their exoskeletons.

Probably the great majority of trilobite remains known as fossils are exuviae shed

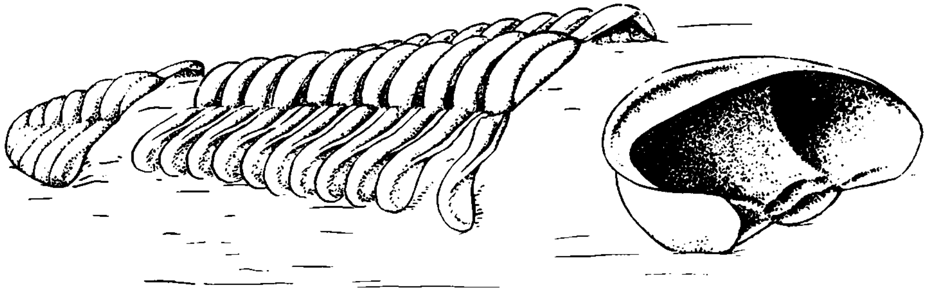

Fig. 83. Phacopid mode of ecdysis. Exuviae of *Nephranops* sp., U.Dev., Ger., showing thoracic and pygidial parts in normal position (ventral face downward), whereas the cephalon has rotated backward about 180° and lies upside down; as the facial sutures are nonfunctional, the librigenae remain attached to the cranidium (after 46).

during molting, either found *"in situ"* or transported and accumulated by waves and sea currents. This is suggested by 2 facts: (1) remains of dead individuals must have been destroyed rapidly by bottom scavengers, whereas the empty exuviae devoid of soft tissues were left undisturbed; and (2) a single individual, attaining the normal life expectancy of the species, probably molted many times. Raw (1927) estimated that not less than 29 molts took place in *Leptoplastoides salteri* from early protaspid to late holaspid stages, and it seems likely that in large trilobites the number of molts was considerably greater. This means that, even if one accepts the postulate that a trilobite carcass had the same chance of preservation as the exuviae, probably not more than 10 per cent of the fossil remains would correspond to those of dead animals.

It is generally accepted that the cephalic sutures played an important role during ecdysis, acting as lines of weakness along which different cephalic exoskeletal pieces cleaved apart, providing spaces through which the animal could crawl out of the old integument. It seems certain, however, that the junction line between cephalon and thorax also played an important part in molting, particularly in those trilobites that, like most phacopids, had nonfunctional facial sutures. The different sutural patterns must have controlled the mechanics of molting in different trilobites, but our knowledge of the modes in which ecdysis was accomplished is unsatisfactory and confined to the data furnished by comparatively scarce specimens interpreted as representing undisturbed exuviae. The best understood are, at present, the phacopid and the olenid modes of molting.

The **phacopid mode**, illustrated by Salter (1864), was analyzed in detail by Richter (1937), who styled it *"Salter'sche Einbettung"* (Salterian molting).[1] The term "phacopid mode" seems more appropriate. According to Richter, it characterizes several Devonian phacopids, including several species of *Phacops, Nephranops, Trimerocephalus, Dianops, Cryphops, Phacopidella,* and *Asteropyge,* in which the facial sutures are nonfunctional. The exuviae consist of thorax and pygidium in normal position and of a complete cephalon (librigenae firmly attached to the cranidium) lying somewhat in front of the thorax in upside-down position (Fig. 83). The main line of ecdysis seems to have been the junction between cephalon and thorax. As these 2 pieces cleaved apart, the animal crawled backward and buckled upward, forcing its head through the opening while shedding the old cephalon, which was tilted forward, rotating on its anterior margin. Once the cephalic region was free, the animal crawled forward, leaving behind the old thoracic and pygidial integuments and causing the old cephalon to overturn completely, so as to rest on its dorsal surface with its anterior margin facing the thorax.

A somewhat similar mode of molting seems to have characterized some telephinid trilobites. A specimen of *Telephina spinifera* from the Upper Ordovician of Virginia, illustrated by Fischer (1946) and re-

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[1] This was first illustrated by J. de C. Sowerby in 1840 and later by Phillips (1841) and Sandberger & Sandberger (1850).—C.J.S.

garded by GLAESSNER (1948) as representing undisturbed exuviae, shows the thorax and cranidium in a position similar to that of the phacopid postecdysial attitude, but in this case the librigenae (still united anteriorly by the narrow cephalic doublure) lie in normal upside-up position between the thorax and the cranidium. In this species, therefore, the facial sutures were functional, and the librigenae, with their very large visual surfaces, were shed independently by wiggling the head, probably before the animal crawled out of its old thoracic integument.

The **olenid mode** of molting has been recently analyzed by HENNINGSMOEN (1957) on the evidence furnished by numerous individuals of *Acerocare ecorne* from the Upper Cambrian of Norway, regarded as undisturbed exuviae. This mode seems to have

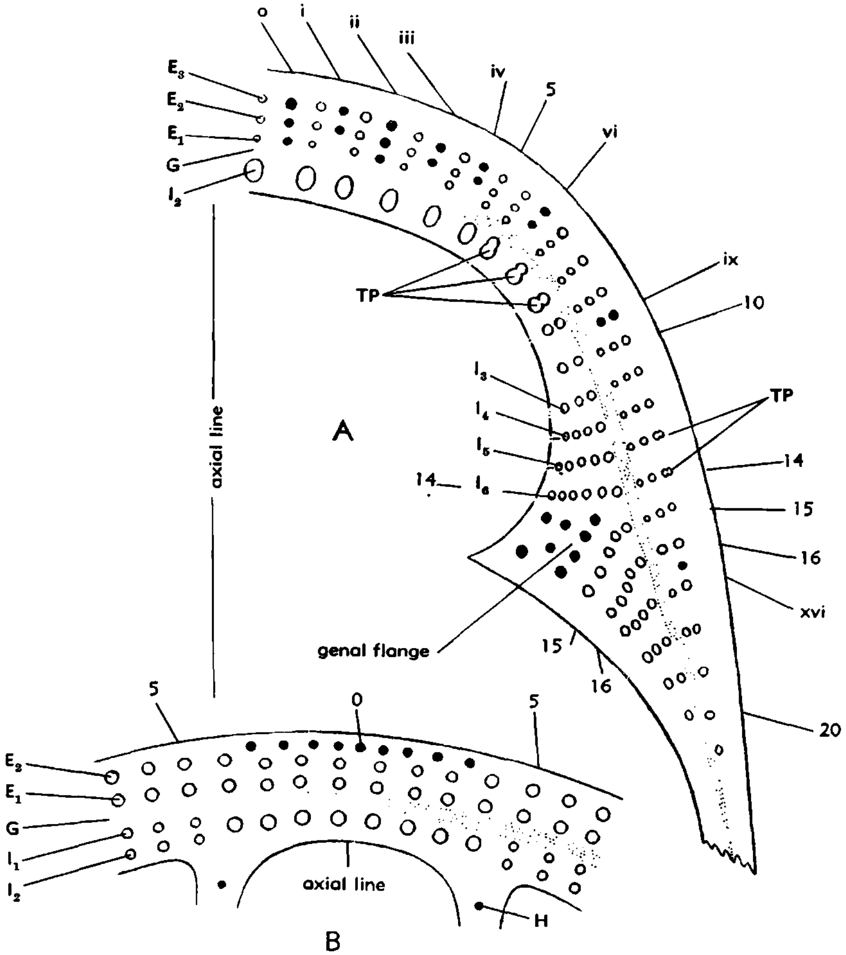

FIG. 84. Notation used for numbering of pits in the Trinucleidae (after 98, 1955).——*A*. Diagram of the lower lamella of a hypothetical trinucleid.——*B*. Diagram of the median part of the upper lamella of a hypothetical trinucleid. [Explanation: adventitious pits (9) marked in black; radii (R) indicated by arabic, and interradii (IR) by roman numerals; 1st to 3rd concentric rows of primary pits external to girder designated E_1, E_2, E_3; 1st to 6th rows of pits internal to girder (G) indicated I_1, I_2, I_3, I_4, I_5, I_6; twin pits (TP), indicated by square brackets in notation given below, are frequently dumbbell-shaped and incompletely divided; pits (marked in black) indicate (i) an interradial position; (ii) a region on the genal flange where the notation cannot be used; in the figure, 8 pits are irregularly arranged on the genal flange between R14-15. The fringe-formula, which applies to half the complete fringe as illustrated, is $E_1$1—21, $E_2$1—18, $E_3$1—15, ($E_4$13-14): e_1o,ii,e_2o—iv,vi,ix,xvi,e_3o—iv,vi,ix; I_1I—20, ($I_2$6—8), $I_2$9—10, $I_3$11—18, $I_4$12—17, $I_5$13—16, $I_6$14.]

characterized many other trilobites belonging to this family. Among the Lower Ordovician olenids from Argentina described by HARRINGTON & LEANZA (1957), specimens belonging to not less than 7 species consist of undisturbed exuviae closely similar to the Norwegian material. These include species of *Parabolina, Saltaspis, Angelina, Parabolinella, Plicatolina,* and *Triarthrus.* The undisturbed exuviae consist of a cranidial-thoracic-pygidial unit and of a librigenal unit which lies below the cranidium and is somewhat displaced backward. As interpreted by HENNINGSMOEN, fission occurred along the facial sutures, which were connected anteriorly by a transverse marginal stretch. By slight wiggling of the head the molting trilobite was able to enlarge the opening so as to free itself from the old librigenal integument, which then came to rest beneath the cephalic region. As no median or connective sutures were present in the Olenidae, the 2 librigenae formed a single piece connected anteriorly by the narrow cephalic doublure. Once the librigenae were shed, the trilobite crawled forward, leaving the old thoracic and pygidial integument behind and in so doing, pushing the librigenal exuviae slightly backward (the librigenae being still connected by the ventral membrane that supported the free hypostoma). As a result, the exuviae consist of a cranidial-thoracic-pygidial complex and a backward displaced librigenal unit that underlies the cranidium and anterior part of the thorax. In some specimens of *Acerocare ecorne* the cranidium is missing, and this led HENNINGSMOEN to suggest that, in molting of some specimens, ecdysis may have been laborious, the freed trilobite carrying

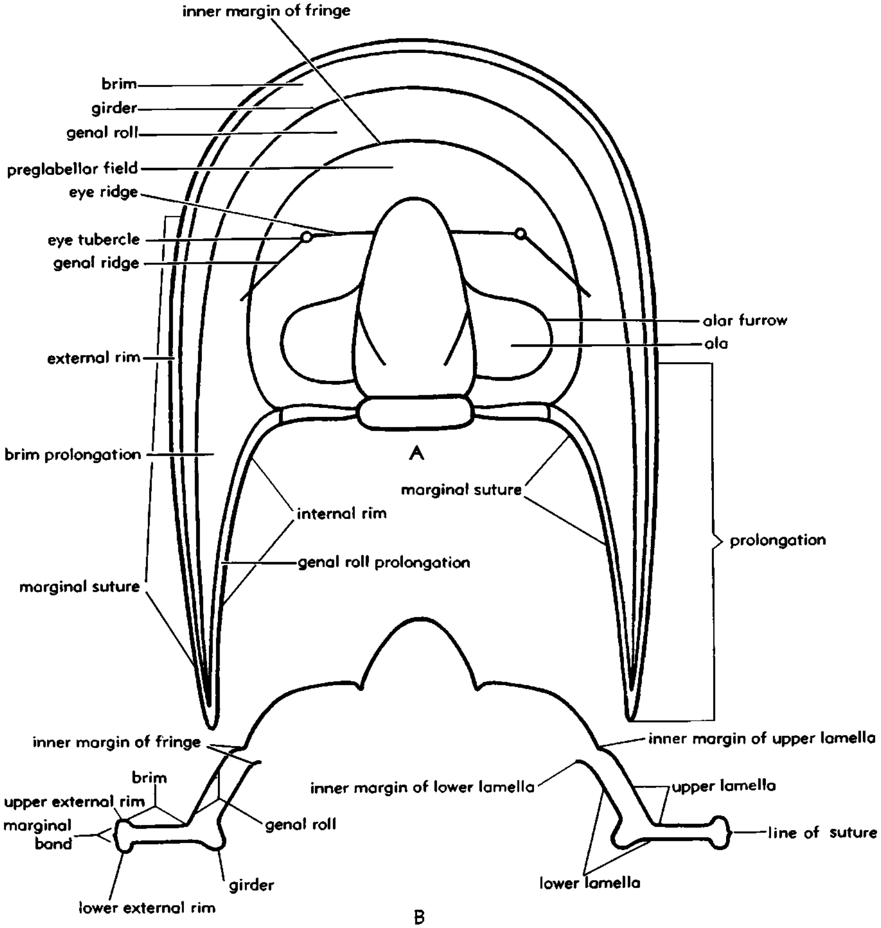

FIG. 85. Cephalic nomenclature of Harpidae; *A,B,* dorsal view and transverse section of cephalon.

away the almost loose cranidial integument that finally was shed at some distance from the remainder of the exuviae. Similar examples are known in Argentine specimens of *Parabolina argentina, Saltaspis steinmanni,* and *Triarthrus parchaensis.*

A mode of molting somewhat similar to that of the Olenidae seems to have characterized some Richardsonellidae, particularly *Pseudokainella* and *Apatokephalus,* as can be inferred from specimens illustrated by HARRINGTON & LEANZA (1957) from the Lower Ordovician rocks of Argentina. In these genera, however, the librigenae are always separated, indicating the presence of functional median (?or connective) sutures.

A small (1.5 cm.) cephalon of *Paedeumias transitans* from the Lower Cambrian of Pennsylvania, illustrated by WALCOTT (1910) and RESSER (1937), has been interpreted by SWINNERTON (1919) and HUPÉ (1953) as probably representing undisturbed exuviae. The cephalon has the rostral plate (bearing the stalked hypostoma) still attached to its rear part, but the plate lies directly behind the cephalon and on the same surface, having rotated 180° on its posterior extremities and so as to rest upside down on its dorsal (internal) face. HUPÉ interpreted the remains as cephalic exuviae shed in a manner similar to that of the phacopid mode of molting, but this can hardly be the case. The remains suggest that the perrostral suture was the main line of ecdysis, and not the junction between cephalon and thorax, as in the phacopid trilobites. The wide gap left by the fission along the perrostral suture must have provided a very easy means of escape for the molting trilobite, which had simply to crawl forward to free itself from the old integument. It is difficult to imagine how, in so doing, the trilobite could have caused the rostral plate (and ventral cephalic membrane) to rotate downward and backward by about 180°. It is conceivable that such a rotation may have occurred accidentally in small specimens, but it seems completely out of the question for large individuals.

FEATURES OF TRINUCLEIDS AND HARPIDS

Morphological characters of trinucleid and harpid trilobites, omitted in earlier discussion, are illustrated in Figures 84 and 85, with indication of nomenclature of parts.

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MORPHOLOGICAL TERMS APPLIED TO TRILOBITA

By H. J. Harrington, R. C. Moore, and C. J. Stubblefield

The somatic terminology of trilobites in the English language has undergone considerable changes since the early descriptions by Green, Milne Edwards, and M'Coy. Several attempts have been made during the last 25 years to stabilize nomenclature, and important papers on the subject have been published by Warburg, Howell, *et al.*, Whittington, Rasetti, Jaanusson, Ross, Whittard, and Henningsmoen; but to this day no comprehensive glossary of terms has been published. The following attempt to list morphological terms used by different authors has as one of its purposes the stabilizing of nomenclature by redefinition of terms and introduction of new names where thought to be necessary.

Most important terms are printed in boldface capital letters (as **ANTERIOR BORDER**), useful but less important terms in boldface small letters (as **abaxial**), and least important (in part obsolete) terms in italic letters (as *antennary pit*).

GLOSSARY OF TRILOBITE MORPHOLOGICAL TERMS

abaxial. Away from axial line.

adaxial. Toward axial line.

aggregate eye. See schizochroal eye.

ala (pl. **alae**). Smooth semicircular area adjoining posterior portion of glabella, outlined distally by furrow and commonly depressed below adjacent part of gena, as in Harpidae. *See* paraglabellar area.

alar furrow. Curved furrow bounding ala peripherally as in Harpidae.

anaprotaspis (pl., **anaprotaspides**). Smallest protaspides in a size series, in which protopygidium is extremely small and ill defined.

antenna (pl. **antennae**). Multijointed sensory appendage attached to front part of cephalon on ventral side.

antennary pit. See fossula.

antenniform cercus (pl., cerci). Uniramous appendage on ventral side of last pygidial segment, known only in *Olenoides serratus* (syn., caudal ramus, cercus, uropod).

antennular pit. See fossula.

anterior area (of fixed cheek). See anterior area (of fixigena).

anterior area (of fixigena). Portion of fixigena in front of eye ridge. If eye ridges are absent, posterior boundary of the area is marked off by imaginary line connecting anterior extremity of palpebral lobe with anterolateral border of glabella (syn., anterior area of fixed cheeks, anterior region of fixed cheek or of fixigena).

ANTERIOR BORDER. Portion of cephalic border between anterior sections of facial sutures (if present); otherwise ill defined.

ANTERIOR BORDER FURROW (OF CEPHALON). Portion of border furrow bounding anterior border (syn., front furrow, frontal furrow).

anterior branch (of facial suture). See anterior section (of facial suture).

anterior flange. Narrow border extending along anterior edge of adaxial portion of a pleura, as in *Ceraurinella.*

ANTERIOR LATERAL GLABELLAR FURROW. First lateral glabellar furrow when numbering from front to back (*see* lateral glabellar furrow).

ANTERIOR LATERAL GLABELLAR LOBE. Lateral portion of glabellar region between anterior lateral and median glabellar furrow, or between anterior lateral and preoccipital glabellar furrows.

anterior limb. See frontal area.

anterior lobe (of glabella). See frontal lobe.

anterior lobe (of hypostoma). Portion of middle body of hypostoma in front of middle furrow.

anterior median process. See frontal process.

anterior pit. See fossula.

anterior pleural band. Strip of thoracic or pygidial pleura bounded posteriorly by pleural furrow.

anterior pleural spine. Extension of distal end of an anterior pleural band.

anterior region (of fixigena or fixed cheek). See anterior area (of fixigena).

ANTERIOR SECTION (OF FACIAL SUTURE). Portion of facial suture lying in front of eye [syn., anterior branch (of facial suture), preocular branch (of facial suture)].

anterior wing (of hypostoma). Extension of anterolateral borders of hypostoma.

apodemal pit. Excavation in external surface of a tergite corresponding to apodeme on internal surface, as in *Ceraurinella* (syn., appendiferal pit).

apodeme. Process for attachment of muscles or ligaments, formed by inbending or thickening of dorsal exoskeleton on internal side of a tergite (syn., appendifer).

appendifer. See apodeme.

appendiferal pit. See apodemal pit.

area. Portion of region or lobe.

articulating boss (and socket). Corresponding structures on the margins of thoracic segments, in some cases situated in the axial furrows, as in Remopleurididae.

ARTICULATING FURROW. Transverse groove between main portions of articulating half ring.

ARTICULATING HALF RING. Anterior extension of axial ring which bends downward to pass under posterior edge of ring just in front of it (syn., half ring).

associated. See attributed.

attributed. Term used for isolated parts of exoskeleton found near together and considered to belong to the same species.

AXIAL FURROW. Groove outlining axial regions of cephalon, thorax and pygidium (syn., dorsal furrow).

axial glabellar furrow. Furrow in axial line of cranidium extending onto frontal lobe of glabella from preglabellar furrow, as in Encrinuridae and Cheiruridae.

axial line. See sagittal line.

axial lobe. See axis.

AXIAL NODE. Medial (or paired) tubercle on external surface of axial ring.

axial region. See axis.

AXIAL RING. Central portion of thoracic or pygidial tergite bounded laterally by axial furrow (syn., ring).

AXIAL SPINE. Medial (or paired) pointed structure projecting from external surface of axial ring.

AXIS (pl., **AXES**). Medial region of dorsal exoskeleton, outlined by axial furrows (syn., axial lobe, axial region, rachis, rhachis).

axis (of pygidium). Medial region of pygidium, outlined by axial furrows (syn., pygothorax).

axis (of thorax). Medial region of thorax, outlined by axial furrows (syn., axothorax).

axothorax. See axis (of thorax).

basal furrow. See preoccipital glabellar furrow.

basal lobe (of glabella). Lateral lobe adjacent to posterolateral extremity of glabella, as in Agnostida and *Schizoproetus. See* lateral preoccipital lobe.

basipodite. See trochanter.

Bertillon pattern. Pattern of subconcentrically arranged, raised, terrace lines on external surface, simulating a fingerprint.

bicomposite glabellar lobe. Lateral glabellar lobe representing fused anterior and median lateral glabellar lobes, separated from frontomedian lobe of glabella by anterior lateral glabellar furrow, as in Lichidae.

biramous appendage. Ventral appendage consisting of outer branch (pre-epipodite) and inner branch (telopodite).

BORDER. Outer, dorsal flange of cephalon and pygidium usually bounded by border furrow (syn., marginal limb, marginal rim).

BORDER FURROW. Furrow bounding border of cephalon and pygidium (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).

brim. Peripheral portion of fringe, bounded on inward side by girder or corresponding inflection of upper lamella, as in Harpidae, Harpididae, and Trinucleidae (formerly used also in the sense of "frontal area" or "preglabellar field").

brim prolongation. Peripheral portion of fringe prolongation, bounded by girder; represents an extension of brim, as in Harpidae and Harpididae.

burlingiiform sutures. Proparian sutures in which the anterior and posterior sections are subparallel, diverging outward-forward at an angle of about 45° to axial line of cephalon (as in *Burlingia*).

buttress (of fixed cheek). See buttress of fixigena.

buttress (of fixigena). Projection of fixigena into axial furrow, meeting a papillate glabellar lobe and bridging over axial furrow, as in Calymenidae (syn., buttress of fixed cheeks).

Carapace. *See* dorsal exoskeleton.

caudal ramus (pl., *rami*). *See* antenniform cercus.

caudal shield. See pygidium.

caudal spine. See posterior spine.

cedariiform suture. Opisthoparian suture in which posterior sections run outward across the lateral border furrow before curving backward and inward to posterior margin, as in *Cedaria* (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., median lobe of glabella, central region of glabella, median cervical lobe).

central body (of hypostoma). See middle body (of hypostoma).

central region (of glabella). See central area (of glabella).

cephalic region. Area of trilobite body formed by fusion of several anterior somites.

cephalic spine. Spine carried by cephalon.

CEPHALON (pl., **CEPHALA**). Anterior area of dorsal exoskeleton separated from thorax by an articulation (syn., head, head shield).

cercus (pl., *cerci*). *See* antenniform cercus.

cervical lobe. See preoccipital glabellar lobe.

cheek. See genal region.

cheek area. See genal region.

cheek lobe. See gena.

cheek region. See genal region.

cheek roll. See genal roll.

cheek roll prolongation. See genal roll prolongation.

composite internal mold. Mold showing the internal surface of dorsal exoskeleton and impression of internal surface of doublure.

compound eye. See holochroal eye.

CONNECTIVE SUTURE. Longitudinal suture transecting doublure in front of hypostoma (paired).

corner furrow. Groove extending obliquely outward from axial furrow at anterolateral borders of glabella, as in *Strenuella.*

coxa. Proximal joint of biramous appendage (syn., coxite, coxopodite).

coxite. See coxa.

coxopodite. See coxa.

CRANIDIUM (pl., **CRANIDIA**). Central dorsal portion of cephalon bounded laterally by facial sutures.

crenulation. Rounded scallop in a series cutting a margin.

dalmanitiform suture. Proparian suture in which anterior sections meet on dorsal side of cephalon near anterior margin, as in *Dalmanites.*

DEGREE OF MERASPID PERIOD. Successive stages in development characterized by number of thoracic segments, from 0 to holaspid number minus one.

denticle. Small tooth or projection.

distal. End of a part or organ away from the point of origin of medial line of the body.

DORSAL EXOSKELETON. Resistant, mineralized dorsal integument extended onto ventral side in a reflexed border or doublure (syn., carapace, dorsal shield, test).

dorsal furrow. See axial furrow.

dorsal shield. See dorsal exoskeleton.

DOUBLURE. Reflexed continuation of dorsal exoskeleton onto ventral side as a rim or shelf.

ecdysis. Act of molting or shedding outer cuticular layer.

endite. Median or inner lobe of segment (podite) of biramous appendage.

endopodite. See telopodite.

entomaspidiform suture. Opisthoparian suture in which the anterior sections are retrodivergent, running outward-backward from the eyes to the lateral margins (as in *Entomaspis*).

ephebic stage. Mature or adult growth stage, loosely applied to part of the holaspid period.

epimera. See pleura.

epistoma. See rostral plate.

epistomal plate. See rostral plate.

epistome. See rostral plate.

exite. Lateral or outer lobe of joint (podite) of biramous appendage.

exopodite. See pre-epipodite.

EXOSKELETON. Resistant external integument covering part of body and appendages (*see* dorsal exoskeleton).

exsagittal. Term used to describe a measurement parallel to, but outside of the medial line (abbrev., *exsag.*).

external mold. Mold of outer surface of dorsal exoskeleton.

external rim. Outer smooth border of fringe along anterior and lateral edges extending back to posterior tip of the prolongation, as in Harpidae, Harpididae, and Trinucleidae.

exuviae. Any parts of trilobite exoskeleton that are shed or cast off.

EYE. Visual organ on external side of cephalon, bearing eye lenses or facets.

eye lappet. See visual surface of eye.

eye list. See eye ridge.

eye lobe. Ensemble of palpebral lobe and eye.

eye platform. Librigenal area adjacent to visual surface of eye.

EYE RIDGE. Raised band extending from anterior end of eye to or just back of anterolateral angles of glabella, usually simple but may be bifid, as in *Pruvostina,* or trifid, as in *Daguinaspis* (syn., eye list, ocular band, ocular ridge, paired eye ridges).

eye tubercle. Raised knob bearing simple eyes, as in Trinucleidae.

FACET. Small triangular area located at anterolateral corners of pygidium and lying at a depressed angle to surface of last thoracic segment, also developed on anterolateral portion of thoracic pleurae, as in *Phacops* and *Bumastus.*

FACIAL SUTURE. One of 2 lateral sutures starting symmetrically on posterior or lateral doublure, crossing the border and taking a symmetrical course to bound adaxial side of visual surface of eye, continuing forward either to unite anteriorly on dorsal surface or marginally; a facial suture may exist where compound eye is absent, its course being then similar to that in nearest eye-bearing relative. Separates cranidium from librigena.

false eye ridge. See sutural ridge.

femur. Third joint of telopodite.

fixed cheek. See fixigena.

FIXIGENA (pl., **FIXIGENAE**). Portion of cranidium between glabella and facial suture (syn., fixed cheek).

fixigenal boss. Fixigenal protuberance at level of last lateral glabellar lobe, as in *Neoredlichia.*

FIXIGENAL SPINE. Any spine borne by fixigena.

flange. See fringe.

fossula (pl., **fossulae**). Small circular or oval depression which may occur in axial furrow at or near anterolateral edges of glabella (syn., anterior pit, antennary pit, antennular pit, pseudantennary pit, pore).

fossular apodeme. Process formed by inbending of dorsal integument corresponding to fossulae on external side.

free cheek. See librigena.

fringe. External, pitted portion of cephalon in Harpidae, Harpididae, and Trinucleidae (syn., flange).

front furrow. See anterior border furrow.

FRONTAL AREA. Portion of cranidium between anterior margin, facial sutures, front of glabella and eye ridges; if eye ridges are absent, the posterolateral boundaries of this area are marked off by imaginary lines connecting anterior extremities of palpebral lobes with anterolateral borders of glabella (syn., preglabellar area, anterior limb, limb); distinct from preglabellar field.

frontal glabellar spine. Median structure projecting forward from frontal part of glabella, as in *Lonchodomas.*

frontal furrow. See anterior border furrow.

FRONTAL LOBE (OF GLABELLA). Lobe of glabella between preglabellar furrow and most anterior lateral glabellar furrows (syn., anterior lobe of glabella).

frontal process. Projection of anterior border and doublure of cephalon into a stout prolongation in cases bi- or trifurcate anteriorly, as in *Neoprobolium* (syn., anterior median process).

frontal spine. Projection of anterior border and doublure of cephalon ending anteriorly in a point, as in *Seleneceme.*

fronto-median lobe. Frontal lobe and central area of glabella, as in Lichidae and Odontopleuridae.

fulcral process. Projection on anterior edge at fulcrum (and inner edge of doublure), as in *Ceraurinella.*

fulcral socket. Excavation on posterior edge at fulcrum, as in *Ceraurinella.*

FULCRUM (pl., **FULCRA**). Geniculation of individual pleurae separating a proximal from distal portion.

GENA (pl., **GENAE**). Area enclosed within cephalic border furrows and axial furrows (used if suture is marginal or absent, as in Olenellidae, Agnostida) (syn., cheek lobe).

GENAL ANGLE. Posterolateral corner of cephalon.

genal caeca. Radiating and more or less anastomosing fine ridges on periglabellar portion of cephalon.

genal field. Portion of librigena between facial suture and border furrow.

genal lobe. See genal region.

GENAL REGION. Area enclosed within cephalic margin and axial furrows (syn., cheek, cheek area, cheek region, genal lobe).

genal ridge. Raised narrow band running outward and backward from outer side of eye or eye tubercle toward genal angle, as in Harpidae.

genal roll. Inner portion of fringe bounded on the outer side by girder or corresponding inflection of upper lamella and on inner side by genal regions, as in Harpidae, Harpididae, and Trinucleidae (syn., cheek roll).

genal roll prolongation. Inner portion of fringe prolongation, bounded outward by girder; represents an extension of genal roll, as in Harpidae and Harpididae (syn., cheek roll prolongation).

GENAL SPINE. Posterior extension of border and doublure at genal angle forming a pointed projection.

geniculate. Bent abruptly or at an angle.

gerontic stage. Senile or old growth stages, to be applied when general evidence of senility is available.

girder. Thickening or ridge of lower lamella parallel to cephalic margin, found at some distance from external rim at angulation of lamella, as in Harpidae, Harpididae, and Trinucleidae.

GLABELLA (pl., **GLABELLAE**). Raised axial portion of cephalon, bounded by axial furrows and by occipital furrow (syn., hologlabella). In some trilobites (Illaenidae, Asaphidae, Odontopleuridae) this term is used to include the occipital ring.

glabellar furrow. See lateral glabellar furrow.

glabellar lobe. See lateral glabellar lobe.

GLABELLAR NODE. Median (or paired) tubercles developed in some part of fronto-median lobe of glabella (syn., glabellar tubercle).

glabellar tongue. Subparallel-sided axial part of cranidium anterior to eye lobes, bounded by confluent sections of facial sutures, and continuous with remainder of glabella, which latter occupies axial region between eye lobes (as in Remopleurididae).

glabellar tubercle. See glabellar node.

GONATOPARIAN SUTURE. Facial suture with posterior sections reaching cephalic margin at genal angles.

granule. Minute protuberance from exoskeleton, smaller than tubercle or node.

half ring. See articulating half ring.

head. See cephalon.

head shield. See cephalon.

HOLASPIS (pl., **HOLASPIDES**). Exoskeleton at any particular stage of development during holaspid period.

HOLASPID PERIOD. Period of growth after specific number of thoracic segments has been attained.

holochroal eye. Compound eye consisting of numerous adjoining planoconvex or biconvex lenses, covered by a continuous cornea (syn., compound eye).

hologlabella. See glabella.

horn. See prolongation.

hyperglabella. Glabella with 7 segments, seen in immature forms of certain genera such as *Daguinaspis.*

HYPOSTOMA (pl., **HYPOSTOMATA**). Small plate anterior to or covering mouth opening on ventral surface of cephalon (syn., labrum, hypostome, epistoma of some early authors).

HYPOSTOMAL SUTURE. Line of junction between posterior margin of frontal doublure or rostral plate and anterior margin of hypostoma.

hypostome. See hypostoma.

inner margin (of fringe). Line separating genal regions and preglabellar field (if present) from pitted area and running into posterior border, as in Harpidae (syn., lateral line of fringe).

inner margin (of lower lamella). Free inner edge of lower lamella, as in Harpidae and Trinucleidae.

inner margin (of upper lamella). Boundary between genal region and fringe on dorsal side of cephalon; coincides with inner margin of fringe, as in Harpidae and Trinucleidae.

integument. Enveloping layer of body (syn., tegument).

intercalary lobe. See median preoccipital lobe.

intercheek suture. See median suture.

intergenal spine. See metafixigenal spine (also used as metagenal spine).

internal mold. Mold of interior surface of dorsal exoskeleton or of surface of doublure, hypostoma, metastoma or large spine.

internal rim. Smooth inner border of fringe, adjacent to thorax, and extending from posterior margin of genal regions to posterior tips of prolongations, as in Harpidae.

interocular spine. See metafixigenal spine.

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.

INTRAMARGINAL SUTURE. Suture running along border of cephalon, close to margin.

ISOPYGOUS. Exoskeleton with pygidium similar in size to that of cephalon.

isoteliform suture. Opisthoparian suture of certain Asaphidae where anterior sections meet in an ogive on exterior surface of dorsal exoskeleton, as in *Isotelus.*

kainelliform suture. Opisthoparian suture in which anterior sections first strongly diverge outward and then bend sharply inward and frontward, meeting anterior cephalic margin at its median point, as in *Kainella.*

labium. See metastoma.

labrum. See hypostoma.

larva. Early form of invertebrate that, while immature, is unlike its parents and must pass through more or less of a metamorphosis before assuming adult characteristics (syn., larval stage).

larval stage. See larva.

lateral articulating furrow (of pleura). Transverse groove parallel to and a little behind anterior margin of proximal half of a thoracic pleura, as in *Rossaspis.*

LATERAL BORDER (OF CEPHALON). Portion of cephalic border between anterior section of facial suture and genal angle.

LATERAL BORDER FURROW (OF CEPHALON). Portion of border furrow bounding lateral border.

LATERAL GLABELLAR FURROW. Narrow groove extending inward on each side of glabella from axial furrow part way across glabella; occurs in bilaterally symmetrical pairs (syn., median lateral glabellar furrows, glabellar furrow). Usually these are referred to by numbering from front to back (or by the adjectives anterior, median and preoccipital when 3 pairs are present), but some writers prefer to number preoccipital lobe as first and continue forward; this last convention is used here as 1p, 2p, etc.

LATERAL GLABELLAR LOBE. Portion of glabella outlined and more or less separated by successive pairs of lateral glabellar furrows (syn., glabellar lobe).

lateral line (of fringe). See inner margin of fringe.

lateral lobe (of pygidium). See pleural field (of pygidium).

lateral notch (of hypostoma). Incision between shoulder and anterior wing of hypostoma.

lateral occipital lobe. Lateral or anterolateral portion of occipital ring, if differentiated (syn., occipital lobe).

LATERAL PREOCCIPITAL LOBE. Lateral portion of glabellar region directly in front of occipital ring where differentiated, as in *Otarion, Ditomopyge. See* basal lobe (of glabella).

lateral tongue furrow. Portion of axial furrow bounding sides of glabellar tongue, as in *Remopleurides.*

LIBRIGENA (pl., **LIBRIGENAE**). Lateral portion of cephalon outside facial suture (syn., free cheek, movable cheek, paria).

LIBRIGENAL SPINE. Spine borne by librigena (syn., parial spine).

limb. See frontal area.

longitudinal glabellar furrow. Posteriorly directed extension of anterior glabellar furrow, as in Lichidae and Odontopleuridae.

longitudinal preglabellar furrow. Median furrow along sagittal line in front of glabella, as in Agnostida and Dimeropygidae.

lower (external or internal) rim. Smooth, raised or thickened portions of lower lamella of fringe, as in Harpidae, Harpididae, and Trinucleidae.

lower lamella. Inferior plate of fringe, as in Harpidae, Harpididae, and Trinucleidae.

macropleura (pl., **macropleurae**). Pleura, much larger than average (syn., macropleural segment).

macropleural segment. See macropleura.

macropleural spine. Pleural spine, much larger than average.

MACROPYGOUS. Having a large pygidium.

macrospine. Axial spine, much larger than average.

macula (pl., **maculae**). Small, usually smooth area lying laterally in front of middle furrow of hypostoma; it may be sunk, flat, or elevated.

MARGIN. Edge of cephalon, pygidium, thoracic pleurae or sternite.

marginal band. Narrow vertical band uniting upper and lower edges of rim, as in Harpidae.

marginal furrow. See border furrow.

marginal limb. See border.

marginal pit. See border pit.

marginal rim. See border.

marginal spine (of cephalon). Spine in a series projecting from cephalic border and doublure, as in *Odontopleura.*

marginal spine (of pygidium). Spine in a series projecting from lateral border and doublure of pygidium.

MARGINAL SUTURE. Suture running along edge of cephalon, as in Harpidae.

median border spine. See posterior spine.

median cervical lobe. See central area (of glabella).

MEDIAN LATERAL GLABELLAR FURROW. Second lateral glabellar furrow when numbering from front to back, in case 3 pairs of such furrows are present (*see* lateral glabellar furrow).

MEDIAN LATERAL GLABELLAR LOBE. Lateral portion of glabellar region between median lateral glabellar furrow and preoccipital glabellar furrow.

median lobe (of glabella). See central area (of glabella).

median preoccipital lobe. Median portion of glabellar region between lateral preoccipital lobes, as in *Ditomopyge* [syn., intercalary lobe, preoccipital lobe *(partim)*].

MEDIAN SUTURE. Median longitudinal suture transecting doublure in front of hypostoma (syn., intercheek suture).

MERASPID PERIOD. Period of development from appearance of first transverse joint in exoskeleton until specific number of thoracic segments less one has been attained.

MERASPIS (pl., **MERASPIDES**). Exoskeleton at any particular degree of development during meraspid period.

mesotergite. Axial portion of a tergite.

metacranidial spine. See metafixigenal spine (also used as metagenal spine).

METAFIXIGENAL SPINE. Spine projecting from border and doublure of fixigena inside genal angle [syn., intergenal spine *(partim),* interocular spine, metacranidial spine *(partim)*].

METAGENAL SPINE. Spine projecting from border and doublure inside genal angle in trilobites with no facial suture, as in Olenellidae [syn., intergenal spine *(partim)*, metacranidial spine *(partim)*].

metamere. See segment.

metaparian suture. Nonfunctional opisthoparian suture in state of complete symphysis in which trace of fused anterior section on dorsal surface of cephalon curves outward and backward from eye, cutting posterior margin inside genal angle, as in some Olenellidae.

METAPROTASPIS (pl., **METAPROTASPIDES**). Large protaspides, or the larger protaspides in a size-series, in which the protopygidium is relatively large and well defined.

metastoma (pl., **metastomata**). Small plate lying posterior to mouth opening on ventral side of body (syn., labium, metastome, postoral plate).

metastome. See metastoma.

MICROPYGOUS. Having a small pygidium.

middle body (of hypostoma). Swollen middle portion of hypostoma (syn., central body of hypostoma).

middle furrow. Transverse furrow dividing middle body of hypostoma into anterior and posterior lobes.

movable cheek. See librigena.

muscle scar. Smooth, or slightly depressed paired areas, in cases darker in color than surrounding regions, in external surface of axial region of exoskeleton, interpreted as areas of muscle attachment.

neanic stage. Immature or adolescent growth stage, loosely applied to part of the holaspid period.

neck furrow. See occipital furrow.

neck node. See occipital node.

neck ring. See occipital ring.

neck spine. See occipital spine.

nepionic stage. Infantile or young growth stage, applied to the meraspid period as here defined.

node. Swelling on any part of exoskeleton resembling a knot or knob (syn., tubercle).

nuchal furrow. See occipital furrow.

nuchal node. See occipital node.

nuchal ring. See occipital ring.

nuchal spine. See occipital spine.

OCCIPITAL FURROW. Transverse groove running from axial furrow to axial furrow forming posterior boundary of glabella (syn., neck furrow, nuchal furrow).

occipital lobe. See lateral occipital lobe.

OCCIPITAL NODE. Median (or paired) tubercle developed on exterior of occipital ring (syn., neck node, nuchal node).

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 (syn., neck ring, nuchal ring).

OCCIPITAL SPINE. Median (or paired) pointed structure projecting from exterior of occipital ring (syn., neck spine, nuchal spine).

ocular band. See eye ridge.

ocular platform. Area of librigena adjacent to visual surface of eye.

ocular ridge. See eye ridge.

OPISTHOPARIAN SUTURE. Facial suture with posterior sections cutting posterior margin of cephalon inside genal angle, which is carried by librigena.

opisthothorax. Posterior portion of thorax with reduced pleurae, observed in certain Olenellidae.

paired eye ridges. See eye ridge.

palpebral area (of fixed cheek). See palpebral area (of fixigena).

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., palpebral area or region of fixed cheek).

PALPEBRAL FURROW. Usually curved groove separating palpebral lobe from palpebral area of fixigena.

PALPEBRAL LOBE. Protruding flange of fixigena bounded distally by facial suture and included within arc of proximal edge of visual surface of eye.

palpebral region (of fixed cheek). See palpebral area of fixigena.

palpebral region (of fixigena). See palpebral area of fixigena.

palpebral rim. Raised or thickened portion of palpebral lobe bordering facial suture.

palpebro-ocular ridge. Raised strip connecting proximal side of eye with axial furrow, as in *Protopliomerops;* the ridge contracts near glabella and expands adjacent to eye, appearing as a combination of palpebral lobe and eye ridge.

pander organ. See panderian opening and panderian protuberance.

panderian opening. Small rounded or elliptical hole in posterior fixigenal and thoracic pleural doublure close to panderian protuberance; in some cases developed as a notch on inner margin of doublure [syn., panderian organ *(partim)*].

panderian organ. See panderian opening and panderian protuberance.

panderian protuberance. Small rounded, elliptical, or elongate protuberance in posterior fixigenal and thoracic pleural doublure; in some cases developed as raised anterior edge of a notch on inner margin of doublure [syn., panderian organ *(partim)*].

parafrontal band. Narrow raised band encircling anterior border of frontal lobe of glabella forming continuation of eye ridges, as in *Termierella.*

paraglabellar area. Arcuate tract on fixigena adjoining base of glabella on either side, commonly defined by independent convexity and faint bounding furrows, as in Homalonotidae. *See* ala.

paraprotaspis (pl., *paraprotaspides*). Late protaspid stage, not precisely defined.

paria. See librigena.

parial spine. See librigenal spine.

patella. Fourth joint of a telopodite.

perfixigenal spine. Spine carried by fixigena in front of librigena (syn., procranidial spine, pergenal spine in Olenellidae).

pergenal spine. See perfixigenal spine.

periglabellar area. Ill-defined portion of cephalon encircling glabella.

PERROSTRAL SUTURE. Ventral-intramarginal cephalic suture crossing genal angle below spine, as in Olenellidae (syn., ventromarginal suture).

pit. Depression, hollow, or excavation developed on any part of exoskeleton.

plate. Skeletal part of cephalon separated by sutures from other plates.

PLEURA (pl., **PLEURAE**). Lateral portion of thoracic segment or pygidium (syn., epimera, pleuron).

pleural band. Anterior and posterior strips resulting from transverse division of a 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., pleural platform, pygopleura, lateral lobe of pygidium).

PLEURAL FURROW. Groove along surface of thoracic or pygidial pleura.

pleural lobe. See pleural region.

pleural platform. See pleural field.

PLEURAL PYGIDIAL SPINE. Projection of lateral border and doublure of pygidium corresponding to outward extension of a pleura.

PLEURAL REGION (OF THORAX). Longitudinal lateral portion of thorax (syn., pleural lobe, side lobe, pleurothorax).

pleural rib. See rib.

PLEURAL SPINE. Pointed extension of distal end of a pleura.

pleuron (pl., *pleura*). *See* pleura.

pleurothorax. See pleural region (of thorax).

podite. Each joint of a biramous appendage.

pore. See fossula.

postaxial field. Area on pygidium between posterior end of axis and posterior margin.

postaxial furrow. Longitudinal groove bounding postaxial ridge of pygidium.

postaxial keel. See postaxial ridge.

postaxial ridge. Raised median portion of pygidium behind axis (syn., postaxial keel).

posterior area (of fixed cheek). See posterior area (of fixigena).

POSTERIOR AREA (OF FIXIGENA). Postocular portion of fixigena (syn., posterolateral limb, posterior limb, postocular area or region of fixed cheek, posterior region of fixigena, posterior region of fixed cheek, posterior area of fixed cheek).

posterior band of occipital ring. Narrow (*sag.* and *exsag.*) band, widest in mid-line, situated below and behind main part of occipital ring.

POSTERIOR BORDER (OF CEPHALON). Portion of cephalic border between genal angle and occipital ring.

POSTERIOR BORDER FURROW (OF CEPHALON). Portion of border furrow bounding posterior border.

posterior branch (of facial suture). See posterior section (of facial suture).

posterior flange. Narrow border extending along posterior edge of adaxial part of a pleura, as in *Ceraurinella.*

posterior genal ridge. See postocular ridge.

posterior limb. See posterior area (of fixigena).

posterior lobe (of glabella). Main glabellar lobe of Agnostida.

posterior lobe (of hypostoma). Portion of middle body of hypostoma behind middle furrow.

POSTERIOR MARGIN (OF CEPHALON). Edge of cephalon between genal angles.

posterior pleural band. Strip of thoracic or pygidial pleura bounded anteriorly by pleural furrow.

posterior pleural spine. Pointed extension of distal end of a posterior pleural band.

posterior region (of fixed cheek). See posterior area (of fixigena).

posterior region (of fixigena). See posterior area (of fixigena).

POSTERIOR SECTION (OF FACIAL SUTURE). Portion of facial suture lying behind eye [syn., posterior branch (of facial suture), postocular branch (of facial suture)].

POSTERIOR SPINE. Posterior extension of border and doublure of pygidium (syn., median border spine, caudal spine).

posterior wing (of hypostoma). Extension of posterolateral doublure of hypostoma.

posterolateral limb. See posterior area (of fixigena).

posterolateral spine (of pygidium). Spine (paired) at posterolateral border of pygidium, as in Agnostida and Dikelocephalidae.

post-eyeline. See postocular ridge.

postocular area (of fixed cheek). See posterior area (of fixigena).

postocular branch (of facial suture). See posterior section (of facial suture).

postocular region (of fixed cheek). See posterior area (of fixigena).

postocular ridge. Raised line running obliquely outward and backward from back end of eye toward but not necessarily touching posterior margin of cephalon, as in Olenellidae (syn., post-eyeline).

postoral plate. See metastoma.

precoxa. Extra basal joint inserted between coxa of a biramous appendage and body wall (syn., subcoxa, sympodite, protopodite).

pre-epipodite. Outer and upper branch of a paired biramous appendage, attached to posterior face of precoxa (syn., exopodite).

prefemur. Second segment of a telopodite.

preglabellar area. See frontal area.

PREGLABELLAR FIELD. Portion of cranidium lying between front of glabella and anterior border furrow; distinct from frontal area.

PREGLABELLAR FURROW. Portion of axial furrow outlining front of glabella. *See* longitudinal preglabellar furrow.

preglabellar keel. See preglabellar ridge.

preglabellar pit. Pit in longitudinal furrow in preglabellar field, as in Dimeropygidae.

preglabellar ridge. Longitudinal median ridge crossing preglabellar field (syn., preglabellar keel).

PREOCCIPITAL GLABELLAR FURROW. Furrow separating preoccipital glabellar lobe from main part of glabella (syn., basal furrow).

PREOCCIPITAL GLABELLAR LOBE. Lateral portion of glabellar region directly in front of occipital ring when differentiated (syn., basal lobe of glabella, cervical lobe). *See* median preoccipital lobe.

preoccipital glabellar spine. Pointed projection from preoccipital part of glabella, as in *Orometopus.*

preocular branch (of facial suture). See anterior section (of facial suture).

preocular ridge. Raised line curving outward and backward from anterior end of eye running toward but not necessarily touching posterior margin of cephalon, as in *Fallotaspis.*

pretarsus. Terminal joint of a telopodite.

procranidial spine. See perfixigenal spine.

PROFIXIGENAL SPINE. Spine projecting from border and doublure of fixigena in front of genal angle, as in *Sphaerocoryphe granulatus.*

PROLIBRIGENAL SPINE. Spine projecting from border and doublure of librigena in front of genal angle, as in *Paracalmonia pessula.*

prolongation. Extension of fringe beyond posterior margin of genal regions, as in Harpidae and Harpididae (syn., horn).

PROPARIAN SUTURE. Facial suture with posterior sections cutting lateral margin of cephalon in front of genal angles which are carried by fixigenae.

PROTASPID PERIOD. Period of development during which there is no transverse joint in the exoskeleton.

PROTASPIS (pl., **PROTASPIDES**). Smallest known exoskeletons, subhemispherical to spherical in form; may exhibit a size-series, but lacking a transverse joint.

prothorax. Anterior portion of thorax with normal pleurae, observed in certain Olenellidae.

protopodite. See precoxa.

PROTOPYGIDIUM. Postcephalic portion of a protaspis.

proximal. End of a part or organ which is nearest to point of origin or mesial line of body.

pseudantennary pit. See fossula.

pseudopalpebral furrow. Furrow running obliquely across eye ridge, as in some *Resserops.*

pseudoproparian suture. See cedariiform suture.

ptychopariiform suture. Opisthoparian suture in which anterior section is directed outward and frontward to margin and then marginally (or along doublure) to center, as in *Ptychoparia.*

pustule. Small pimple-like elevation or spot resembling a blister developed on any part of exoskeleton.

pygaxis. See axis (of pygidium).

pygidial region. Area of trilobite body formed by fusion of several posterior somites.

PYGIDIUM (pl., **PYGIDIA**). Posterior part of dorsal exoskeleton separated from thorax by an articulation (syn., tail, tail shield, caudal shield).

pygopleura. See pleural field (of pygidium).

rachis (pl., *rachises*). *See* axis.

REGION. Each portion of dorsal exoskeleton resulting from its longitudinal trilobation.

rhachis (pl., *rhachises*). *See* axis.

RIB. Portion of pygidial pleural region bounded by 2 successive pleural furrows (syn., pleural rib).

rib furrow. See interpleural furrow.

ring. See axial ring.

RING FURROW. Groove bounding successive axial rings of pygidium.

ring process. Projection extending inward from posterolateral corner of axial ring, fitting into socket in next posterior ring, as in *Ceraurinella.*

ring socket. Hollow formed by extremities of articulating furrow and articulating half-ring for reception of ring process of next anterior ring, as in *Ceraurinella.*

rostral flange. Hindmost part of rostral plate when it is strongly curved in anterior or dorsal direction so as to form a fold, as in *Illaenus.*

ROSTRAL PLATE. Median cephalic ventral plate of variable size and relations, may be bounded anteriorly and laterally by the perrostral suture (Olenellidae) or bounded anteriorly by the rostral suture and laterally by the paired connective sutures, and in the Homalonotidae it is partly dorsal (syn., epistoma, epistomal plate, epistome, rostrum).

ROSTRAL SUTURE. Anterior portion of facial suture forming line of junction between anterior margin of rostral plate and cranidium.

rostrum. See rostral plate.

sagittal. Term used to describe a measurement in median line (abbrev., *sag.*).

sagittal line. Medial line of body (syn., axial line).

schizochroal eye. Eye with visual surface consisting of a 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. Hard part of exoskeleton belonging to each body segment.

scrobiculate. Having numerous small, shallow depressions or hollows; pitted.

SEGMENT. Each of the metameric transverse elements forming body; also used as a general term for successive units of an appendage (syn., metamere, somite).

shield. See carapace.

shoulder. Anterolateral part of lateral border of hypostoma, generally the widest and most inflated part, projecting ventrally.

side lobe. See pleural region.

somite. See segment.

spatulate. Any part shaped like a spatula; spoon-shaped.

SPINE. Pointed projection from exoskeleton.

sternite. Hard ventral covering of body segment.

subcephalic furrow. See vincular furrow.

subcoxa. See precoxa.

subcranial furrow. See vincular furrow.

subocular area. Small smooth area of librigena adjoining posterior portion of eye, as in *Phillipsia hildae*.

subocular groove. Smooth bandlike depression of librigena surrounding visual surface of eye, as in *Griffithides indicus*.

sutural ridge. Narrow ridge upon (or beside) which either section of facial suture may run on exterior surface of dorsal exoskeleton (syn., false eye ridge).

SUTURE. Line of union, or seam, in immovable articulation, consisting of very narrow uncalcified band perceivable on external side of cephalon or between cephalic sternites.

sympodite. See precoxa.

tail. See pygidium.

tail shield. See pygidium.

tarsus. Sixth joint of a telopodite.

tegument. See integument.

telopodite. Free postcoxal inner branch (walking leg) of a biramous appendage, attached to ventrolateral portion of precoxa (syn., endopodite).

telson. Terminal or anal segment (sometimes incorrectly used for first opisthothoracic macrospine of Olenellidae).

tergite. Hard dorsal covering of each body segment.

TERMINAL AXIAL PIECE (OR RING). Last segment of axis of pygidium.

terminal axial segment. See terminal axial piece.

TERMINAL AXIAL SPINE. Projection of median dorsal surface of terminal portion of axis of pygidium.

terrace lines. Fine raised lines on doublure (and in some trilobites also on border) running subparallel to margins or arranged in Bertillon pattern.

test. See dorsal exoskeleton.

thoracic region. Area of trilobite body formed by the ensemble of metameric somites interposed between cephalic and pygidial regions.

THORACIC SEGMENT. Transverse division of thorax consisting of 2 pleurae and axial ring.

tibia. Fifth joint of a telopodite.

transglabellar furrow. Continuous furrow across glabella resulting from meeting of adaxial ends of a pair of lateral glabellar furrows.

TRANSITORY PYGIDIUM. Fused segments of the posterior region during the meraspid period.

transverse. Term used to describe a measurement at right angles to median line (abbrev., *tr.*).

traversing pad. Distinctly thickened posterior pleural band, as in Asteropyginae.

tricomposite glabellar lobe. Lateral glabellar lobe representing fused anterior, median and posterior lateral glabellar lobes, separated from frontomedial lobe of glabella by the longitudinal furrow, as in some Lichidae.

trochanter. Basal joint of a telopodite (syn., basipodite).

tropidia. Crest on fixigena or librigena or both, running parallel to cephalic margin, as in some Proetidae.

tubercle. Small knoblike prominence on any part of exoskeleton (syn., node).

upper lamella. Upper or dorsal plate of fringe, as in Harpidae, Harpididae, and Trinucleidae.

upper rim (external or internal). Smooth, raised portion of upper lamella of fringe, as in Harpidae, Harpididae, and Trinucleidae.

uropod. See antenniform cercus.

ventromarginal suture. See perrostral suture.

vincular furrow. Ventral groove along anterior (as in Phacopinae) or posterolateral (as in Phacopidellinae) cephalic doublure for reception of posterior margin of pygidium or thoracic pleurae extremity at enrollment (syn., subcephalic furrow, subcranial furrow).

visual surface of eye. External surface of eye showing outline of lenses (syn., eye lappet).

wing process (of hypostoma). Rounded boss or thornlike structure which may be developed on inner surface of anterior wing of hypostoma.