Treatise on Invertebrate Paleontology

Part V

Hemichordata

Second Revision

Including Enteropneusta, Pterobranchia (Graptolithina)

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PART V
HEMICHORDATA

Including Enteropneusta, Pterobranchia (Graptolithina)

Second Revision

Jörg Maletz, Coordinating Author

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INFORMATION ON TREATISE VOLUMES

The *Treatise on Invertebrate Paleontology* is published by the University of Kansas Paleontological Institute, www.paleo.ku.edu. The *Treatise* is organized in lettered Parts (A–W) to indicate their systematic sequence but also allowing publication of units in whatever order each is finalized. It is published in three formats. Individual chapters are published when completed in the *Treatise Online* series. When a volume is complete, it is published both as a book and as an online volume in the *Digital Treatise* series. In addition, *Paleontological Institute Special Publications* series are published periodically. The web address above provides information for ordering *Treatise* publications. Please encourage academic libraries to subscribe to all Paleontological Institute publications.

PUBLISHED VOLUMES

Part A. Introduction: Fossilization (Taphonomy), Biogeography, and Biostratigraphy, xxiii + 569 p., 169 fig., 1979.

Part B. Protoctista 1 (Charophyta), xvi + 170 p., 79 fig., 9 tables, 2005.

Part B. Prokaryota (Bacteria and Archaea), xvii + 179 p., 48 fig., 3 tables, 2023.

Part C. Protista 2 (Sarcodina, Chiefly "Thecamoebians" and Foraminiferida), Volumes 1 and 2, xxxi + 900 p., 653 fig., 1964.

Part D. Protista 3 (Protozoa: Chiefly Radiolaria, Tintinnina), xii + 195 p., 92 fig., 1954.

Part E. Archaeocyatha and Porifera, xviii + 122 p., 89 fig., 1955.

Part E, Revised. Archaeocyatha, Volume 1, xxx + 158 p., 107 fig., 1972.

Part E, Revised. Porifera, Volume 2 (Introduction to the Porifera), xxvii + 349 p., 135 fig., 10 tables, 2003.

Part E, Revised. Porifera, Volume 3 (Demospongea, Hexactinellida, Heteractinida, Calcarea), xxxi + 872 p., 506 fig., 1 table, 2004.

Part E, Revised. Porifera, Volume 4 and 5 (Hypercalcified Porifera), liii + 1223 p., 665 fig., 42 tables, 2015.

Part F. Coelenterata, xx + 498 p., 358 fig., 1956.

Part F. Coelenterata, Supplement 1 (Rugosa and Tabulata), Volumes 1 and 2, xl + 762 p., 462 fig., 1981.

Part G. Bryozoa, xiii + 253 p., 175 fig., 1953.

Part G, Revised. Bryozoa, Volume 1 (Introduction, Order Cystoporata, Order Cryptostomata), xxvi + 625 p., 295 fig., 1983.

Part H. Brachiopoda, Volumes 1 and 2, xxxii + 927 p., 746 fig., 1965.

Part H, Revised. Brachiopoda, Volume 1 (Introduction), xx + 539 p., 417 fig., 40 tables, 1997.

Part H, Revised. Brachiopoda, Volumes 2 and 3 (Linguliformea, Craniiformea, Rhynchonelliformea [part]), xxx + 919 p., 616 fig., 17 tables, 2000.

Part H, Revised. Brachiopoda, Volume 4 (Rhynchonelliformea [part]), xxxix + 768 p., 484 fig., 3 tables, 2002.

Part H, Revised. Brachiopoda, Volume 5 (Rhynchonelliformea [part]), xlvi + 631 p., 398 fig., 2006.

Part H, Revised. Brachiopoda, Volume 6 (Supplement), l + 906 p., 461 fig., 38 tables, CD of compiled references from volumes 1–6, 2007.

Part I. Mollusca 1 (Mollusca General Features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda General Features, Archaeogastropoda, Mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii + 351 p., 216 fig., 1960.

Part K. Mollusca 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii + 519 p., 361 fig., 1964.
Part L. Mollusca 4 (Cephalopoda: Ammonoidea), xxii + 490 p., 558 fig., 1957.
Part L, Revised. Mollusca 4, Volume 2 (Carboniferous and Permian Ammonoidea), xxix + 258 p., 139 fig., 1 table, 2009.
Part L, Revised. Mollusca 4, Volume 4 (Cretaceous Ammonoidea), xx + 362 p., 216 fig., 1996.
Part N. Mollusca 6 (Bivalvia), Volumes 1 and 2 (of 3), xxxvii + 952 p., 613 fig., 1969; Volume 3, iv + 272 p., 153 fig., 1971.
Part O. Arthropoda 1 (Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha), xix + 560 p., 415 fig., 1959.
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Part P. Arthropoda 2 (Chelicerata, Pycnogonida, Palaeoisopus), xvii + 181 p., 123 fig., 1955 [1956].
Part Q. Arthropoda 3 (Crustacea, Ostracoda), xxiii + 442 p., 334 fig., 1961.
Part R. Arthropoda 4, Volumes 1 and 2 (Crustacea Exclusive of Ostracoda, Myriapoda, Hexapoda), xxxvi + 651 p., 397 fig., 1969.
Part R. Arthropoda 4, Volumes 3 and 4 (Hexapoda), xxii + 655 p., 265 fig., 1992.
Part S. Echinodermata 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), Volumes 1 and 2, xxx + 650 p., 400 fig., 1967 [1968].
Part T. Echinodermata 2 (Crinoidea), Volumes 1–3, xxxviii + 1,027 p., 619 fig., 1978.
Part T, Revised. Echinodermata 2 (Crinoidea), Volume 3, xxix + 261 p., 112 fig., 2011.
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Part V, Revised. Graptolithina, xxxii + 163 p., 109 fig., 1970.
Part W. Miscellanea (Conodonts, Conoidal Shells of Uncertain Affinities, Worms, Trace Fossils, Problematica), xxv + 259 p., 153 fig., 1962.
Part W, Revised. Miscellanea, Supplement 1 (Trace Fossils and Problematica), xxi + 269 p., 110 fig., 1975.
Part W, Revised. Miscellanea, Supplement 2 (Conodonta), xxviii + 202 p., frontis., 122 fig., 1981.

THIS VOLUME

Part V, Second Revision. Hemichordata (incl. Graptolithina), xxx + 548 p., 310 fig., 2023.

VOLUMES IN PREPARATION

Part B. Protista 1 (Chrysomonadida, Coccolithophorida, Diatomacea).
Part E, Revised. Porifera (additional volumes).
Part F, Revised. Cnidaria (Scleractinia).
Part G, Revised. Bryozoa (additional volumes).
Part K, Revised. Mollusca 3 (Nautiloidea).
Part L, Revised. Mollusca 4 (Ammonoidea) (additional volumes).
Part M. Mollusca 5 (Coleoidea).
Part N, Revised. Mollusca 6 (Bivalvia), Volume 1.
Part O, Revised. Arthropoda 1 (Trilobita) (additional volumes).
Part P, Revised. Arthropoda 2 (Chelicerata).

Part Q, Revised. ARTHROPODA 3 (Ostracoda).
Part R, Revised. ARTHROPODA 4 (Crustacea Exclusive of Ostracoda).
Part T, Revised. ECHINODERMATA 2 (Crinoidea) (additional volumes).
Part W, Revised. TRACE FOSSILS.

EDITORIAL PREFACE

Paul A. Selden[1] and William I. Ausich[2]

[1]Director 2007–2020, [2]Interim Director 2020–2022]

From the outset, the aim of the *Treatise on Invertebrate Paleontology* has been to present a comprehensive and authoritative, yet compact, statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early *Treatise* volumes was undertaken by a small group with a synoptic view of the taxa being monographed. Two, or perhaps three, specialists worked together, sometimes co-opting others for coverage of highly specialized taxa. Recently, however, both new *Treatise* volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. This volume, Part V, Hemichordata (Second Revision of Graptolithina) has been guided by Coordinating Author Jörg Maletz. The Treatise editor for the project was also a team effort. The planning and most of the text was submitted, edited, and published online during the editorship of Paul Selden. After Paul retired in 2020, William Ausich took up the mantle as interim editor. Editorial matters specific to this volume are discussed near the end of this editorial preface.

ZOOLOGICAL NAMES

Questions about the proper use of zoological names arise continually, especially questions regarding both the acceptability of names and alterations of names that are allowed or even required. Regulations prepared by the International Commission on Zoological Nomenclature (ICZN) and published in the *International Code of Zoological Nomenclature* (4th edition, 1999), hereinafter referred to as the *Code,* provide procedures for answering such questions. The prime objective of the *Code* is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding unwarranted restrictions on freedom of thought and action of systematists. Priority of names is a basic principle of the *Code;* but, under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Code is updated periodically and is now available online [www.iczn.org/the-code/the-international-code-of-zoological-nomenclature/the-code-online]. A significant recent change to nomenclatoral practice is that new nomenclatoral acts must be registered on Zoobank [zoobank.org] for recognition by the ICZN. Zoobank is the offical register of the ICZN and includes registry of nomenclatoral acts of genera and species, authors, publications, and type specimens.

Among other requirements, the revised *Code* is clear that the type genus of family-level taxa must be specified. In this volume we have continued the practice that has characterized most previous volumes of the *Treatise*, namely that the type genus of all family-level taxa is the first listed and diagnosed. In spite of the revisions, the nomenclatorial tasks that confront zoological taxonomists are formidable and have often justified the complaint that the study of zoology and paleontology is too often merely the study of names rather than the study of animals. It is incumbent on all systematists, therefore, at the outset of their work to pay careful attention to the *Code* to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise*.

Terminology is explained, and examples are given of the style employed in the nomenclatorial parts of the systematic descriptions.

GROUPS OF TAXONOMIC CATEGORIES

Each taxon belongs to a category in the Linnaean hierarchical classification. The *Code* recognizes three groups of categories, a species-group, a genus-group, and a family-group. Taxa of lower rank than subspecies are excluded from the rules of zoological nomenclature, and those of higher rank than superfamily are also not regulated by the *Code.* It is both natural and convenient to discuss nomenclatorial matters in general terms first and then to consider each of these three, recognized groups separately. Especially important is the provision that within each group the categories are coordinate, that is, equal in rank, whereas categories of different groups are not coordinate.

FORMS OF NAMES

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

ORIGINAL SPELLINGS

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

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

Incorrect original spellings are any that fail to satisfy requirements of the *Code,* represent an inadvertent error, or are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and, therefore, cannot enter into homonymy or be used as replacement names. They call for correction. For example, a name originally published with a diacritical mark, apostrophe, dieresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel in a name derived from a German word or personal name unfortunately requires the insertion of *e* after the vowel. Where original spelling is judged to be incorrect solely because of inadequacies of the Greek or Latin scholarship of the author, nomenclatorial changes conflict with the primary purpose of zoological nomenclature as an information retrieval system. One looks forward with hope to further revisions of the *Code* wherein rules are emplaced that enhance stability rather than classical scholarship, thereby facilitating access to information.

SUBSEQUENT SPELLINGS

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

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

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

AVAILABLE AND UNAVAILABLE NAMES

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

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the *Code,* which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition, or indication (*Code,* Article 12) and names published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen novum*) of a preexisting available name (*Code,* Article 13.1), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (*Code,* Article 13.2). *Nomina nuda* have no status in nomenclature, and they are not correctable to establish original authorship and date.

VALID AND INVALID NAMES

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

One encounters a sort of nomenclatorial no-man's land in considering the status of such zoological names as *nomina dubia* (doubtful names), which may include both available and unavailable names. The unavailable ones can well be ignored, but names considered to be available contribute

to uncertainty and instability in the systematic literature. These can ordinarily be removed only by appeal to the ICZN for special action. Because few systematists care to seek such remedy, such invalid but available names persist in the literature.

NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES

SPECIES-GROUP NAMES

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

GENUS-GROUP NAMES

Conditions warranting change of the originally published, valid form of generic and subgeneric names are sufficiently rare that lengthy discussion is unnecessary. Only elimination of diacritical marks and hyphens in some names in this category and replacement of homonyms seem to furnish basis for valid emendation. Many names that formerly were regarded as homonyms are no longer so regarded, because two names that differ only by a single letter or in original publication by the presence of a diacritical mark in one are now construed to be entirely distinct (but see *Code,* Article 58).

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

FAMILY-GROUP NAMES

Family-Group Names: Authorship and Date

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

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

Family-Group Names: Use of *nomen translatum*

The *Code* (Article 29.2) specifies the suffixes for tribe (-ini), subfamily (-inae), family (-idae) and superfamily (-oidea), the formerly widely used ending (-acea) for superfamily having been disallowed. All these family-group categories are defined as coordinate (*Code*, Article 36.1): "A name estab-

lished for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at other ranks in the family group; all these taxa have the same type genus, and their names are formed from the stem of the name of the type genus (Art. 29.3] with appropriate change of suffix [Art. 34.1]. The name has the same authorship and date at every rank." Such changes of rank and concomitant changes of endings as elevation of a subfamily to family rank or of a family to superfamily rank, if introduced subsequent to designation of the original taxon or based on the same nominotypical genus, are *nomina translata*. In the *Treatise,* it is desirable to distinguish the valid alteration in the changed ending of each transferred family-group name by the term *nomen translatum,* abbreviated to *nom. transl.* Similarly for clarity, authors should record the author, date, and page of the alteration, as in the following example.

Family HEXAGENITIDAE
Lameere, 1917

[*nom. transl.* Demoulin, 1954, p. 566, *ex* Hexagenitinae Lameere, 1917, p. 74]

This is especially important for superfamilies, for the information of interest is the author who initially introduced a taxon rather than the author of the superfamily as defined by the *Code.* For example:

Superfamily AGNOSTOIDEA
M'Coy, 1849

[*nom. transl.* Shergold, Laurie, & Sun, 1990, p. 32, *ex* Agnostinae M'Coy, 1849, p. 402]

The latter is merely the individual who first defined some lower-ranked, family-group taxon that contains the nominotypical genus of the superfamily. On the other hand, the publication that introduces the superfamily by *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the taxon.

Family-Group Names: Use of *nomen correctum*

Valid name changes classed as *nomina correcta* do not depend on transfer from one category of the family group to another but most commonly involve correction of the stem of the nominotypical genus. In addition, they include somewhat arbitrarily chosen modifications of endings for names of tribes or superfamilies. Examples of the use of *nomen correctum* are the following.

Family STREPTELASMATIDAE
Nicholson, 1889

[*nom. correct.* Wedekind, 1927, p. 7, *pro* Streptelasmidae Nicholson in Nicholson & Lydekker, 1889, p. 297]

Family PALAEOSCORPIDAE
Lehmann, 1944

[*nom. correct.* Petrunkevitch, 1955, p. 73, *pro* Palaeoscorpionidae Lehmann, 1944, p. 177]

Family-Group Names: Replacements

Family-group names are formed by adding combinations of letters, which are prescribed for all family-group categories, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but among all those included it must be the first published as name giver to a family-group taxon. Once fixed, the family-group name remains tied to the nominotypical genus even if the generic name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* requires replacement of a family-group name only if the nominotypical genus is found to have been a junior homonym when it was proposed (*Code,* Article 39), in which case ". . . it must be replaced either by the next oldest available name from among its synonyms [Art. 23.3.5], including the names of its subordinate family-group taxa, or, if there is no such synonym, by a new name based on the valid name . . . of the former type genus." Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name. Recommendation 40A of the *Code,* however, specifies that for subsequent application of the rule of

priority, the family-group name ". . . should be cited with its original author and date (see Recommendation 22A.2.2), followed by the date of its priority as determined by this Article; the date of priority should be enclosed in parentheses." Many family-group names that have been in use for a long time are *nomina nuda,* because they fail to satisfy criteria of availability (*Code,* Article 11.7). These demand replacement by valid names.

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

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

SUPRAFAMILIAL TAXA: TAXA ABOVE FAMILY-GROUP

International rules of zoological nomenclature as given in the *Code* affect only lower-rank categories: subspecies to superfamily. Suprafamilial categories (suborder to kingdom) are either not mentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological Nomenclature* (1953, Articles 59 to 69) proposed adopting rules for naming suborders and higher taxa up to and including phylum, with provision for designating a type genus for each, in such manner as not to interfere with the taxonomic freedom of workers. Procedures were outlined for applying the rule of priority and rule of homonymy to suprafamilial taxa and for dealing with the names of such taxa and their authorship, with assigned dates, if they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

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

The considerations just stated do not prevent the editors of the *Treatise* from making rules for dealing with suprafamilial groups of animals described and illustrated in this publication. Some uniformity is needed, especially for the guidance of

Treatise authors. This policy should accord with recognized general practice among zoologists; but where general practice is indeterminate or nonexistent, our own procedure in suprafamilial nomenclature needs to be specified as clearly as possible. This pertains especially to decisions about names themselves, about citation of authors and dates, and about treatment of suprafamilial taxa that, on taxonomic grounds, are changed from their originally assigned rank. Accordingly, a few rules expressing *Treatise* policy are given here, some with examples of their application.

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

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

3. The rules of priority and homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatorial stability and to avoid confusion these rules are widely applied by zoologists to taxa above the family-group level wherever they do not infringe on taxonomic freedom and long-established usage.

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

Order CORYNEXOCHIDA Kobayashi, 1935

[*nom. transl.* Moore, 1959, p. 217, *ex* suborder Corynexochida Kobayashi, 1935, p. 81]

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

Order DISPARIDA Moore & Laudon, 1943

[*nom. correct.* Moore in Moore, Lalicker, & Fischer, 1952, p. 613, *pro* order Disparata Moore & Laudon, 1943, p. 24]

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

Order HYBOCRINIDA Jaekel, 1918

[*nom. transl. et correct.* Moore in Moore, Lalicker, & Fischer, 1952, p. 613, *ex* suborder Hybocrinites Jaekel, 1918, p. 90]

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

Subclass ENDOCERATOIDEA Teichert, 1933

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

Order ENDOCERIDA Teichert, 1933

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

TAXONOMIC EMENDATION

Emendation has two distinct meanings as regards zoological nomenclature. These are alteration of a name itself in various ways for various reasons, as has been reviewed, and alteration of the taxonomic scope or concept for which a name is used. The *Code* (Article 33.1 and Glossary) concerns itself only with the first type of emendation, applying the term to intentional, either justified or unjustified changes of the original spelling of a name. The second type of emendation primarily concerns classification and inherently is not associated with change of name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleontologists, who have emended zoological names refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation *emend.* then must accompany the name with statement of the author and date of the emendation. On the other hand, many systematists think that publication of *emend.* with a zoological name is valueless because alteration of a taxonomic concept is introduced whenever a subspecies, species, genus, or other taxon is incorporated into or removed from a higher zoological taxon. Inevitably associated with such classificatory expansions and restrictions is some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat more extensive revisions are put forward, generally with a published statement of the reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as an aid to subsequent workers in taking account of the altered nomenclatorial usage and to indicate where in the literature cogent discussion may be found. Authors of contributions to the *Treatise* are encouraged to include records of all especially noteworthy emendations of this nature, using the abbreviation *emend.* with the name to which it refers and citing the author, date, and page of the emendation. Examples from *Treatise* volumes follow.

Order ORTHIDA Schuchert & Cooper, 1932

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

Subfamily ROVEACRININAE Peck, 1943

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

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE SPECIES

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

Orionastraea Smith, 1917, p. 294 [**Sarcinula phillipsi* McCoy, 1849, p. 125; OD].

Schoenophyllum Simpson, 1900, p. 214 [**S. aggregatum;* OD].

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

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

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

Prionocyclus Meek, 1871b, p. 298 [**Ammonites serratocarinatus* Meek, 1871a, p. 429, *non* Stoliczka, 1864, p. 57; *=Prionocyclus wyomingensis* Meek, 1876, p. 452].

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

Fixation of Type Species Originally

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

Fixation of Type Species Subsequently

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

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

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

Another mode of fixing the type species of a genus is through action of the International Commission of Zoological Nomenclature using its plenary powers. Definition in this way may set aside application of the *Code* so as to arrive at a decision considered to be in

the best interest of continuity and stability of zoological nomenclature. When made, it is binding and commonly is cited in the *Treatise* by the letters ICZN, accompanied by the date of announced decision and reference to the appropriate numbered opinion.

Subsequent designation of a type species is admissible only for genera established prior to 1931. A new genus-group name established after 1930 and not accompanied by fixation of a type species through original designation or original indication is invalid (*Code,* Article 13.3). Effort of a subsequent author to validate such a name by subsequent designation of a type species constitutes an original publication, making the name available under authorship and date of the subsequent author.

HOMONYMS

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

Hallophora BASSLER, 1911, p. 325, *nom. nov. pro Callophora* HALL, 1852, p. 144, *non* GRAY, 1848.

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

Mysterium DE LAUBENFELS, herein, *nom. nov. pro Mystrium* SCHRAMMEN, 1936, p. 183, *non* ROGER, 1862 [**Mystrium porosum* SCHRAMMEN, 1936, p. 183; OD].

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

Synonymous Homonyms

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

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

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

SYNONYMS

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

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

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

OTHER EDITORIAL MATTERS

BIOGEOGRAPHY

Purists, *Treatise* editors among them, would like nothing better than a stable world with a stable geography that makes possible a stable biogeographical classification. Global events of the past few years have shown how rapidly geography can change, and in all likelihood we have not witnessed the last of such change as new, so-called republics continue to spring up around the globe. One expects confusion among readers in the future as they try to decipher such geographical terms as USSR, Yugoslavia, or Ceylon. Such confusion is unavoidable, as books must be completed and published at some real time. Libraries would be limited indeed if publication were always to be delayed until the political world had settled down. In addition, such terms as central Europe and western Europe are likely to mean different things to different people. Some imprecision is introduced by the use of all such terms, of course, but it is probably no greater than the imprecision that stems from the fact that the work of paleontology is not yet finished, and the geographical ranges of many genera are imperfectly known.

Other geographic terms can also have varying degrees of formality. In general, *Treatise* policy is to use adjectives rather than nouns to refer to directions. Thus, we use *southern* and *western* in place of *South* and *West* unless a term has been formally defined as a geographic entity (e.g., South America or West Virginia). Note that we have referred to western Texas rather than West Texas, which is said to be not a state but a state of mind.

NAMES OF AUTHORS: TRANSLATION AND TRANSLITERATION

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

Second, most but by no means all Chinese list their family name first followed by given names. People with Chinese names who study in the West, however, often reverse the order, putting the family name last as is the Western custom.

In previous *Treatise* volumes, traditional Chinese name order was followed when citing a Chinese language publication, in an attempt to list authors ias they appear in the source being cited. However, the increasingly global nature of scientific publishing has rendered this past *Treatise* policy cumbersome and prone to error. Therefore, starting with this volume, *Treatise* is using the Western name order style for all authors, regardless of country of origin or language of publishing. The aim is for consistency and should not imply disrespect for Chinese tradition.

In this volume, we also use the full given name for Chinese authors rather than initials when the name is known (Yuandong Zhang instead of Y.-D. Zhang). Some authors cited in this volume share both a family name and the same initials with another cited author.

Several systems exist for transliterating the Cyrillic alphabet into the roman alphabet. On the recommendation of skilled bibliographic librarians, we have adopted the American Library Association/Library of Congress romanization table for Russian and other languages using the Cyrillic alphabet.

MATTERS SPECIFIC TO THIS VOLUME

Authorship entails both credit and responsibility. As the knowledge of paleontology grows and paleontologists become more specialized, preparation of *Treatise* volumes must necessarily involve larger and larger teams of researchers, each focusing on increasingly narrow aspects of the higher taxon under revision. In this volume, we have taken special pains to acknowledge authorship of small subsections. Readers citing the volume are encouraged to pay close attention to the actual authorship of a section or subsection.

Stratigraphic nomenclature in the *Treatise* follows that recommended by the International Commission of Stratigraphy, which updates their International Chronostratigraphic Chart periodically (www.stratigraphy.org).

Unlike other volumes, stratigraphic ranges are listed herein to the level of biozones, due to the unique role graptolites play in determining ages and ranges.

Few authors, including in the *Treatise*, consistently provide the names and publication dates of sources that first declared a name to be a synonym of another genus or type species. This is surprising because such information is an important part of the history of a taxon. Identifying synonyms is particularly of crucial importance in the study of graptolites because fossils from as early as the Cambrian are often fragments, and reclassification is common. Graptolite family, genera, and species names have been in flux for centuries. In the interest of being as thorough as possible, the authors of this volume have endeavored to note author, date, and page numbers of researchers first synonymizing a name. We list such sources, identified as "synonymized by…" (abbreviated to "syn. by").Therefore entries might read:

...[=*Prochnygraptus* Přibyl, & Štorch, 1985, p. 159 (type, *Monograptus singularis* Törnquist,1892, p. 22, OD); syn. by Zalasiewicz, 1995, p. 34]

...[=*Dibranchiograptus* Hundt, 1949a, p. 19 (type, *D. bibrachiatus,* OD), syn., herein]

All sections in this volume first appeared as chapters in *Treatise Online,* published between 2014 and 2022. This presents new dilemmas. For instance, credits for previously published figures are identified by publication and date at the end of figure captions; "new" is used if a figure is being published for the first time. In that regard, we treat *Treatise Online* and *Treatise* (the printed volume) as the same entity, therefore "new" will appear herein, even if technically published online earlier.

Authors who wish to cite *Treatise* material may choose to cite the online publication, which is the earliest date—often referred to in the text as "originally published as..." (a listing of all Part V *Treatise Online* chapters are on p. xxvii). Please note that editorial changes have been made subsequent to *Treatise Online* versions. Therefore, the printed

volume represents the most accurate and up-to-date information.

ACKNOWLEDGMENTS

This second revision of Part V began under the supervision of the late Assistant Editor, Jill Hardesty and Editor and Director Paul Selden. Assistant Editor Elizabeth Black took on the task in 2016 in the early stages of submission of manuscripts. As chapters were finished, they were made available to the community in *Treatise Online*. Becoming the Interim Director as the project was in its final phases, William Ausich took on the formidable task of moving this volume through the various stages of final editing and into production. In this, able assistance was provided by other members of the editorial team, including Denise Mayse, Office Manager and Copy Editor, with her excellent attention to detail while proofing, checking the references, and various other tasks, and Mike Cormack with his outstanding computer skills and management of subscriptions and *Treatise Online*. Six months before this volume went to the printer, Bruce Lieberman became Director and Editor, and his input was invaluable in the last stages.

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

Paul Selden
William Ausich

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REPOSITORIES AND THEIR ABBREVIATIONS

Institutional acronyms for the repositories of specimens mentioned and illustrated in this volume:

AMF: Australian Museum, Sydney, Australia

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

BAF: Palaeontological collection, Department of Geology, TU Bergakademie Freiberg, Germany

BB: Bedřich Bouček collection, Czech Geological Survey, Prague, Czech Republic

BELUM: Ulster Museum, Belfast, Northern Ireland

BGR: Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany

BGS GSM: British Geological Survey, Geological Survey Museum, Keyworth, Nottingham, UK

BSPGM: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany

BU: Lapworth Museum, Birmingham University, Birmingham, UK

CCG: Changchun College of Geology, Changchun, Jilin Province, China

CGS: Czech Geological Survey, Prague, Czech Republic

CGM: Central Geological Museum named after F. N. Tchernyshev, St. Petersburg, Russia

CMC: Cincinnati Museum Center, Cincinnati, Ohio, USA (collection formerly at University of Minnesota)

CNIGR: Museum of the A. P. Karpinsky All-Union Geological Research Institute (VSEGEI), St. Petersburg, Russia

CPC: Commonwealth Palaeontological Collections, Geoscience Australia, Canberra, Australia (previously Bureau of Mineral Resources, BMR)

CSGM: Central Siberian Geological Museum, Novosibirsk, Russia (see **IGiG**)

DPI: La Plata Museum, La Plata, Argentina

DPM: Departamento de Paleontologia, Universidad Complutense, Madrid, Spain

FGWG: Universität Greifswald, Institut für Geographie und Geologie, Greifswalder Geologische Sammlungen, Greifswald, Germany

FMNH: Field Museum, Chicago, Illinois, USA

GIT: Tallinn University of Technology, Geoscience collections of Estonia, Tallinn, Estonia

GLAHM: Hunterian Museum, University of Glasgow, Glasgow, UK

GM: Geological Museum, K. I. Satpayev Institute of Geological Sciences, Almaty, Kazakhstan

GMCH: Geological Museum of China, Beijing, China

GPIT: Geologisch-Paläontologisches Institut der Universität Tübingen, Tübingen, Germany

GSC: Geological Survey of Canada, Ottawa, Canada

GSE: Geological Survey Museum (British Geological Survey), Keyworth, Nottingham, UK

GSM: Geological Survey Museum, London, UK

IGiG: Central Siberian Geological Museum, Novosibirsk, Russia

i751: Museo Civico di Storia Naturale di Milano, Milano, Italy

KR: TU Clausthal, Institut für Geologie und Paläontologie, Clausthal-Zellerfeld, Germany

LO: Lunds Originale, Department of Geology, Lund University, Lund, Sweden

MB.G.: Museum für Naturkunde, Berlin, Germany

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

MGM: Museo Geominero, Spanish Geological Survey (IGME), Madrid, Spain

MGUH: Geological Museum of the University of Copenhagen, Copenhagen, Denmark

MNHN: Muséum National d'Histoire Naturelle, Paris, France

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

NHMUK: The Natural History Museum, London, UK (formerly BMNH)

NMG: Naturkundemuseum, Gera, Germany

NM: National Museum, Department of Paleontology, Prague, Czech Republic

NMV: Museums Victoria, Melbourne, Australia

NMW: National Museum of Wales, Cardiff, UK

NRM: Naturhistoriska Riksmuseet Stockholm, Stockholm, Sweden

NYSM: New York State Museum, Albany, New York, USA

OMR: B. Horák Museum, Rokychany, Czech Republic

OSU: Orton Geological Museum, Ohio State University, Columbus, Ohio, USA

OU: Otago University, Department of Geology, Geology Museum, Dunedin, New Zealand

PMO: Natural History Museum, Paleontological Type collections, University of Oslo, Oslo, Norway

PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Uppsala, Sweden

PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Uppsala, Sweden (previously UM)

PKUM: Geological Museum of Peking University, Beijing, China

ROM: Royal Ontario Museum, Toronto, Canada

RPM: Redpath Museum, McGill University, Montreal, Québec, Canada

SGU: Sveriges Geologiska Undersökning, Uppsala, Sweden

SM: Sedgwick Museum of Earth Sciences, Cambridge, UK

SMF: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

SNOMNH: Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA

SVEGEI: F. N. Tchernyshev Central Geological Museum, St. Petersburg, Russia

T: West Bohemian Museum, Pilsen, Czech Republic

TUG: University of Tartu, Natural History Museum, Tartu, Estonia

UM: Ulster Museum, Belfast, UK

UMMP: University of Michigan, Museum of Paleontology, Ann Arbor, Michigan, USA

USNM: US National Museum of Natural History, Washington, DC, USA

UQ: Queensland Museum, South Brisbane, Queensland, Australia

UUG: Czech Geological Survey (Česká geologická služba), Prague, Czech Republic

UWO: University of Western Ontario, London, Ontario, Canada

VU: Geological Museum, Department of Geology and Mineralogy, Vilnius University, Vilnius, Lithuania

ZPAL: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland (older ZPAL materials do not have type numbers)

ORIGINAL PUBLICATION IN *TREATISE ONLINE*

All content in this volume was originally published online. Below are the relevant *Treatise Online* chapters with their original titles in the order reflected in this volume (not in date order). Authors wishing to cite the online published material, may follow the suggested citations below. They may be accessed at paleo.ku.edu/treatiseonline. The Reference Section also cites online chapters by authors where relevant.

Chapter 1: Introduction to the Hemichordata.
Maletz, Jörg, & Christopher B. Cameron 2021. Part V, Second Revision, Chapter 1: Introduction to the Hemichordata. Treatise Online 157:1–9, 2 fig.

Chapter 2. Class Enteropneusta:
Cameron, Christopher B. 2018. Part V, Second Revision, Chapter 2: Class Enteropneusta: Introduction, morphology, life habits, systematic descriptions, and future research. Treatise Online 109:1–22, 8 fig.

Chapter 3: Introduction to the class Pterobranchia.
Maletz, Jörg, & Christopher B. Cameron. 2016. Part V, Second Revision, Chapter 3: Introduction to the class Pterobranchia Lankester, 1877. Treatise Online 82:1–15, 8 fig.

Chapter 4: Morphology of the Pterobranch Tubarium.
Maletz, Jörg, Alfred C. Lenz, & Denis E. B. Bates. 2016. Part V, Second Revision, Chapter 4: Morphology of the Pterobranch Tubarium. Treatise Online 76:1–63, 44 fig.

Chapter 5: Hemichordate taphonomy.
Maletz, Jörg. 2018. Part V, Second Revision, Chapter 5: Hemichordate taphonomy. Treatise Online 110:1–15, 5 fig.

Chapter 6: Paleoecology of the Pterobranchia.
Cooper, Roger A., Sue Rigby, Denis E. B. Bates, & Jörg Maletz. 2017. Part V, Second Revision, Chapter 6: Paleoecology of the Pterobranchia (Cephalodiscida and Graptolithina). Treatise Online 86:1–16, 9 fig.

Chapter 7: Biostratigraphy.
Maletz, Jörg. 2021. Part V, Second Revision, Chapter 7: Biostratigraphy. Treatise Online 146:1–22, 7 fig.

Chapter 8: Paleogeography of the Hemichordata.
Maletz, Jörg. 2020. Part V, Second Revision, Chapter 8: Paleogeography of the Hemichordata. Treatise Online 133:1–12, 4 fig.

Chapter 9: Geological applications.
Maletz, Jörg, & Alfons H. M. VandenBerg. 2021. Part V, Second Revision, Chapter 9: Geological applications. Treatise Online 155:1–12, 3 fig.

Chapter 10: Evolutionary history.
Maletz, Jörg. 2020. Part V, Second Revision, Chapter 10: Evolutionary history. Treatise Online 143:1–16, 6 fig.

Chapter 11: Graptolite Preparation and Illustration Techniques.
Denis E. B. Bates, Jörg Maletz, & Jan Zalasiewicz. 2015. Part V, Revised, Volume 1, Chapter 11: Graptolite Preparation and Illustration Techniques. Treatise Online 65:1–20, 17 fig.

Chapter 12: Glossary of the Hemichordata.
Jörg Maletz, Denis E. B. Bates, Edsel D. Brussa, Roger A. Cooper, Alfred C. Lenz, John F. Riva, Blanca A. Toro, & Yuandong Zhang. 2014. Part V, Revised Chapter 12: Glossary of the Hemichordata. Treatise Online 62:1–23, 6 fig.

Chapter 13: The history of graptolite classification.
Maletz, Jörg. 2017. Part V, Second Revision, Chapter 13: The history of graptolite classification. Treatise Online 88:1–11, 4 fig., 1 table.

Chapter 14: Order Cephalodiscida.
Maletz, Jörg, & Paul Gonzalez. 2017. Part V, Second Revision, Chapter 14: Order Cephalodiscida: Introduction and systematic descriptions. Treatise Online 100:1–8, 4 fig.

Chapter 15: Subclass Graptolithina and *incertae sedis* family Rhabdopleuridae.
Maletz, Jörg, & Elena Beli. 2018. Part V, Second Revision, Chapter 15: Subclass Graptolithina and *incertae sedis* family Rhabdopleuridae: Introduction and systematic descriptions. Treatise Online 101:1–14, 8 fig.

Chapter 16: Order Graptolithina, uncertain families.
Maletz, Jörg. 2019. Part V, Second Revision, Chapter 16: Order Graptolithina, uncertain families: Introduction, morphology, and systematic descriptions. Treatise Online 122:1–19, 12 fig.

Chapter 17: Order Dendroidea.
Maletz, Jörg. 2020. Part V, Second Revision, Chapter 17: Order Dendroidea: Introduction, morphology, and systematic descriptions. Treatise Online 139:1–23, 12 fig.

Chapter 18: Order Graptoloidea and Family Anisograptidae.
Maletz, Jörg, Blanca A. Toro, & Yuandong Zhang. 2017. Part V, Second Revision, Chapter 18: Order Graptoloidea and Family Anisograptidae: Introduction, morphology, and systematic descriptions.Treatise Online 85:1–14, 9 fig.

Chapter 19: Suborder Sinograptina.
Maletz, Jörg, Yuandong Zhang, & Alfons H. M. VandenBerg. 2018. Part V, Second Revision, Chapter 19: Suborder Sinograptina: Introduction, morphology, and systematic descriptions. Treatise Online 107:1–23, 17 fig.

Chapter 20: Suborder Dichograptina.
Maletz, Jörg, Blanca A. Toro, Yuandong Zhang, & Alfons H. M. VandenBerg. 2018. Part V, Second Revision, Chapter 20: Suborder Dichograptina: Introduction, morphology, and systematic descriptions. Treatise Online 108:1–28, 19 fig.

Chapter 21: Suborder Glossograptina.
Maletz, Jörg, & Yuandong Zhang. 2016. Part V, Second Revision, Chapter 21: Suborder Glossograptina: Introduction, Morphology, and Systematic Descriptions. Treatise Online 79:1–22, 20 fig.

Chapter 22: Suborder Axonophora, Infraorder Diplograptina I.
Maletz, Jörg. 2019. Part V, Second Revision, Chapter 22: Suborder Axonophora, Infraorder Diplograptina I

(Diplograptidae, Lasiograptidae): Introduction, morphology, and systematic descriptions. Treatise Online 127:1–26, 14 fig.

Chapter 23: Suborder Axonophora, Infraorder Diplograptina II.
Maletz, Jörg. 2020. Part V, Second Revision, Chapter 23: Suborder Axonophora, Infraorder Diplograptina II (Climacograptidae, Dicranograptidae): Introduction, morphology, and systematic descriptions. Treatise Online 129:1–20, 10 fig.

Chapter 24: Infraorder Neograptina and family Normalograptidae.
Maletz, Jörg. 2019. Part V, Second Revision, Chapter 24: Infraorder Neograptina and family Normalograptidae: Introduction, morphology, and systematic descriptions. Treatise Online 116:1–15, 8 fig.

Chapter 25: Superfamily Retiolitoidea and family Neodiplograptidae.
Maletz, Jörg. 2019. Part V, Second Revision, Chapter 25: Superfamily Retiolitoidea and family Neodiplograptidae: Introduction, morphology, and systematic descriptions. Treatise Online 117:1–8, 4 fig.

Chapter 26: Family Retiolitidae.
Lenz, Alfred C., Denis E. B. Bates, Anna Kozłowska, and Jörg Maletz. 2018. Part V, Second Revision, Chapter 26: Family Retiolitidae: Introduction, morphology, and systematic descriptions. Treatise Online 114:1–37, 24 fig.

Chapter 27: Superfamily Monograptoidea and family Dimorphograptidae.
Maletz, Jörg. 2017. Part V, Second Revision, Chapter 27: Superfamily Monograptoidea and family Dimorphograptidae: Introduction, morphology, and systematic descriptions. Treatise Online 87:1–9, 6 fig.

Chapter 28: Family Monograptidae.
Maletz, Jörg, & David K. Loydell. 2021. Part V, Second Revision, Chapter 28: Family Monograptidae: Introduction, morphology, and systematic descriptions. Treatise Online 156:1–43, 19 fig.

Chapter 29: Uncertain genera.
Maletz, Jörg, & Michael Steiner. 2021. Part V, Second Revision, Chapter 29: Uncertain genera. Treatise Online 152:1–17, 3 fig.

COORDINATING AUTHOR'S PREFACE

Jörg Maletz

INTRODUCTION

This Second Revision of the Part V *Treatise on Invertebrate Paleontology,* dealing with the phylum Hemichordata, is a considerably extended version of the Graptolite Treatises of Bulman (1955, 1970), which primarily covered the Graptolithina, at the time interpreted as an extinct class of the Hemichordata. With the recognition of the Graptolithina as fossil members of the Pterobranchia and the identification of the benthic colonial pterobranch *Rhabdopleura* as an extant graptolite (Mitchell & others, 2013), the focus in this volume is extended to include the record of fossil Hemichordata and to also examine the soft-body anatomy in more detail. Zooidal anatomy is important for the interpretation of the fossil graptolites and their life style and points to the importance of modern biology in understanding the fossil record.

The two editions of Bulman's *Treatise* (1955, 1970) have been the standard for graptolite research for seven decades, but their precursor in the *Handbuch der Paläozoologie* (Bulman, 1938) seems to be nearly forgotten and is difficult to obtain. This volume could be regarded as the first version of the Graptolite Treatise, because it covers in a similar manner all the main aspects of graptolite taxonomy and its understanding at the time of publication and was obviously the basic source for the later versions. Unfortunately, it was published at the wrong time and in the wrong country. Bulman (1938) established all the basic taxonomic concepts in the volume, even introducing a number of new taxa.

Bulman's work on the graptolites and their taxonomy in the two previous *Treatise* volumes is neither the only one nor the first attempt at a general overview of graptolites. However, most general treatments did not attain the influence and acceptance in the international scientific community, either due to the language in which they were published or the time of publication. Hall (1868) and Frech (1897) provided an understanding of graptolite research during their times and achieved important and valuable insights. General overviews by Dawydoff (1948), Waterlot (1953), Münch (1952), Mu and Lee (1960), and Obut (1957, 1964) had less impact due to the language barriers (published in French, German, Chinese, and Russian, respectively), but nevertheless they were important in shaping the opinions of generations of researchers.

Discussions to produce a new Graptolite *Treatise* began more than 20 years ago, with Chuck Mitchell and Mike Melchin initiating the first steps with then *Treatise* Editor Roger Kaessler. Along the way, there were meetings in Prague (1999, 2008), Nanjing (2007), and Sardinia (2009). Twelve years into the project, I became Coordinating Author when Chuck Mitchell was unable to continue due to other commitments. I began producing a newsletter in 2010 to track progress and keep in touch with authors.

SCOPE OF THE VOLUME

This volume is aimed at providing the most complete and up-to-date information on the fossil Hemichordata, their taxonomy, and their use in the geological sciences. The inclusion of not only the Pterobranchia (Graptolithina) but also the Enteropneusta shows our increased knowledge of the relationships of this fascinating fossil group with extant groups of organisms. This approach connects the fossil graptolites with their closest relatives, largely known from extant organisms.

Graptolites, the main focus of this volume, have been used successfully in the understanding of lithostratigraphic succes-

sions, unraveling structural complexities in geology and, thus, are important biological objects enabling numerous geological interpretations, as detailed on p. 127–134 (first published as Maletz & VandenBerg, 2021, *Treatise Online*). Lapworth (1878) first used graptolites to decipher the tectonic complexities in the succession of the Moffat Series, a milestone in graptolite research (Fortey, 1993; Hamilton, 2001) and a first hint on the importance of graptolite research to applied geology. Graptolite fusellum has been used to determine temperature and burial histories of Paleozoic sediments (e.g., Goodarzi & Norford, 1985). Graptolite research, thus, goes far beyond the identification of taxa and the relative dating of successions that included graptolites as index fossils. It is not just a discipline for taxonomists and fossil collectors; the geological application of graptolites is still developing and modern data collection and database interpretations may infuse new life into graptolite research. In recent years, paleodiversity studies using graptolite faunas have become the focus of research on extinction and origination intervals in Earth's history (e.g., Crampton & others, 2020).

The Enteropneusta, unfortunately, have been neglected in the past because so few fossil ones were recognized, and even the extant enteropneusts were rarely investigated in much detail. Only through the renewed interest in the Burgess Shale biota and their preservation, fossil Enteropneusta have gained more interest. As a result, new fossil taxa have been studied and described, including ones that are tubicolous (e.g., Caron, Conway Morris, & Cameron, 2013; Nanglu, Conway Morris, & Cameron, 2016; Cameron, 2018) and one with tentaculate arms (Nanglu, Caron, & Cameron, 2020), two characteristics that were previously regarded as restricted to the Pterobranchia.

ADDITIONAL INFORMATION

Color versions of many of the specimens and illustrations in this volume are available in *Treatise Online*. A reference to a color version is included in captions when color contributes vital information.

The systematic description section, which begins on p. 189, also includes additional introductory information and morphology details for each taxon group.

ACKNOWLEDGEMENTS

As the coordinating author of this volume, I wish to thank all my co-authors (listed on p. xxiv) and also all specialists who provided information, illustrations, and reviews of the individual chapters. I should not forget the hard working team at the *Treatise* office in Kansas who were essential to the production of this volume—Director Paul Selden, who supervised the project from 2007 to mid-2020, Assistant Editor Elizabeth Black who handled all but the first two chapters submitted; Michael Cormack for *Treatise Online* support; Denise Mayse, whose copyediting and proofing was essential; and Interim Editor William Ausich, who shepherded the project through its final stages.

Unfortunately, a number of our colleagues have left us during this long process, and we will always remember their input. Thus, a special thank you goes to Edsel D. Brussa (1961–2008), Roger A. Cooper (1939–2020), John F. Riva (1929–2020) and also to Assistant Editor Jill Hardesty (1965–2015), who initially supervised the editorial work for this *Treatise* volume.

INTRODUCTION TO THE PHYLUM HEMICHORDATA

Jörg Maletz and Christopher B. Cameron

The recognition of fossil Hemichordata is quite difficult as these organisms in general are soft-bodied and rarely leave any trace of their existence (Maletz, 2020a). Thus, the fossil record is relatively poor. Of the three extant groups of Hemichordata (Enteropneusta, Pterobranchia, and Planctosphaeroidea), only the tube-building Pterobranchia (Fig. 1.2–1.4) are common in the fossil record due to the preservability of their organic housing, the tubarium (Fig. 1.2). The Enteropneusta (Fig. 1.1) possess a fossil record reaching back into the middle Cambrian, but the Planctosphaeroidea (Fig. 1.5) are only known from a few larvae (e.g., Spengel 1932; Hyman, 1959; Hart, Miller, & Madin, 1994).

All extant Hemichordata share a tripartite body plan of their wormlike soft-bodied organization as a characteristic feature. Modern taxa investigated with DNA analysis indicate a phylogenetic position of the Hemichordata as a sister group to the echinoderms (e.g., Halanych, 1996; Cannon & others, 2009; Li & others, 2019) (Fig. 2). The extant Pterobranchia may have evolved from an enteropneust-like ancestor through a reduction in size and morphological complexity, a colonial or pseudocolonial life style, and development of the colony zooids through asexual budding (Cameron, Garey, & Swalla, 2000). Interestingly, a miniaturization also occurs in enteropneusts (e.g., *Meioglossus* Worsaae & others, 2012).

Bateson (1885a) introduced the term Hemichordata for the Enteropneusta, but it was Fowler (1892a, p. 132) who revised the Hemichordata to also include the colonial Pterobranchia. The status of the Planctosphaeroidea in the Hemichordata is still uncertain (see p. 189). The Hemichordata are comparable to the Helminthomorpha of Grobben (1908, p. 505), who included the Enteropneusta and Pterobranchia. Spengel (1932, p. 26) included *Planctosphaera* as a third class in the Helminthomorpha. The Helminthomorpha Grobben, 1908 has commonly been used in German literature and may easily be confused with the Helminthomorpha Pocock, 1887, a clade of millipedes.

The Hemichordata range in length from less than 1 mm (Worsaae & others, 2012) to more than 2 m. Of the living hemichordates, the Enteropneusta are the most well known members. They are benthic marine worms that are distributed from the shallow intertidal zone to the deep sea and appear not to be limited by temperature barriers. They are usually infaunal elements, but deep-water enteropneusts include epibenthic demersal drifters (Osborn & others, 2012). The enteropneust *Saxipendium coronatum* Woodwick & Sensenbaugh, 1985 is known to congregate on rock surfaces near hydrothermal vents.

Uncertainty about the relationships of the Hemichordata has been present since the first enteropneust was discovered in 1821 and was thought to be an atypical holothurian (Eschscholtz, 1825). Hyman (1959) provided a thorough historical treatment of early hemichordate classifications. Kowalewsky (1866) provided the first anatomical study of an acorn worm including the discovery of pharyngeal openings that aligned the Enteropneusta with the Chordata. Metschnikoff (1869) found that the tornaria larva was an enteropneust rather than an asteroid larva, adding weight to the echinoderm and enteropneust relationship. Then, Bateson (1885a) placed a subphylum Hemichordata in the phylum Chordata based on the presence of a notochord, the central nervous system, and the gill slits. This position was protested by Spengel (1893) and subsequently abandoned by the German, French, and American treatises

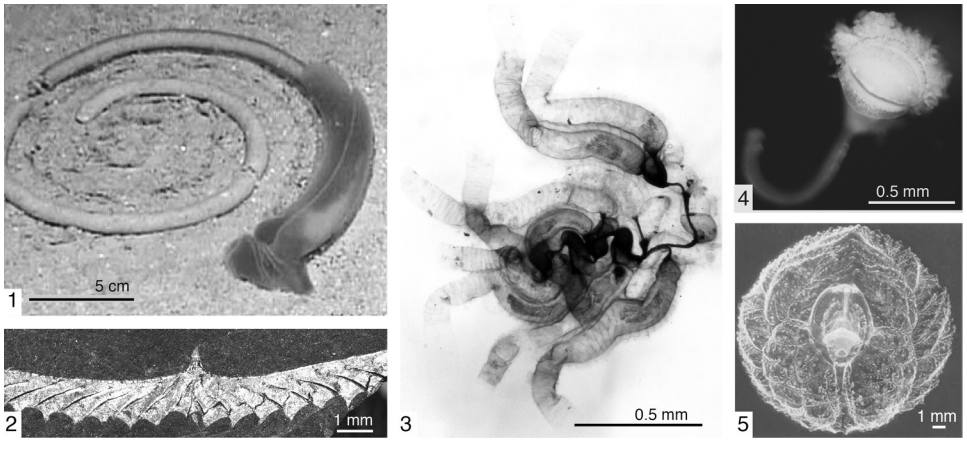


Fig. 1. Examples of the Hemichordata. *1,* Torquaratorid enteropneust with fecal string (Holland & others, 2005, fig. 3E); *2, Expansograptus hirundo* (Salter, 1863a), flattened tubarium, PMO 234.064, Tøyen Shale, Oslo region, Norway (new); *3, Rhabdopleura compacta* Hincks, 1880a, tubarium with zooids (Cavers, 2005, fig. 1.1); *4, Cephalodiscus planitectus* Miyamoto, Nishikawa, & Namikawa, 2020, ventral view of zooid (Miyamoto, Nishikawa, & Namikawa, 2020, fig. 2C); *5, Planctosphaera pelagica* Spengel, 1932 (Hart, Miller, & Madin, 1994, fig. 1B). Color images available, *Treatise Online* 157.

on invertebrates, namely van der Horst (1939), Dawydoff (1948), and Hyman (1959). The similarities and close relationship of the hemichordates to the echinoderms was the predominant view for the latter half of the twentieth century, although the common ancestor remained contentious. On one side, Bather (1900) referred to the dipleurula larva, a name introduced by Semon (1888), as a common ancestor. The larva shared features of the enteropneust tornaria or asteroid auricularia. It was soft, bilaterally symmetric with a ventral mouth, apical organ, ciliated bands, and three pairs of coelomic sacs that were arranged on either side of the gut (Gislén, 1930), referred to as the protocoel, mesocoel, and metacoel. The protocoel opened to the exterior by a ciliated duct and pore. The hypothesis that this dipleurula elongated to become the ancestral chordate animal (Garstang, 1928) gained acceptance.

Grobben (1923) advanced the hypothesis that the echinoderms are derived from the pterobranchs. The ancestor was similar to *Cephalodiscus* M'Intosh, 1882 in that it had five pairs of arms with tentacles. The cephalic shield was comparable in position to the attachment pit of the crinoid and asteroid larvae that was drawn out to become a stalk. Most people regarded the pterobranchs as more primitive than enteropneusts because of their simple nervous system. The echinoderms then would have evolved by the extension of the protocoel (echinoderm hydrocoel) into multiple arms. The protocoel opened to the exterior by a pore. The digestive tract was comprised of an esophagus, stomach, and intestine and curved to open into an anus on the anterior ventral side. This ancestor metamorphosed into an echinoderm with the right protocoel and five arms diminished, and the body attained a circular disklike shape. The remaining arms radiated in five directions to form the echinoderm rays. Jeffries (1986) developed a similar calcichordate hypothesis whereby the echinoderms and the chordates evolved from a pterobranch-like ancestor that had fallen over and then elaborated one side. The prevailing hypotheses of the twentieth century was that pterobranchs were either basal deuterostomes (Gee, 1996; Nielsen, Scharf, & Eibye-Jacobsen, 1996) or plesiomorphic hemichordates (Hyman, 1959; Barrington, 1965).

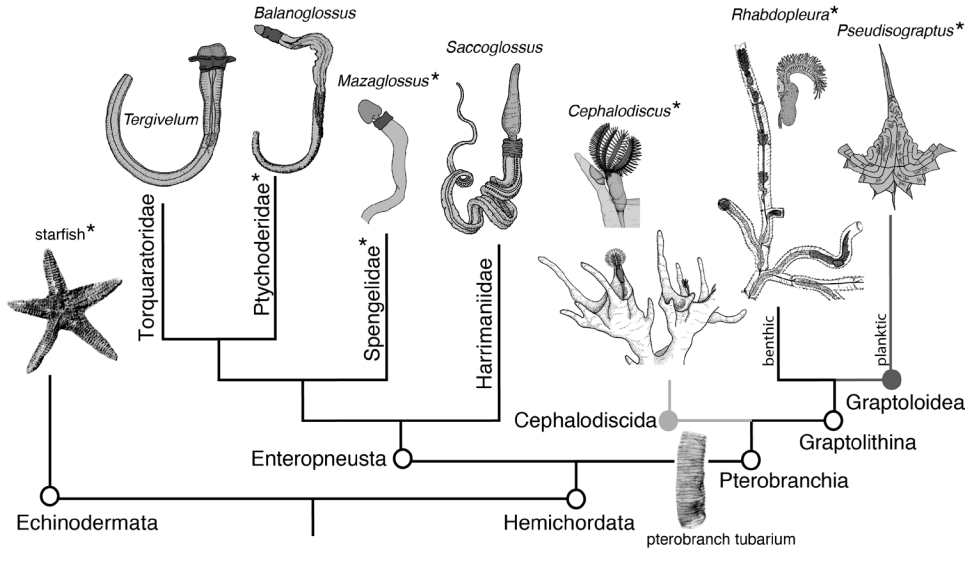


FIG. 2. Phylogenetic understanding of the Hemichordata. Taxon names with * indicate taxa known also from fossils or only from fossil material (new).

The GUTMANN (1981) hypothesis posits that the ancestral deuterostome, based on a functional-mechanical analysis, was a metameric, coelomate wormlike animal with complex body muscles that formed the basis of a hydrostatic skeleton. The sequence of morphological changes leading to the chordate ancestor was, in chronological order, the appearance of a notochord, the dorsal hollow nerve cord, the post-anal tail, and the branchial basket. This primitive chordate would have been most like a lancelet. From here, the enteropneusts lost the notochord, dorsal nerve cord, and segmented condition and developed a muscular burrowing proboscis. The collar originated to prevent water from exiting the mouth. Pterobranchs then arose from this acorn worm by a reduction in the branchial basket and an elaboration of the collar into arms and tentacles, and finally, the appearance of the tubarium. By this hypothesis, echinoderms arose from the pterobranch-like ancestor by specializing for sessile life, developing feeding tentacles and losing the branchial basket.

The twenty-first century saw the dawn of a new hypothesis, that the common ancestor to the deuterostomes was an enteropneust-like worm with chordate-like gills (CAMERON, GAREY, & SWALLA, 2000). This worm hypothesis was further elaborated by CAMERON (2002a, 2005), who stated that the ancestral deuterostome was a benthic vermiform organism with a terminal mouth and anus and a pharynx perforated with gill slits bordered by gill bars of collagen used in filter feeding (CAMERON, 2002a). This organism possessed a simple nerve plexus with little sign of regionalization. The enteropneust collar cord is not a homolog of the chordate dorsal nerve cord. It had a cluster of vacuolated cells with myofilaments, expanded extracellular matrix, and extracellular spaces developed from the middorsal wall of the archenteron that provided the foundation for the independent evolution of the chordate notochord and enteropneust stomochord. Iodotyrosine was produced in cells lining the gut, but these cells had not yet coalesced into an endostyle. It is not known if this animal had trimeric or metameric coeloms, but the ancestor probably had well-developed circular and longitudinal muscles (CAMERON, 2005). On the branch

to the Ambulacraria, the dipleurula larva appeared. The first echinoderm adult was bilaterally symmetric (Rahman & others, 2015) and may have possessed echinoderm-like ossicles (Cameron & Bishop, 2012) and gill slits (e.g., *Jaekelocarpus* Kolata, Frest, & Mapes, 1991, see Dominguez, Jacobson, & Jeffries, 2002). The first pterobranchs, then, similarly evolved from an acorn worm-like ancestor.

The discovery of two Cambrian Burgess Shale enteropneust fossils that are tubicolous (Cameron, 2018), and another with arms and tentacles (Nanglu, Caron, & Cameron, 2020) suggest that these traits originated before the pterobranchs. Therefore, the major innovations of pterobranchs are coloniality and a reduction in size that resulted in the loss of the gill skeleton, branchiomeric nephridia, and three pairs of coelomic diverticula—the perihaemal, peripharyngeal, and peribuccal coeloms (Cameron, 2005). The hypothesis that the ancestor to the deuterostomes was an enteropneust-like worm is supported by morphological and molecular phylogenetic trees (Cameron, 2005; Cannon & others, 2009), molecular development (Lowe, 2021), and comparative genomics (Simakov & others, 2015). An important caveat to this hypothesis, which points to fruitful future avenues of research, is the almost total absence of pterobranch molecular developmental studies (Sato & others, 2009) and the absence of a pterobranch genome.

The preservation of the Hemichordata as fossils depends strongly on the type of sediments in which they are embedded and the environmental conditions in these sediments (Maletz, 2020a). In general, indications of the organic soft tissue of organisms is only preserved under very special conditions and can be found in rare Lagerstätten, such as the Burgess Shale of British Columbia, the Chengjiang fauna of China (Cameron, 2018), and the Mazon Creek fauna of North America (Cameron, 2016).

The fossil record of the Pterobranchia is extensive, as evidenced by the common occurrence of graptolite tubaria in Paleozoic sediments, but does not include any identifiable organically preserved zooids (Maletz, 2020a; Ramírez-Guerrero & Cameron, 2021).

INTRODUCTION TO THE CLASS ENTEROPNEUSTA

Christopher B. Cameron

MORPHOLOGY

The Enteropneusta are free living, solitary marine worms.Their occurrence ranges from the Cambrian to the present. The acorn worm body is arranged into an anterior proboscis, a collar, and a posterior trunk (Fig. 3). Body length can vary from less than 1 mm (Worsaae & others, 2012) to 1.5 m (Spengel, 1893). The proboscis is muscular, and its epidermis is replete with sensory, ciliated, and glandular cells (Benito & Pardos, 1997). Acorn worms deposit-feed by trapping sediment in mucus and transporting it to the mouth with cilia. A pre-oral ciliary organ on the posterior proboscis (Brambell & Cole, 1939) (Fig. 4.1) directs the food-laden mucous thread into the mouth (Gonzalez & Cameron, 2009). The proboscis coelom contains a turgid stomochord (Fig. 3, Fig. 4.2a), an anterior projection of the dorsal collar buccal cavity that consists of vacuolated cells arranged around a central ciliated cavity and encapsulated in a collagen sheath (Welsch & Storch, 1970). The result is a rigid structure against which the pericardium (heart) compresses the intervening blood sinus so that urine can be forced across the glomerulus (kidney) into the proboscis coelom (Balser & Ruppert, 1990). The stomochord is not a homolog of the chordate notochord (Satoh & others, 2014). The right protocoelom is small or absent, and the left coelom is dominant and extends a ciliated duct, which is lined with nephridia (mesothelial, monociliated podocytes and myocytes) to the exterior via a left dorsal lateral urinary proboscis pore (Ruppert & Balser, 1986) (Fig. 3). There is extensive inter- and intraspecific variation in the form of this proboscis heart-kidney-coelom complex (Deland & others, 2010). The stomochord is supported ventrally by a collagenous Y-shaped nuchal skeleton (Fig. 3, Fig. 4.2a–b). The skeleton extends posteriorly through the neck and bifurcates into paired horns in the collar (Spengel, 1893; Horst, 1939; Ezhova & Malakhov, 2009).

The collar lip forms the mouth anteriorly, and its interior is the buccal cavity (Fig. 3). In some species, the anterior lip is muscular and flexible, adept at guiding sediment laden strings of mucus from the proboscis into the mouth or rejecting them over the lip and onto the collar. The collar epidermis is usually differentiated into histologically distinct zones of transverse bands of numerous gland cells and dense bands of cilia (Benito & Pardos, 1997; Horst, 1939), with distinct mucin and glycoprotein secretory patterns (Simakov & others, 2015). The acorn worm nervous system is an epidermal plexus with two longitudinal intraepidermal nerve cords in the trunk and a neurulated cord in the collar (Bullock, 1940; Knight-Jones, 1953). Sensory cells, ganglion cells, interneuronal junctions, and motor innervation are arranged diffusely (Bullock, 1940; Benito & Pardos, 1997). The collar cord is intraepithelial even where the epithelium containing the nerves becomes internalized, and most commonly has paired, parallel, and discontinuous lacuna that are lined with cilia. There is no central nervous system. The collar cord is a simple conduction pathway (Cameron & Mackie, 1996) and is aligned with the perihaemal muscles, suggesting a role in the rapid contraction of the proboscis (Ruppert, 2005). This cord is unlike the hollow, neuroepithelium in the rays of echinoderms or the hollow, neural tube of chordates (Bullock, 1940; Cameron & Mackie, 1996; Ruppert, 2005). Paired diverticula of the trunk coeloms, called perihaemal and peribuccal coeloms, project anteriorly into the collar (Fig. 3). Paired mesocoel ducts connect the collar coeloms to the first pair of gill pore atria in the anterior trunk (Fig. 3). The acorn worm trunk bears middorsal and midventral longitudinal grooves that

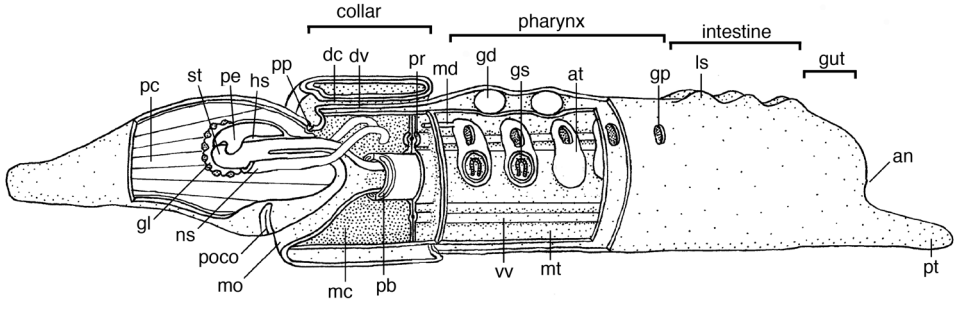


FIG. 3. Illustration of a generalized morphology of an enteropneust. Anus (*an*), atrium (*at*), dorsal nerve cord (*dc*), dorsal blood vessel (*dv*), gonad (*gd*), filtration glomerulus (*gl*), gill pore (*gp*), gill slit (*gs*), heart sinus (*hs*), liver sacs (*ls*), mesocoel (*mc*), paired mesocoel ducts (*md*), mouth (*mo*), metacoels (*mt*), Y-shaped nuchal skeleton (*ns*), peribuccal coeloms (*pb*), protocoel (*pc*), pericardium (*pe*), ventral post-anal tail (*pt*), preoral ciliary organ (*poco*), urinary pore (*pp*), perihaemal coeloms (*pr*), stomochord (*st*), and ventral blood vessel (*vv*) (adapted from Cameron 2005, fig. 1).

correspond to the location of longitudinal nerves and blood vessels (PARDOS & BENITO, 1990) (Fig. 3). The dorsal and ventral nerve cords are connected anteriorly by a circumpharyngeal ring (BULLOCK, 1940; KAUL-STREHLOW & others, 2015). The ventral cord is the fastest conducting cord due to its proximity to the large ventral longitudinal muscles (PICKENS, 1970; CAMERON & MACKIE, 1996). The trunk is differentiated into regions along its length that correspond to the specializations of the gut. The anterior region bears paired dorsolateral series of gills, followed by an esophagus and an intestine that terminates at an anus (Fig. 3). The gill slits, demarcated by a series of M-shaped collagenous gill bars, are connected to the outside pores by atrial cavities, akin to those of cephalochordates. The ciliated bars pump water through the pharynx, slits, and pores, removing food particles from suspension (CAMERON, 2002a; GONZALEZ & CAMERON, 2009). Support for the hypothesis that gills are a deuterostome plesiomorphy are shared patterns of genes expressed during gill and pharynx development and the organization of these genes in synteny in acorn worms and vertebrates (GILLIS, FRITZENWANKER, & LOWE, 2012; SIMAKOV & others, 2015). The food and mucus are then transported down the gill bars to the ventral gut, concentrated into a mucous food cord, and then transported posteriorly through the esophagus. Iodine^{125} binding experiments suggest that an endostyle function may reside in the entire pharyngeal lining of Enteropneusta and in *Schizocardium* SPENGEL, 1893, in which an epibranchial ridge is organized into zones of cells, reminiscent of the chordate endostyle (RUPPERT, CAMERON, & FRICK, 1999; RUPPERT, 2005; see also SATOH & others, 2014) (Fig. 4.3). The muscular esophagus functions to eliminate excess water from the food cord as it passes to the intestine. Anteriorly, the intestine is usually darkly pigmented. It is a simple tube except in *Schizocardium* and the family Ptychoderidae, in which it develops dorsally projecting rows of hepatic sacs, presumably to deal with a diet of heavy sediment. Gonads occur along the pharyngeal region, and in the family Ptychoderidae, they develop in external paired longitudinal ridges or wings. A few species have a curious pygochord structure in the posterior ventral trunk that WILLEY (1899) suggested may be a homolog to the chordate notochord. It is comprised of vacuolated cells positioned between the posterior ventral trunk mesenteries (WILLEY, 1899; SPENGEL, 1903; URIBE & LARRAIN, 1992; MIYAMOTO & SAITO, 2007) or intestine (HORST, 1939). PUNNETT (1906) suggested that the structure may be a vestigial collateral intestine, which may instead function to support the fragile trunk as it projects from the burrow to eject fecal sediment. Distinct

protuberances characterize the epidermis of the acorn worm trunk. These are formed by secretory and sclerocyte cells that occlude extracellular spaces, where microscopic calcium carbonate ossicles develop. In *Ptychodera* (Fig. 4.4a) and *Saccoglossus* (Fig. 4.4b), the ossicles form a polycrystalline aggregate of laminar layers, with perforations that are comparable to echinoderm stereom (Cameron & Bishop, 2012). The functions of the pygochord and the ossicles are unknown.

DEVELOPMENT AND REPRODUCTION

The sexes are separated except for *Yoda purpurata* Priede & others, 2012, which is a hermaphrodite (see Priede & others, 2012). Fertilization is external (Burdon-Jones 1951; Lowe & others 2004) although vivipary is known for *Xenopleura vivipara* Gilchrist, 1925 and the deep-sea *Coleodesmium karaensis* Osborn & others, 2013, which broods their embryos in sacs that connect to a gonadal wing by a narrow stock (Osborn & others, 2013). In most species, eggs are released in a jelly coating that breaks down following fertilization (Colwin & Colwin, 1954). All subsequent development occurs in the seawater. Cleavage is holoblastic, radial, and more or less equal. Cell fates and axis specifications are in most respects similar to that of an echinoderm (Henry, Tagawa, & Martindale, 2001). A coeloblastula is followed by gastrulation by invagination. The blastopore is located posteriorly but closes before a new anus and mouth are formed (Burdon-Jones, 1952; Colwin & Colwin, 1953). The fertilization envelope weakens and ruptures, releasing ciliated, swimming embryos by late gastrula. The organization of the coelomic sacs is comparable to echinoderms. The ambulacrarian coeloms are organized anterior to posterior as paired protocoel, mesocoels, and metacoels (Crawford & Chia, 1978). They develop as independent pouches from the archenteron by enterocoely (Kaul-Strehlow & Stach, 2013). Reports of schizocoely have not been substantiated (Hadfield, 1975). Gemmill (1914) provided a thorough comparative study of coelomogenesis in the asteroid (starfish), *Asterias rubens* Linnaeus, 1758 and an enteropneust (summarized in Cameron, 2005).

Harrimaniid worms (e.g., *Saccoglossus*) develop from a large, yolky egg to a ciliated, non-feeding larva with a telotrochal band and apical tuft that allows for a brief swimming and exploratory period (Colwin & Colwin, 1953). Following settlement, the juvenile worm has a ciliated, adhesive, post-anal tail (Fig. 5.3) that allows for rapid forward and reverse locomotion, adhesion, and release (Burdon-Jones, 1952; Burdon-Jones 1956; Cameron, 2002b; Stach & Kaul, 2011) that may be a homolog to the pterobranch stalk (Burdon-Jones, 1952; Hyman, 1959; Lester, 1985; Cameron, 2005). Ptychoderid worms (e.g., *Ptychodera*) shed small transparent eggs. Development is rapid and indirect via a tornaria larva that resembles an echinoderm auricularia (Morgan, 1891; Gemmill, 1914; Gislén, 1930; Tagawa & others, 1998; Urata & Yamaguchi, 2004) (Fig. 5.4). These dipleurula larvae are delicate and transparent with a preoral ciliated feeding band (Fig. 5.4) that creates an upstream feeding current using monociliated cells (Morgan, 1891; Strathmann & Bonar, 1976) and a perioral ciliated band that manipulates and conveys food into the esophagus (Lacalli & Gilmour, 2001). The free-swimming, feeding tornaria are able to turn due to a band of multiciliated cells that comprise the locomotory telotroch (Fig. 5.4), an acorn worm innovation. The tornaria apical plate retractor muscle (and associated coughing behavior) (Morgan, 1891) is another acorn worm larval apomorphy. Tornaria may persist in the plankton for months before metamorphosis and settlement to a suitable juvenile worm habitat. The larval body elongates differentiating the three body regions and organs. The larval apical tuft, nervous system, and feeding band are lost, followed by the telotroch band. The gills develop as

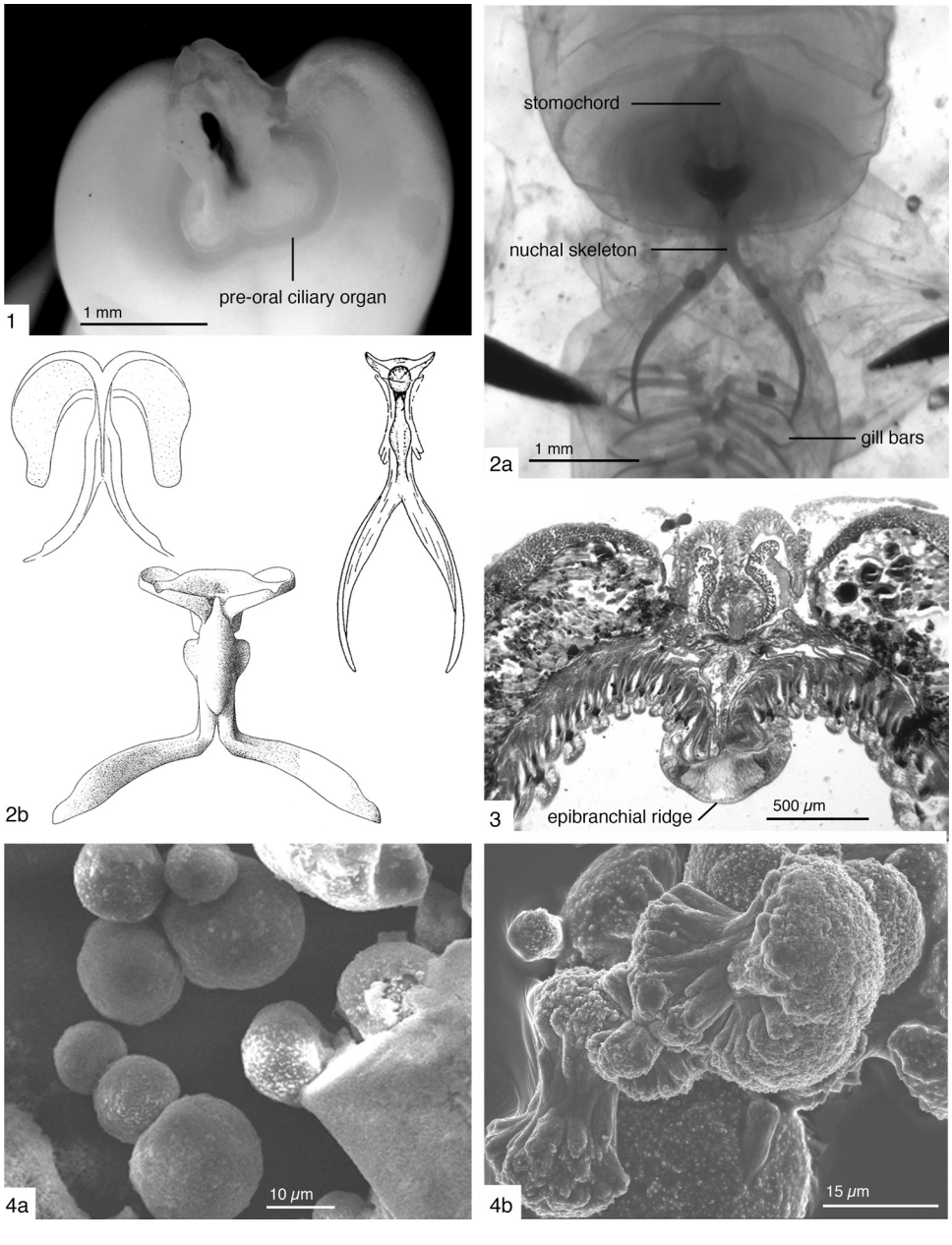


FIG. 4. Acorn worm anatomy. *1,* Pre-oral ciliary organ of *Protoglossus graveolens* GIRAY & KING, 1996; *2a,* stomochord, nuchal skeleton, and gill bars of *P. graveolens; 2b,* illustrations of nuchal skeletons, in clockwise order, *Protoglossus koehleri* (CAULLERY & MESNIL, 1900), *Saccoglossus ruber* TATTERSALL, 1905, and *Balanoglossus hydrocephalus* HORST, 1940; *3,* epibranchial ridge of *Schizocardium peruvianum* SPENGEL, 1893; *4a,* ossicles of *Ptychodera flava* var. ESCHSCHOLTZ, 1825, Galapagos; *4b,* ossicles of *Saccoglossus bromophenolosus* KING, GIRAY, & KORNFIELD, 1994 (all, new).

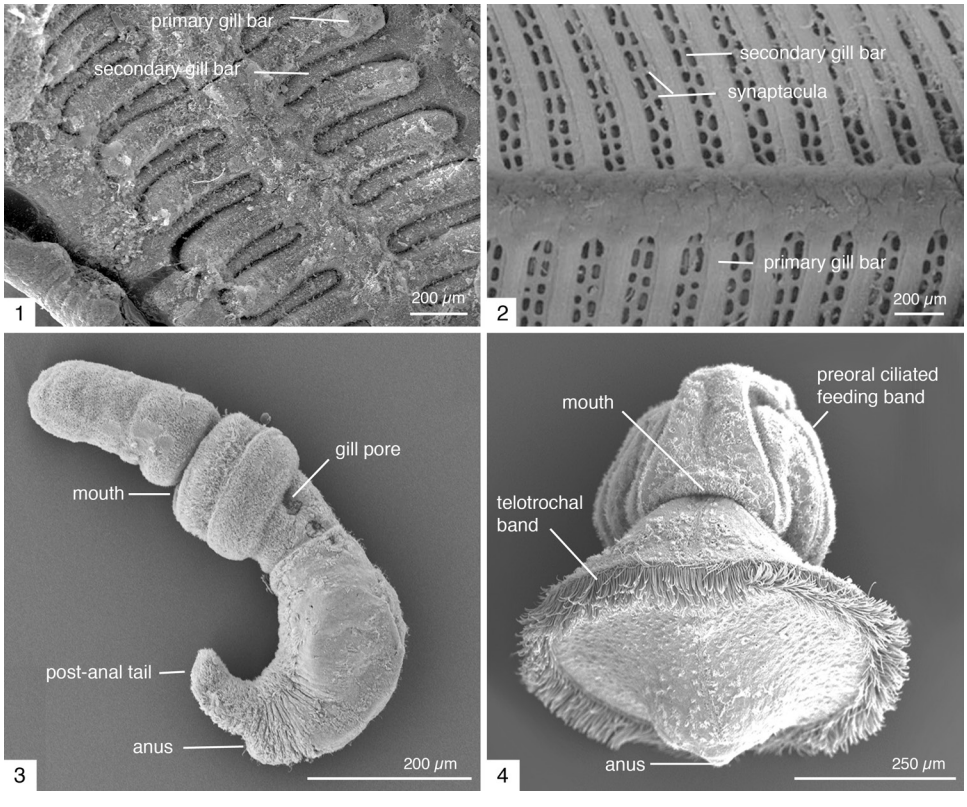


FIG. 5. SEM photos of details. *1,* Gill region of *Harrimania planktophilus* CAMERON, 2002b; *2,* gill region of *Ptychodera* sp.; *3, Saccoglossus kowalevskii* AGASSIZ, 1873 at the three-gill pore stage, showing a typical harrimaniid juvenile post-anal tail; *4,* posteriofrontal view of a tornaria larva of *Schizocardium* sp., showing the swimming telotrochal band (all, new).

out-pockets of the gut that open to the exterior by paired dorsolateral pores. Nothing is known of torquaratorid development, but the exceptionally large egg size (OSBORN & others, 2012; PRIEDE & others, 2012) hints that development is direct, via a loss of a feeding tornaria, parallel to the ontological loss of the larva in the line to modern harrimaniids.

Asexual reproduction by fragmentation is widespread among enteropneusts, including ptychoderids (GILCHRIST, 1923; PACKARD, 1968; MIYAMOTO & SAITO, 2010; HUMPHREYS & others, 2010), a spengelid (URATA, IWASAKI, & OHTSUKA, 2012), and the minute harrimaniid *Meioglossus psammophilus* WORSAAE & others, 2012, which lacks males and reproduces by paratomy. Regeneration is particularly well developed in the ptychoderids, a group especially susceptible to breakage due to their larger and fragile bodies. The posterior fragments are particularly good at regeneration, although some experimentally bisected animals can regenerate new individuals from both anterior and posterior fragments (WILLEY, 1899; DAWYDOFF, 1909, 1948; RAO, 1955; TWEEDELL, 1961; PACKARD, 1968; PETERSEN & DITADI, 1971; RYCHEL & SWALLA, 2009; HUMPHREYS & others, 2010; MIYAMOTO & SAITO, 2010). The cells that participate in blastema formation and morphogenesis during regeneration have not been identified (RYCHEL & SWALLA, 2009; MIYAMOTO & SAITO, 2010).

LIFE HABITS

Acorn worms are exclusively marine and usually burrow into the sand or mud or are associated with the underside of rocks, although species have also been found entangled in kelp holdfasts (Ritter, 1900). To burrow, they penetrate the sediment using muscular peristaltic contractions of the proboscis and transport the sediment using the ciliated epidermis of the proboscis and collar.

Burrow structure varies greatly. They may be Y-shaped, with one arm forming a feeding funnel (Duncan, 1987), U-shaped (Rao, 1954), coiled (Burdon-Jones, 1950) (Fig. 6.1), sinuous, irregular (Brambell & Goodhart, 1941; Knight-Jones, 1953), poorly defined (Burdon-Jones, 1956), or absent for animals that occupy interstitial spaces (Cameron, 2002b; Worsaae & others, 2012). Most acorn worms form mucus-lined burrows (Fig. 6.1) that smell of haloindols or brominated phenols (Higa, Fujiyama, & Scheuer, 1980; Giray & King, 1997; Woodin, Walla, & Lincoln, 1987). In the absence of a burrow or in response to stress, a mucous tube may be produced (Burdon-Jones, 1952; Halanych & others, 2013). The antibiotic properties of the phenols stabilize the sediment around the burrow (Cedhagen & Hansson, 2013) and likely repel predators, such as gastropods on the coasts of Japan and South Carolina that have been known to nip the tail from defecating ptychoderids (K. Tagawa, E. E. Ruppert, personal communications). *Saxipendium* Woodwick & Sensenbaugh, 1985 cling to rocky outcroppings near hydrothermal vents (Woodwick & Sensenbaugh, 1985), and members of the deep-sea family Torquaratoridae reside on the seafloor.

Enteropneusta are mucociliary feeders that collect their food particles on the proboscis with abundant mucin and glycoprotein secretions and transport them to the mouth with cilia (Barrington, 1940; Knight-Jones, 1953; Burdon-Jones, 1962; I. M. Thomas, 1972). Many are facultative filter feeders that pump water into the mouth, then through the pharynx and gills slits using cilia that line the gill bars (Barrington, 1940; Knight-Jones, 1953; Burdon-Jones, 1962; Cameron, 2002a; Gonzalez & Cameron, 2009). Balanoglossids ingest copious amounts of sand, in some cases forming feeding funnels at the mouth of the burrow system. *Saccoglossus* extend a long proboscis from the burrow to exploit surface sediments and marine snow, sometimes forming feeding rosettes. To defecate, the worm protrudes its posterior from the burrow system and ejects the fecal casting with rapid force. These surface castings are typically the best clue that acorn worms reside below the sediment surface (Fig. 6.2).

Torquaratorids have evolved several unique traits for life in the deep sea. Most notably, they are commonly brightly colored; and, rather than residing in burrows, they are epibenthic deposit feeders (Fig. 6.3). The collar of many species is elongated into lips that are used to collect and transport sediment to the mouth (Holland & others, 2005; Osborn & others, 2012; Priede & others, 2012). Their castings form tightly wound spiral coils to wandering, switchback loops on the sea floor (Bourne & Heezen 1965; Smith, Holland, & Ruhl, 2005) (Fig. 6.3).

Trace fossils may provide some indirect evidence of acorn worms in the fossil record. See Maletz (2014a) for a review of trace fossils with possible enteropneust affinities, including ones of a spiral form. Many typical meandering deep-water trace fossils (e.g., graphoglyptid traces, *Nereites* ichnofacies) may be explained as mucus-coated fecal casts produced by enteropneusts. The gut contents act as ballast, and when voided, the worms may drift through the demersal zone (Smith, Holland, & Ruhl, 2005; Osborn & others, 2012; Holland, Kuhnz, & Osborn, 2012). This adaptation allows for economical, long-distance movements to a new feeding site in an environment where food is typically heterogeneous and limited (Osborn & others, 2012; Jones & others, 2013).

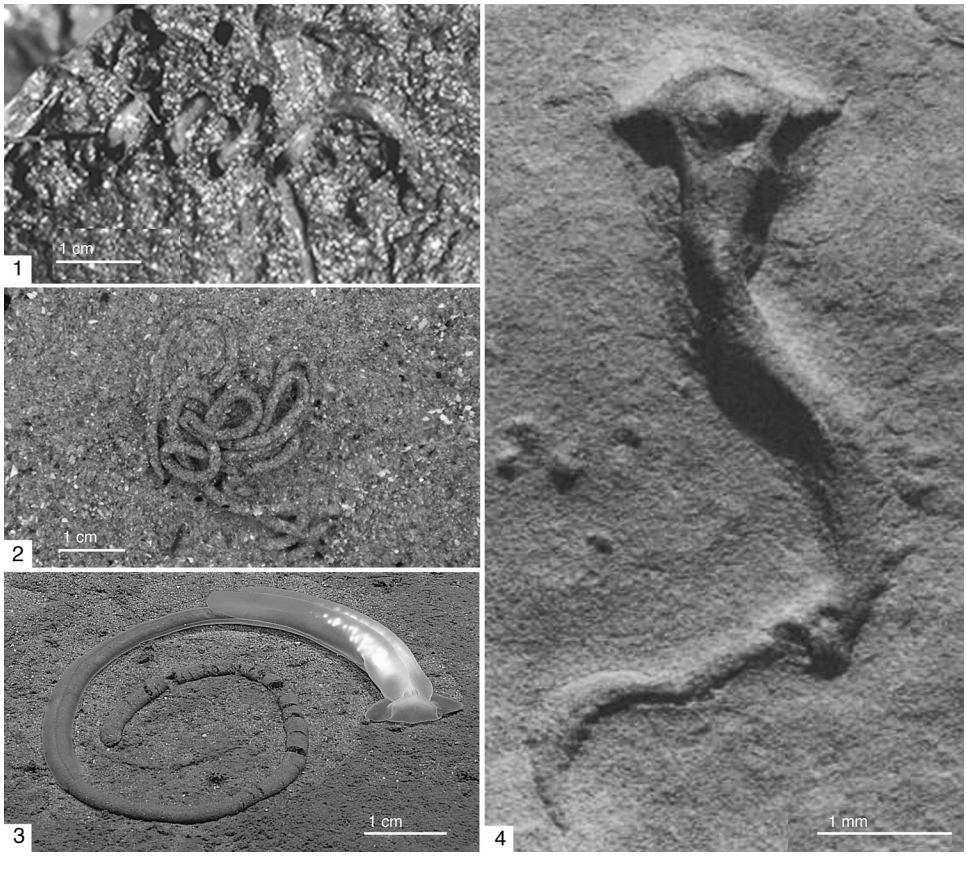


Fig. 6. Enteropneust traces. *1,* Helical-shaped burrow of *Saccoglossus bromophenolosus* King, Giray, & Kornfield, 1994, Willapa Bay, Washington, USA, exposing the brominated lining of the burrow (new, photo, M. K. Gingras); *2,* fecal casting of *Saccoglossus pusillus* Ritter, 1902 (new); *3*, fecal trail of *Tergivelum* sp? (photo courtesy of NOAA Office of Ocean Exploration and Research); *4*, resting trace of torquaratorid enteropneust (Twitchett, 1996, fig. 2.1). Color version of *1–3* in *Treatise Online* 109.

Two species of *Glandicepts* Spengel, 1893 from the west Pacific swim by flattening the trunk in a dorsoventral aspect and then undulate and turn as the worm ascends to the sea surface (Spengel, 1909; Yoshimatu & Nishikawa, 1999; Urata, Iwasaki, & Ohtsuka, 2012). This behavior does not appear to be coordinated with spawning (Urata, Iwasaki, & Ohtsuka, 2012). An unusual feature of some ptychoderids is their ability to produce light when stimulated (Kuwano, 1902; Crozier, 1917; Harvey, 1926; Rao, 1954). This luminescence is neurally mediated and appears to be intracellular, though luminous slime is also produced (Baxter & Pickens, 1964). The role of swimming and bioluminescence in acorn worms is unknown.

EVOLUTION

The embryologist Bateson (1884, 1885a) studied the direct-developing acorn worm *Saccoglossus kowalevskii* Agassiz, 1873 and concluded that the notochord, gill slits, collar nerve cord, and mesoblast development were comparable to amphioxus and therefore regarded enteropneusts as sister to chordates. Earlier, Metschnikoff (1869) studied the development of the genus *Balanoglossus* Delle Chiaje, 1829 and noted

many similarities of the tornaria to echinoderm larvae, so regarded hemichordates as sister taxon to echinoderms, a superphyletic group that he called Ambulacraria. With the advent of modern cladistics and phylogenetic methods, early phylogenies were consistent with these early ideas that envisioned the deuterostome ancestor as either a sessile tentaculate filter-feeding organism similar to a pterobranch (Romer, 1967) or to a dipleurula larva (Garstang, 1928). This dichotomy, and the polyphyletic relationship of enteropneusts (as sister to chordates) and pterobranchs (allied with echinoderms), persisted for nearly a century (Gee, 1996; Holland, Holland, & Holland, 2015; Lowe & others, 2015; Satoh, 2016; Peterson & Eernisse, 2016). These hypotheses have fallen out of favor, replaced by the hypothesis that the deuterostome ancestor was a free-living worm with a pharynx perforated with gill slits, used in filter feeding—similar to a modern enteropneust (e.g., Cameron, Garey, & Swalla, 2000; Cameron, 2002b; Lowe & others, 2015; Satoh, 2016). This hypothesis is consistent with an extensive morphological phylogeny for hemichordates (Cameron, 2005) and current molecular phylogenies, which regard Enteropneusta and Pterobranchia as sister taxa and the monophyletic Hemichordata as sister to the Echinodermata, together forming the Ambulacraria (Fig. 7) (Winchell & others, 2002; Peterson & others, 2013; Cannon & others, 2014; Telford & others, 2014; Simakov & others, 2015).

The class Enteropneusta consists of three major clades, one comprised of the three families Ptychoderidae, Torquaratoridae, and Spengelidae; the monophyletic Harrimaniidae (Osborn & others, 2012; Cannon & others, 2014); and the stem group Cambrian fossils (Fig. 7). According to a molecular clock estimate based on the genomes of *Ptychodera flava* Eschscholtz, 1825 and *Saccoglossus kowalevskii,* the three-family clade and Harrimaniidae clade diverged 373 million years ago (Simakov & others, 2015). Among the larger three-family clade, Spengelidae is sister to the Ptychoderidae and Torquaratoridae (Cameron, 2005; Osborn & others, 2012; Cannon & others, 2014). Osborn and others (2012), sequenced 25 torquaratorids and found them to be a monophyletic sister group to the Ptychoderidae. Based on two unidentified specimens, Cannon and others (2014) suggested that the Torquaratoridae are nested within the family Ptychoderidae (i.e., ptychoderid paraphyly). Torquaratorids have several unique morphological adaptations to life in the deep sea that are absent from ptychoderids. Interestingly, these adaptations did not evolve by parallelism in the deep-sea acorn worms *Glandiceps abyssicola* Spengel, 1893 (Spengelidae) (Holland & others, 2013), *Ritteria* Deland & others, 2010, nor *Saxipendium* (Harrimaniidae) (Deland & others, 2010; Holland, Osborn, & Kuhnz 2012).

The family Harrimaniidae is monophyletic and sister to the three-family clade (Fig. 7). Within the Harrimaniidae there are three clades that differ in the arrangements of their proboscis musculature (Deland & others, 2010). *Saxipendium*, a genus previously assigned to the monospecific family Saxipendidae, has been reclassified as a harrimaniid based in part on the shared presence of diffusely arranged proboscis musculature with *Mesoglossus* Deland & others, 2010 and *Ritteria*. The proboscis muscles of *Saccoglossus* are arranged in concentric rings, whereas radially arranged muscles are the ancestral acorn worm state (Deland & others, 2010).

The three-family clade and Harrimaniidae clade, inclusive of their fossil species, together comprise the crown Enteropneusta and diverged from a common ancestor approximately 373 million years ago (Fig. 7). Neither clade can be regarded as ancestral or derived. Each of the clades (as well as each family and species) exhibits ancestral and derived traits, although in general, the evolution of harrimaniids is characterized by losses of tornaria larval traits, whereas that of ptychoderids is characterized by gains of adult complexity. Harrimaniidae develop via a swimming, non-feeding, ciliated larva that

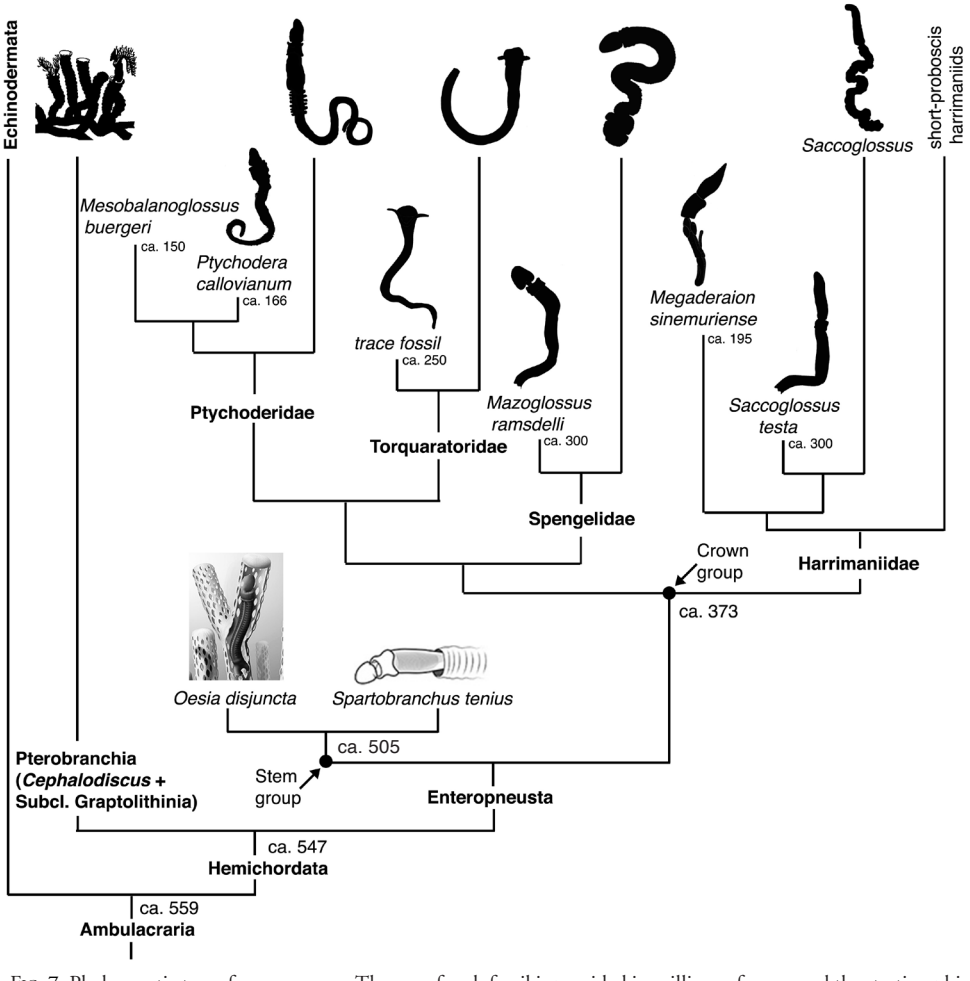


FIG. 7. Phylogenetic tree of acorn worms. The age of each fossil is provided in millions of years, and the stratigraphic details are provided in the text. Neither the tree branch lengths nor the worm silhouettes are to scale. The age of the Ambulacraria, Hemichordata, and crown group are molecular clock estimates from SIMAKOV & others (2015) (adapted from Cameron, 2016).

swims with a telochrochal ciliated band—an acorn worm innovation. The harrimaniid larval telotroch suggests that the tornaria larva was lost in this family.

The modern families are a crown group clade with respect to the Cambrian fossil stem group, which includes *Oesia disjuncta* and *Spartobranchus tenuis* (Fig. 7). These 505 million-year-old fossils are the closest representatives of the ancestral acorn worm condition, and in most respects, they have a harrimaniid-like body plan. The Cambrian fossils lack hepatic sacs, genital wings, and synaptaculae that bridge the primary and secondary gill bars that characterize ptychoderids and the spengelids *Spengelia* WILLEY, 1898 and *Schizocardium*. Thus, this trait evolved by parallelism in Cephalochordata (Fig. 5.1–5.2). Tubes are unique to stem enteropneusts. Those of *Oesia disjuncta* are fibrous (Fig. 8.1), and those of *Spartobranchus tenuis* sometimes branch (Fig. 8.2). Dozens of the *O. disjuncta* and approximately one-quarter of the *S. tenuis* specimens are associated with tubes, suggesting a facultative tubicolous habit (CARON, CONWAY

Morris, & Cameron, 2013; Nanglu & others, 2016). The tubes are interpreted as a homologue to pterobranch tubes, abandoned on the internode branch to the crown enteropneust clade.

PALEONTOLOGY

Fossils of the soft-bodied enteropneusts are rare and typically occur in Konservat-Lagerstätten. The oldest of these are the Cambrian fossils *Oesia disjuncta* Walcott, 1911 and *Spartobranchus tenuis* (Walcott, 1911) from the Burgess Shales of British Columbia, Canada and date to approximately 505 million years ago. *O. disjuncta* is abundant in the Raymond Quarry and the Marble Canyon Quarry (see p. 191, Fig. 116,*2*). Its body is dominated by a broad and long pharynx that extends to nearly the posterior end of the animal. There is no appreciable intestine. A few of the specimens have what appears to be a posterior grasping appendage. Based on these unusual traits, Nanglu and others (2016) speculated that it may be a basal hemichordate, but here it is allied with *S. tenuis* in the stem Enteropneusta with which it shares tubes and a similar age. *O. disjuncta* occupied tubes that were formerly classified as the algae *Margaretia* Walcott, 1931. The tubes are cosmopolitan, comprised of woven fibers that form a sediment anchor basally and project into the water column (Fig. 8.1). The large pharynx, tube-dwelling habit, and the lack of sediment in the gut suggest it was an epibenthic filter feeder. *S. tenuis,* from the Walcott Quarry, has a body plan that resembles that of a modern harrimaniid worm, including an extensive pharynx followed by a vermiform, unembellished intestine (see p. 191, Fig. 116,*1a–b)*. It occupied infaunal tubes that could tear, although fibers are not apparent. The discovery of a torquaratorid inside a mucous tube has led to the idea that *S. tenuis* was a member of the family Torquaratoridae (Halanych & others, 2013; Cannon & others, 2014). This idea is rejected because *S. tenuis* lacks all diagnostic torquaratorid traits, mucus does not fossilize (Nanglu, Caron, & Cameron, 2015), and the Cambrian fossils predate the origin of the crown enteropneusts (Simakov & others, 2015). *S. tenuis* was probably a facultative filter and deposit feeder. The tubes of Cambrian acorn worms provide evidence of a link to the tubarium of pterobranchs, including graptolites (Caron, Conway Morris, & Cameron, 2013; Nanglu & others, 2016).

Following the Cambrian, more than 200 million years passed before the next fossil acorn worms appeared during the Carboniferous, and after the divergence of the modern families at approximately 373 million years ago (Simakov & others, 2015). Though a precarious exercise, the Carboniferous, Triassic, and Jurassic acorn worms have been assigned to the four modern families: Harrimaniidae, Spengelidae, Ptychoderidae, and the deep-sea Torquaratoridae (Cameron, 2016). *Mazoglossus ramsdelli* (see Bardack, 1985, 1997; Maletz, 2014a) and *Saccoglossus testa* Cameron, 2016 are from the Mazon Creek fauna, Illinois, USA (~307–309 million years ago). *M. ramsdelli* Bardack, 1997 has a wide anterior trunk suggesting a well-developed pharynx (see p. 193, Fig. 117,*3*). Gill pores are reported (Bardack, 1985), but having viewed all of the specimens to date, this author was unable to detect them. The enlarged gonadal-branchial region and absence of gonadal wings suggest it was a member of the family Spengelidae (Cameron, 2016). The two *S. testa* specimens, also from Mazon Creek, are located next to each other in a single concretion (see p. 193, Fig. 117,*1*). They possess a long proboscis and therefore likely represent a re-emergence to surface deposit feeding. The proboscis of living saccoglossids are aposomatically colored—usually orange, red, or peach—and chemically defended. The Mazon Creek fauna is replete with predators including horseshoe crabs, sea scorpions, crustaceans, a shark, and the Tully monster (McCoy & others, 2016; Sallan & others, 2017), so, while somewhat speculative, chemical defense and

aposomatic colors may have evolved as early as *S. testa* (Cameron, 2016).

The next evidence of an acorn worm is a resting trace fossil from the Lower Triassic Werfen Formation of northern Italy (Twitchett, 1996) (Fig. 6.4). It has collar lips that extend laterally and a pharynx that narrows posteriorly, characteristic of the Torquaratoridae, a family of surface-dwelling, pelagic deep-sea acorn worms (Holland & others, 2005; Priede & others, 2012). *Megaderaion sinemuriense* Arduini, Pinna, & Teruzzi, 1981 is from the Sinemurian (Lower Jurassic) strata of Osteno, northern Italy (see p. 193, Fig. 117,2). It is a single, small (2 cm) specimen that lacks gonadal wings, hepatic sacs, and an enlarged branchial region, characteristic of the family Harrimaniidae. It resembles *Mesoglossus,* a harrimaniid worm with a medium-long proboscis (Deland & others, 2010).

Ptychodera callovianum (Alessandrello, Bracchi, & Riou, 2004) was a ptychoderid (see p. 193, Fig. 117,*4*) from the lower Callovian (Middle Jurassic) of La Voulte-sur-Rhone, France.The youngest fossil is *Mesobalanoglossus buergeri* Bechly & Frickhinger in Frickhinger, 1999 from the lower Tithonian (Upper Jurassic) Solnhofen Limestones, southern Germany (see p. 193, Fig. 117,*5*). It is assigned to the Ptychoderidae due to its length (68.8 cm) and enlarged genital wings, but the proboscis preservation is poor and the presence of bristles in the pharynx (Frickhinger, 1999) suggest that it was not an acorn worm.

See p. 190–194 for Enteropneusta systematic descriptions.

FUTURE RESEARCH

In the intervening years since the most recent edition of the graptolite *Treatise* (Bulman, 1970) in which only a short note on the Enteropneusta appeared, 22 new, living enteropneust species have been described, and with it, their zoogeographic range is currently better appreciated (see especially, Cameron, Deland, & Bullock, 2010), particularly with respect to their abundance in the deep sea (Osborn & others, 2012; Pried & others, 2012; Cannon, Swalla, & Halanych, 2013). Although fossil enteropneusts were unknown to Bulman (1970), seven fossil acorn worm species are now known to extend from the Jurassic to the Cambrian periods. Fine details of cellular ultrastructure (see especially Pardos & Benito, 1990) have been brought to light, contributing to a better appreciation of the functional morphology of the group. Surprising observations have been made on their life habits. Interest in the molecular developmental of the group has revealed body plan patterns conserved with their common ancestor, chordates (Lowe & others, 2003; Lowe & others, 2006). The current phylogeny is robust, with broad taxonomic sampling (Cannon & others, 2014), with the exception of the family Spengelidae. The genomes of *Saccoglossus kowalevskii* and *Ptychodera flava* have been sequenced, providing a tremendous resource for future investigations (Tagawa, 2016; Simakov & others, 2015). The conserved linkage, or micro-synteny, of transcription

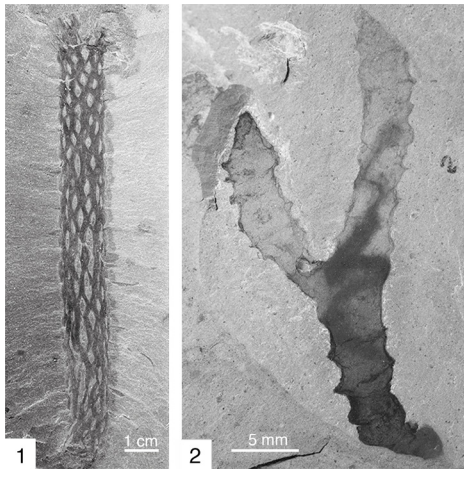


Fig. 8. Tubes of Cambrian fossil acorn worms. *1,* spirally arranged pores perforate the tube of *Oesia disjuncta* Walcott, 1911, ROM 63716 (Nanglu & others, 2016, fig. 4a); *2,* branching tubes of *Spartobranchus tenuis* (Walcott, 1911), ROM 57170 (Caron, Conway Morris, & Cameron, 2013, fig. 2f). Color version, *Treatise Online* 109.

factors involved in gill development have been revealed (Gillis, Fritzenwanker, & Lowe 2012; Simakov & others, 2015). Similar studies on other organ systems will come, and higher levels of conserved linkages, or macro-synteny, may be expected. The genes involved in the biosynthesis and degradation of the sialic acid molecule, a deuterostome synapomorphy (Cameron, 2005), includes nine that arrived as transposons from a prokaryote or protist donor (Simakov & others, 2015). In their review of the development of the group, Kaul-Strehlow and Röttinger (2015) emphasized a need for more investigations on the development of the nervous and muscular systems, and one might add the coelomic, reproductive, and immune systems. There is a single paper on the immunodefense of the group (Tassia, Whelan, & Halanych, 2017). Interest in acorn worm biology has grown—affirmed by the 1st International Hemichordate Meeting, Hopkins Marine Station at Stanford University, December 2016—and the future looks bright.

Future fruitful avenues of research may include: 1) A more extensive sampling of South America, Africa, Asia, as well as deep water worldwide where many species remain to be found. 2) The burrow shape of acorn worms varies tremendously and there seems to be some genus-specific patterns. The fossil record of burrow trace fossils is rich (Bromley, 1996; Seilacher, 2007; Gingras & others, 2008) and may provide some insight on the origin of modern acorn worm genera. Horst (1940) suggested that an enteropneust similar to *Saccoglossus* is responsible for the spiraling trace fossil, *Gyrolithes* Saporta, 1884. This, as well as changes to burrow structure—depending on season or sediment parameters—should be explored. 3) Intensive sampling of many individuals within a species is needed to assess the amount of intraspecific variation, in the structure of the heart-kidney coelomic process, the collagenous gill bars and nuchal skeleton, the ossicles, as well as developmental genes—because variation is what selection works on. Such studies are rare, the most comprehensive study being that of the many *Ptychodera flava* variants from the Indian Ocean (Punnett, 1906). 4) Do closely related species have similar developmental processes—as might be expected—or is the variation substantive, as in the direct developer *Saccogossus kowalevskii* to the tornaria of *Schizocardium californicum* (see Gonzalez, Uhlinger, & Lowe, 2017)? Experimental molecular developmental approaches that include gene knock-down (Tagawa, 2016), RNAi, CRISPR, and single-cell sequencing (Klein & others, 2015), will provide more robust and nuanced tests of homology. 5) Nearly nothing is known of the post-juvenile development of acorn worms, but the powerful potential of these investigations is that the ontological development can be compared with the paleontological equivalents, particularly with the Cambrian forms that are abundant and preserve exquisite details of extracellular matrix structures, including gill bars and tubes. 6) Nothing is written on the quantitative genetics, the population-based studies of continuously varying characters, nor how these characters respond to selection. 7) Slightly more is known about the neural physiology (Pickens, 1970; Cameron & Mackie, 1996) and respiratory physiology of acorn worms (Azariah, Ismail, & Najib, 1975; Ditadi, Mendes, & Biancconcini, 1997). Is the physiological role of the gill slits respiratory as the name Enteropneusta—Greek for gut-breathing—implies, or is the primary role of the acorn worm gills in ammonia exchange or acid-base regulation? Even less is known of embryonic and larval physiology and behavior. Clearly, much more research awaits.

INTRODUCTION TO THE CLASS PTEROBRANCHIA

Jörg Maletz and Christopher B. Cameron

The class Pterobranchia Lankester, 1877 is comprised of sedentary to planktic organisms with communal or colonial zooids that first appeared during the Cambrian and includes extant species, such as *Rhabdopleura* Allman in Norman, 1869a. They are present worldwide in marine environments. Pterobranchia zooids are divided into three body regions: preoral lobe (cephalic shield), collar, and trunk. The collar extends to form one or more pairs of arms, each bearing double row of ciliated tentacles used in feeding. An elongated trunk serves as an interconnection between zooids in colonial forms. Most species feature external organic housing referred to as the tubarium. Tubaria have been preserved in the fossil record and, thus, their structures form the basis for the classification of the Pterobranchia.

The Pterobranchia can be differentiated into two main groups: the pseudocolonial Cephalodiscida and the entirely colonial Graptolithina. The Cephalodiscida include organisms with separate individuals, but clonal, asexually produced zooids are connected to their mother individuals when immature (Fig. 9.1). After reaching maturity, they may separate from their mother zooid and lead an independent life in their communal housing constructions. There is no apparent difference between sexually and clonally produced mature zooids in the Cephalodiscida.

The truly colonial Graptolithina start their colonies from a sexually produced mother zooid, the sicular zooid, comparable to the ancestrula of the Bryozoa. All subsequently produced clonal zooids are interconnected for life through the stolon system (Fig. 9.2). Apart from extinct benthic and planktic graptolites, which constitute the largest group of taxa, the Graptolithina also includes the small group of extant, benthic rhabdopleurids (Mitchell & others, 2013), that remain nearly unchanged since the Early Ordovician (e.g., Andres, 1980; Mierzejewski, 1986).

The Pterobranchia possess a number of special developments and features that set them apart from the rest of the phylum Hemichordata—namely, small-sized, individual zooids with a specialized anatomy, a complex cycle of sexual and asexual reproduction, and most importantly, from a fossil point of view, the secretion of a special housing structure, the tubarium (Fig. 9.2). In short, the Pterobranchia can be described as tube-building, communal to colonial, marine organisms with a benthic to planktic lifestyle and a complex sexual and asexual cycle of reproduction.

EVOLUTIONARY ORIGINS

Latest interpretations (e.g., Cannon & others, 2014; Nanglu, Caron, & Cameron, 2015; Simakov & others, 2015) indicate monophyly of the Pterobranchia relative to the Enteropneusta (Fig. 10). Information on the early evolution of the Pterobranchia is scarce and can only be estimated from the record of a few early to middle Cambrian fossil tubarium fragments. The cladistic analysis of benthic graptolites (Mitchell & others, 2013) indicates a poor resolution of most groups, but the Cephalodiscida can easily be differentiated by their non-colonial development. The invariably colonial Graptolithina have the highest amount of evolutionary diversification with the planktic Graptoloidea as the geologically most important group. The Enteropneusta differ from the Pterobranchia by the position of the anus at the end of their elongated body; the Pterobranchia have a U-shaped gut with the anus positioned directly below the collar.

If these interpretations are correct, the evolution of the pterobranchs may be based on the miniaturization of the individuals associated with a simplification of their body construction and loss of complex internal

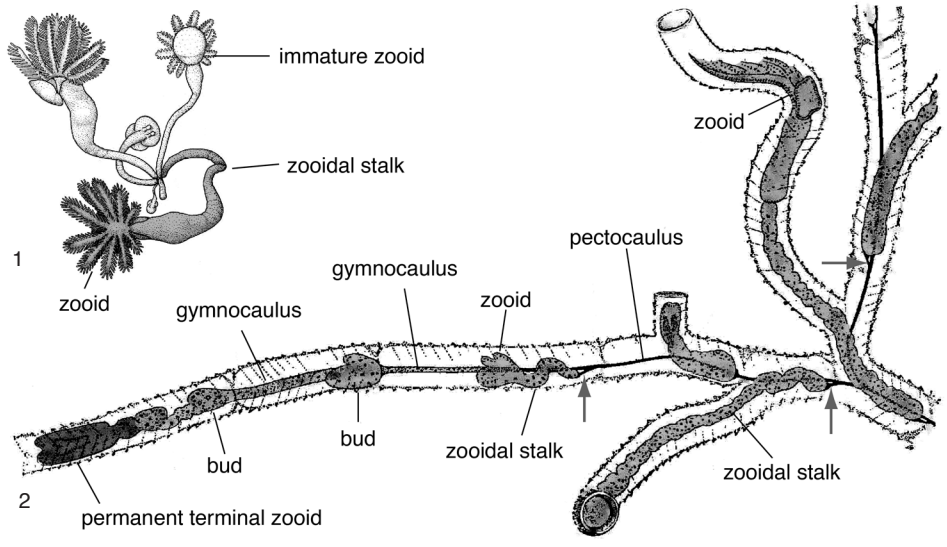


Fig. 9. Pterobranch organization. *1, Cephalodiscus gracilis* M'Intosh, 1882, zooid with juveniles (adapted from Lester, 1985, fig. 2); *2, Rhabdopleura normani* Allman in Norman, 1869a, part of tubarium with permanent terminal zooid, showing terminology of the stolon system (adapted from Ridewood, 1907, fig. 7). *Arrows* point to the short zooidal stolons of the *Rhabdopleura* zooids.

organs and, eventually, the exploration of a colonial lifestyle with the generation of numerous asexually produced members or zooids. The evolution of these characteristics and the origin of the secretion of the typical pterobranch tubarium is not clear. Many of the features of fossil zooids can only be estimated from the characters of extant taxa, as the actual organisms are almost completely unknown from the fossil record.

The miniaturization of the pterobranch zooids can be simply understood by comparing the related enteropneusts, worm-like organisms of up to 2 m in length, with the generally small pterobranch zooids (~0.6–10 mm). However, miniature enteropneusts, measuring less than 1 mm long, have also been discovered (Worsaae & others, 2012). Cephalodiscid zooids can reach lengths of several mm and, thus, are larger than the 0.6–2 mm long rhabdopleurid zooids. The size of the zooids of the extinct taxa of the Graptolithina is more difficult to estimate (e.g., Sudbury, 1991; Rigby & Sudbury, 1995), but considering the small tubes and apertural openings in most taxa, they would not have been larger than the zooids of a modern *Rhabdopleura*.

The construction of the pterobranch tubarium can be quite complex, and details are discussed in this volume's sections on taxonomy of individual groups. The general features of both fossil and extant Pterobranchia are described in *Morphology of the Pterobranch Tubarium* (p. 29–80), first published as Maletz, Lenz, & Bates, *Treatise Online,* 2016. The evolutionary origin of the peculiar housing system of the Pterobranchia is unclear. One possibility, based on the tube-dwelling habitat of the Cambrian acorn worms *Spartobranchus* Caron, Conway Morris, & Cameron, 2013 and *Oesia* Walcott, 1911 may be that tubes are a hemichodate plesiomorphy. If this is true, these tubes were then elaborated on in the Pterobranchia and lost on the branch to the extant worms (Caron, Conway Morris, & Cameron, 2013; Nanglu & others, 2016).

Modern Enteropneusta produce mucus-lined burrows from glands on the proboscis (Nørrevang, 1965; Nanglu, Caron, & Cameron, 2015). The composition of this

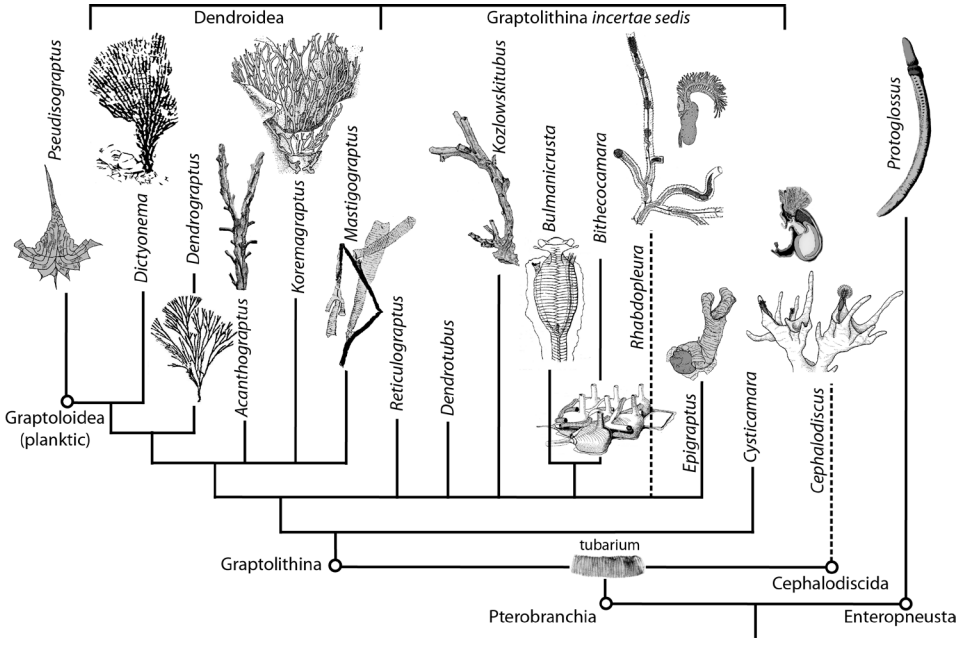


FIG. 10. Relationships of the main groups of the Graptolithina. Diagram based in part on Maletz (2014b). *Dotted lines* in diagram indicate extant members.

mucus and its possible relationship to the secretionary material of the tubaria in the Pterobranchia may be important to study in the future, especially since NANGLU, CARON, AND CAMERON (2015) suggested that the burrows of *Spartobranchus* from the Cambrian Burgess Shale were unlikely to be based on the secretion of mucus alone, because these fragile burrows would then have easily been destroyed. The tubes of *Oesia,* previously described as the alga *Margaretia,* were fibrous but unlike pterobranch tubes, were permeated with holes (NANGLU & others, 2016).

In the Enteropneusta, the proboscis is completely covered with the mucus secreted from its glandular cells, whereas in the Pterobranchia, the glandular secretion is limited to a special area on the proboscis, the cephalic shield (DILLY, 1986, 1988). In *Rhabdopleura,* secretion of the dome of the colony occurs by secretory cells of the ventral epidermis of the larva, and this site probably becomes the ventral surface of the cephalic shield in the later ontogeny of the zooid (LESTER, 1988a, 1988b). There is no information on mucus production in modern pterobranchs. Interestingly, non-fusellar tissue occurs in some rhabdopleurids (e.g., KULICKI, 1971; MIERZEJEWSKI, 1986; MIERZEJEWSKI & KULICKI, 2003a) and may be indicative of early development of tubarium secretion.

PTEROBRANCH ZOOIDS

The zooidal anatomy of the Pterobranchia is known from the few extant taxa and has been described in detail. Pterobranch zooids (Fig. 11–12) are divided into three parts: the cephalic shield or proboscis (protosome), the collar bearing the arms (mesosome), and the trunk (metasome). A slender, flexible zooidal stalk is located at the end of the trunk and connects the individual zooids of the colonies to the stolon system, or pectocaulus, in the Graptolithina (Fig. 9.2), and to a common, motile, ciliated disk in most Cephalodiscida (Fig. 9.1). The zooidal anatomy of the Cephalodiscida (*Cephalodiscus* M'INTOSH, 1882; *Atubaria* SATO, 1936) and Graptolithina (*Rhabdopleura*) differs in a number of modifications of the body, such as the number and development

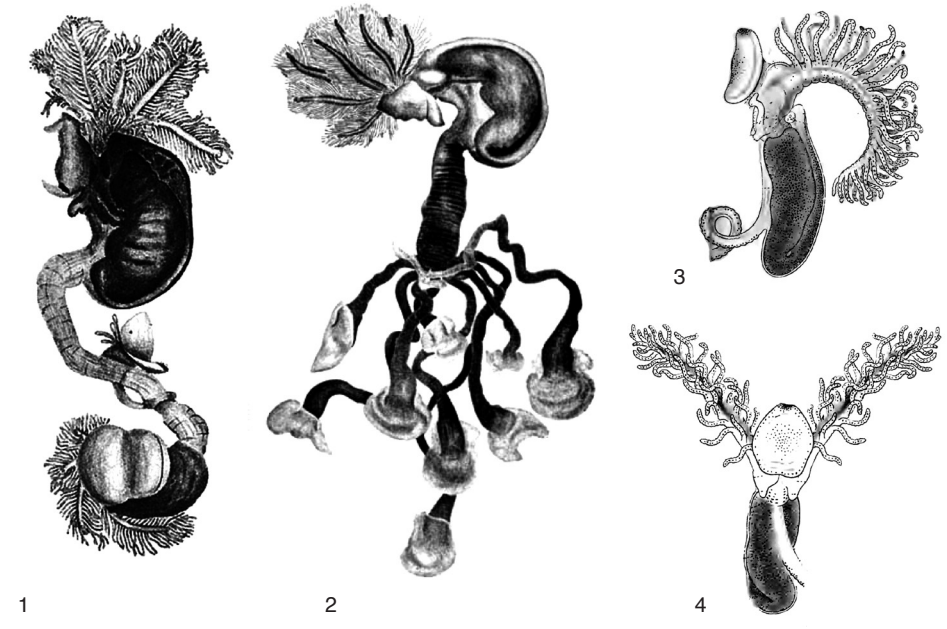


FIG. 11. Pterobranch zooids. *1, Cephalodiscus* (*Acoelothecia*) *kempi* JOHN, 1931, mature zooid with two buds in different stages of development (John, 1931, pl. 35,*2*); *2, Cephalodiscus* (*Cephalodiscus*) *fumosus* JOHN, 1931, mature zooid with at least nine budding individuals (John, 1931, pl. 35,*3*); *3–4, Rhabdopleura normani* ALLMAN in NORMAN, 1869a, lateral (*3*) and ventral (*4*) view of zooids (adapted from Sars, 1874, pl. 1,*1–2*).

of the arms and gonads and the presence or absence of gill pores. Other differences appear in the size of the zooids and their interconnections.

MASTERMAN (1897, 1898a, 1898b, 1900, 1903), HARMER (1905), ANDERSON (1907), SCHEPOTIEFF (1907a, 1908), JOHN (1932), DILLY, WELSCH, and REHKÄMPER (1986a, 1986b, 1986c) and WELSCH, DILLY, and REHKÄMPER (1987) described the anatomy of the zooids of *Cephalodiscus* in some detail. HORST (1939) and HYMAN (1959) provided an overview of the knowledge. STACH, GRUHL, and KAUL-STREHLOW (2012) described the central nervous system. The mature zooids of *Cephalodiscus* (Fig. 11.1–11.2) are ~2–14 mm long and bear four to nine pairs of tentaculated arms on the dorsal side of the collar. The cephalic shield is flexible and possesses a characteristic red pigment line parallel to the posterior edge. The arms form two curved rows on the dorsal side of the collar, whereas the ventral side bears the mouth of the zooid. The arms are extensions of the collar coeloms and have ~25–50 paired tentacles. A terminal glandular or tentacular knob is present in some species of *Cephalodiscus*. The trunk consists of a wide, saclike, anterior part that culmimates in a slender stalk used for attachment. The U-shaped gut and the gonads are located in the trunk (Fig. 12.2). A single pair of gill pores are behind the posterior border of the collar. The zooidal stalk is hollow and has a ciliated adhesive disk at the end, with which the zooid attaches itself to the tubarium. This is also where the asexually produced buds appear (Fig. 11.1–11.2). The zooids of *Cephalodiscus* grow attached to the adhesive disk until they mature (Fig. 11.2), and then they may separate and live free. After maturation, they are also able to produce new zooids by asexual budding.

The zooids of *Atubaria* (Fig. 12.1) are similar to those of *Cephalodiscus* but differ in the development of the arms. The anterointernal arm pair bears a long, tentacular rod distally, covered with granules similar to the

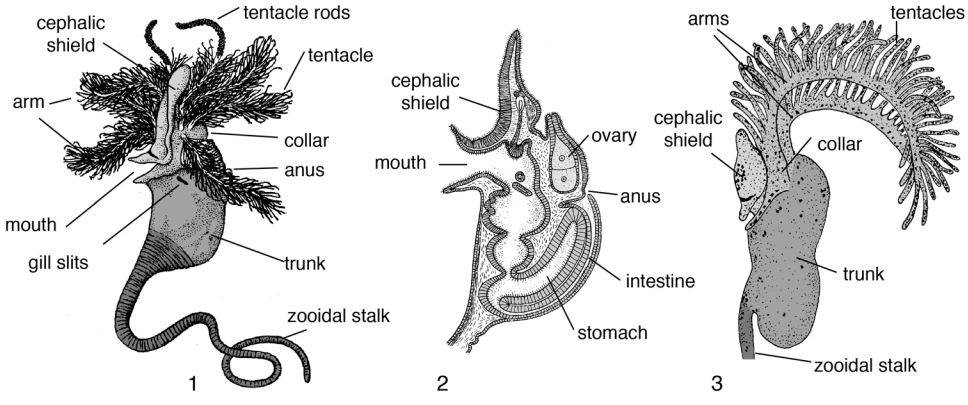


FIG. 12. Zooidal anatomy. *1–2, Atubaria heterolopha* SATO, 1936; *1,* single zooid (adapted from Komai, 1949, fig. 1); *2,* sagittal section of the body of a female zooid (adapted from Komai, 1949, fig. 2); *3, Rhabdopleura normani* ALLMAN in NORMAN, 1869a, single zooid with part of zooidal stalk (adapted from Hyman, 1959, fig. 67C).

clubs on the arms of certain *Cephalodiscus* species. Another difference is the lack of an adhesive disk at the end of the stalk. All known zooids of *Atubaria* are female (SATO, 1936). Nothing is known on the lifestyle and reproduction of this taxon. According to SATO (1936), the two different zooidal forms can be identified as immature and mature specimens, suggesting that the juveniles separate at an early stage from their mother zooid or do not represent clonally reproduced individuals.

Details of the zooidal anatomy of *Rhabdopleura* (Figs. 11.3–11.4) are provided by LANKESTER (1884), SCHEPOTIEFF (1904, 1906, 1907b, 1909), LESTER (1988a, 1988b), and MAYER and BARTHOLOMAEUS (2003). The mature zooids of *Rhabdopleura* are ~1 mm or less in length. They are organized similarly to *Cephalodiscus* and are differentiated into cephalic shield, collar, and trunk regions (Fig. 12.3). The cephalic shield is oval and has a central glandular region for the secretion of the tubarium. The red pigment strip is sometimes present as in *Cephalodiscus*. The collar of *Rhabdopleura* bears a single pair of arms with paired tentacles, and the mouth is on the shorter ventral side.

The zooids of a *Rhabdopleura* colony are interconnected for life through the stolon system or pectocaulus (Fig. 9). A single zooid, the sicular zooid, is the founder of the colony and is the only sexually produced zooid. All subsequent zooids develop asexually on the advancing stolon of the colony. Thus, contrary to the situation in *Cephalodiscus,* each zooid of *Rhabdopleura* is only able to produce a single additional zooid through asexual budding.

HYMAN (1959) provided an overview on the internal anatomy of the pterobranchs, but details are not discussed herein, as the zooidal anatomy is not known from the fossil record and unlikely to be preserved in fossil specimens. The zooids are either male, female, or neuter, but hermaphroditic ones also exist. The most important difference in the anatomy between enteropneusts and pterobranchs is easily visible in the form of the gut. The small pterobranch zooids have a U-shaped gut and the anus is below the collar on the dorsal side of the body, opposite to the mouth (Fig. 12.2).

The sexes are separate in *Cephalodiscus* but impossible to differentiate externally. Male and female zooids may occupy a single tubarium, but tubaria may also include a single sex. Hermaphroditic zooids, in which one gonad is female and the other is male, are not uncommon. HARMER (1905) described *Cephalodiscus sibogae* HARMER, 1905 with neuter and male zooids, but no females. The neuter zooids appear to

normally have four pairs of tentaculate arms and lack gonads, whereas the males have two arms without tentacles, a vestigial digestive tract, and a trunk filled with two large testes.

The stolon system (Fig. 9) is a defining feature of the colonial Graptolithina and connects the individual zooids. The Cephalodiscida do not possess an equivalent of the soft stolon or gymnocaulus, nor do they have the black stolon or pectocaulus (Schepotieff, 1906) of the Graptolithina. Instead, buds develop from a common point or ciliated disk (Fig. 9.1). Cephalodiscid zooids attach to this point by a flexible, extendable zooidal stalk. In *Rhabdopleura,* the zooidal stalk connects the stolon to a gymnocaulus or pectocaulus. These can bifurcate and have the potential to differentiate and form asexual zooid buds. The stolon develops from the gymnocaulus of the advancing terminal zooid in *Rhabdopleura*.

Lankester (1884) described and illustrated the stolon system of *Rhabdopleura normani* Allman in Norman, 1869a in some detail and differentiated the gymnocaulus and pectocaulus. The gymnocaulus, or soft stolon, is the flexible connection of the zooid to the black stolon or pectocaulus, a hard and inflexible structure. A short zooidal stolon as the direct connection between the zooidal stalk and the main stolon can usually be observed; the zooidal stalk is not a continuation of the main stolon (arrows in Fig. 9.2).

According to Lankester (1884), the pectocaulus develops from the gymnocaulus through the formation of a sclerotized cuticle around the gymnocaulus, which he termed the caulotheca or stalk-pipe. Lankester (1884, p. 634) differentiated between the axial stalk and the contractile stalk of the zooid, but remarked that both are "essentially the same thing." The zooidal stalks differ considerably from the gymnocaulus behind the permanent terminal zooid of the Rhabdopleura colony because they are unable to produce new buds for zooidal growth (Fig. 9.2). Therefore, the zooidal stalk is separated here from the gymnocaulus.

Urbanek and Dilly (2000, p. 201) described the stolon of *Rhabdopleura* as a thread of soft tissue produced by the terminal zooid through an extension of its stalk. The gymnocaulus produces a chain of buds behind the terminal zooid, thus forming the colonial organism. According to Urbanek and Dilly (2000), the stolonal threads have distinct diaphragm complexes from which the zooids develop. The origin and construction of these diaphragm complexes are unclear, but a comparison can be made to the dormant buds. These are encased completely into a thickened, pigmented wall or capsule. The diaphragm complexes are similarly constructed but have an open end. Thus, the diaphragm complex may represent a protective shell for the developing buds (see Stebbing, 1970a, p. 210; Urbanek & Dilly, 2000, p. 216). The walls of the stolon, the dormant buds, and the diaphragm complexes are constructed from crassal fabric (Urbanek & Towe, 1974); thus, they may be secreted similarly from the surface of the organism, and in this respect, differ from the tubarium secretion. Contracted specimens of *Rhabdopleura compacta* Hincks, 1880a have the coiled gymnocaulus within the diaphragm complex (Urbanek & Dilly, 2000, p. 216), clearly indicating that the zooids are moving in and out of their tubes.

The development of the stolon is more complex in dendroid graptolites with diad and triad budding, but details are only known from a few taxa (e.g., Bulman, 1945; Kozłowski, 1949, 1963; Bates & Urbanek, 2002; Saunders & others, 2009). Saunders and others (2009) described the development in *Desmograptus micronematodes* (Spencer, 1884) and presented evidence of a development similar to the diaphragm complex of *Rhabdopleura* in the dendroid graptolites. Due to the durability of the stolon system, it may be preserved in many sediments, as evidenced by numerous fragments previously identified as hydroid remains (e.g., Kozłowski, 1959a; Mierejewski, 1986; Maletz, 2014b; Muscente, Allmon, & Xiao, 2015). Studies of the fossil

record of early planktic graptolites rarely mention the presence of a stolon system (e.g., Hutt, 1974a; Legrand, 1974; Cooper & others, 1998), even though it is clear from the tubarium construction that it must have been present. Very likely, the stolon was not strongly sclerotized and, thus, was not preserved in the fossil record.

ONTOGENY AND ASTOGENY

All extant Pterobranchia from which we know any details, may have a life cycle with a double mode of reproduction—sexual reproduction resulting in a single zooid (the sicular zooid), and asexual budding that forms all subsequent zooids in the pterobranch colony (Fig. 13). The ontogeny of the zooids combines with the budding mechanism to form the astogeny of the colony or pseudo-colony. There is no information available on the ontogeny and life cycle in *Atubaria,* even though mature and immature specimens have been discovered. These are all separate individuals, and a clonal origin has not been verified. The evolutionary origin of this asexual, clonal development in the Pterobranchia is not unique in the deuterostomes but can be compared to that of the colonial tunicates. Pterobranchs are unique among animals in that the colonies may be male, female, or contain zooids of both sexes.

Details of the breeding and fertilization are incompletely known for the pseudo-colonial *Cephalodiscus*. It is not known if fertilization is internal and embryos are released from the zooid or if fertilization is external. The embryos develop in the tubarium. Within a short time, they metamorphose into a ciliated larva (Andersson, 1907, fig. 23; Hyman, 1959, fig. 63D) and hatch from the fertilization membrane. The larva was identified as a planula larva in Ramirez-Guerrero, Kocot,& Cameron (2020, p. 847), a lecithotrophic (non-feeding) larva. Schiaparelli, Cattaneo-Vietti, and Miere-jewski(2004) described a protective larval cocoon in *Cephalodiscus densus* Anderson, 1907. The larva may swim freely for a short time before it settles. At metamorphosis, probably during the free-swimming period (John, 1932, p. 201), it attains the typical zooidal shape with the stalk and the arms in a rudimentary state. When the juvenile *Cephalodiscus* finds a suitable place to establish a new colony, it settles, develops the arms and stalk, and begins to secrete its tubarium. Further development and astogenetic growth of the *Cephalodiscus* pseudocolony is by asexual budding. This asexual budding of new zooids occurs near the base of the stalk. Dilly (1985) referred to this site as a sucker, but in *Cephalodiscus gracilis* Harmer, 1905 it is a ciliated and motile pad. This common point or pad is the location of cell division and differentiation resulting in new zooidal buds (Fig. 9.1, Fig. 11.2). Dilly (2014) interpreted these *Cephalodiscus* buds as representing a colonial organism and counted up to an estimated 14 individuals, as he was unable to definitively observe individual zooids. When mature, the zooids can detach themselves from the colony, produce new zooids through asexual budding, and secrete a new pseudo-colonial tubarium.

Lester (1988a, 1988b) described in some detail the life cycle of *Rhabdopleura normani* (Fig. 13), especially the ontogenetic development of the sicular zooid (called ancestrula in Lester, 1988a) from the early larval stage onward. The uniflagellated spermatozoans are elongated, filiform (Lester, 1988a), and are probably released into the seawater. The fertilization site is not known, but may occur within the tubarium, where the eggs are kept in special brood chambers by the female zooids. The females of *Rhabdopleura normani* secrete the initial part of their individual tube, which is coiled at least 360° (Lankester, 1884; Lester, 1988a). This structure is used as a brood chamber in which the embryos hatch. The fertilized egg develops into a ciliated larva and escapes from its parental tube by squeezing itself past the female zooid and the younger embryos and then swims for as many as 24 hours before settling (Fig. 13.1). After finding a suitable place to establish a new colony,

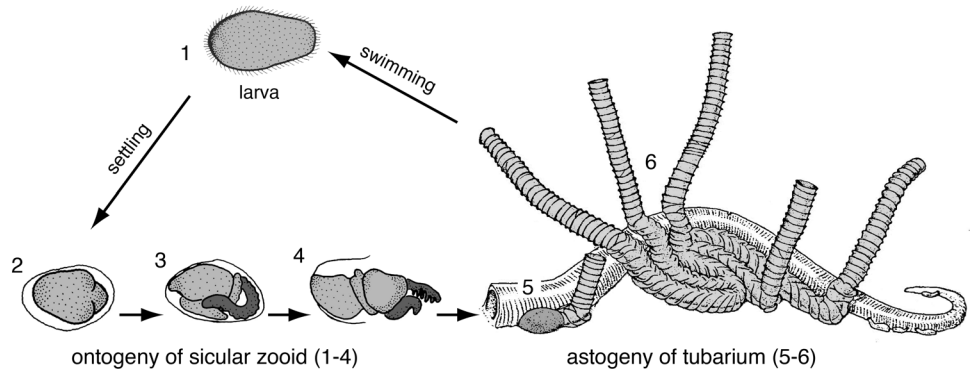


FIG. 13. The ontogeny and astogeny of *Rhabdopleura compacta* HINCKS, 1880a (adapted from Maletz, 2015, fig. 5). *Rhabdopleura* colony is attached to a tube of *Serpula vermicularis* LINNAEUS, 1767 (adapted from Stebbing, 1970b, fig. 3).

the larva secretes the prosicular dome and metamorphoses into a mature zooid (Fig. 13.2–13.4).

The mature sicular zooid attaches with its stalk on one side of the dome and produces a hole in the other side of the dome, through which it emerges to secrete the first tube. The first asexually budded zooid develops from the base of the stalk of this founding sicular zooid (LESTER, 1988a), but further development has not been observed in *Rhabdopleura normani*. A similar development can exist in *Rhabdopleura compacta*. STEBBING (1970a) described the early astogenetic development of the colony of *Rhabdopleura compacta,* and stated that the sicular zooid secretes only a few segments of a creeping tube with the typical dorsal zigzag suture before forming an erect tube with fusellar full rings and the typical collar structures. At this stage, the zooid is fully developed and begins to bud off the asexually produced zooid from the base of the gymnocaulus. This second zooid secretes a septum, separating part of the dome. After this, it breaks down the wall of the dome and secretes its own tube. Further development is not described; thus, it is unclear from what point the next bud originates and which zooid will form the permanent terminal bud.

The sexes are separate in *Rhabdopleura normani* (see LESTER, 1988a), but both may exist in a single colony together with neuter individuals as in *Rhabdopleura compacta* (STEBBING, 1970a). Typically, several sicular zooids are associated and together form intermingling colonies. Thus, it may be difficult to identify and separate individual colonies of *Rhabdopleura*. Zooids that reproduce sexually are apparently morphologically different from other zooids. They generally have reduced arms and tentacles, but also reduced inner organs, suggesting that they do not feed themselves (STEBBING, 1970a).

The life cycle of extinct graptolite taxa (Fig. 14) is expected to be similar to that of the extant *Rhabdopleura,* as all taxa are truly colonial, evidenced by the presence of the common canal connecting the individual thecal tubes (BARRANDE, 1850; MALETZ, 2015). Historically, graptolites have been considered extinct; and no modern relatives have been recognized, even though the graptolites were identified as the group most closely related to the extant *Rhabdopleura*. Therefore, the mystery of the soft-body anatomy of the graptolite zooids remained unresolved, especially because no remains of fossil graptolite zooids that reveal anatomical details have been discovered. The secretion of the graptolite tubarium has been difficult to explain, but problems have also arisen from a lack of information on the secretion of the tubaria in the extant pterobranchs *Rhabdopleura* and *Cephalodiscus*. KIRK (1972a), among others (e.g., BULMAN,

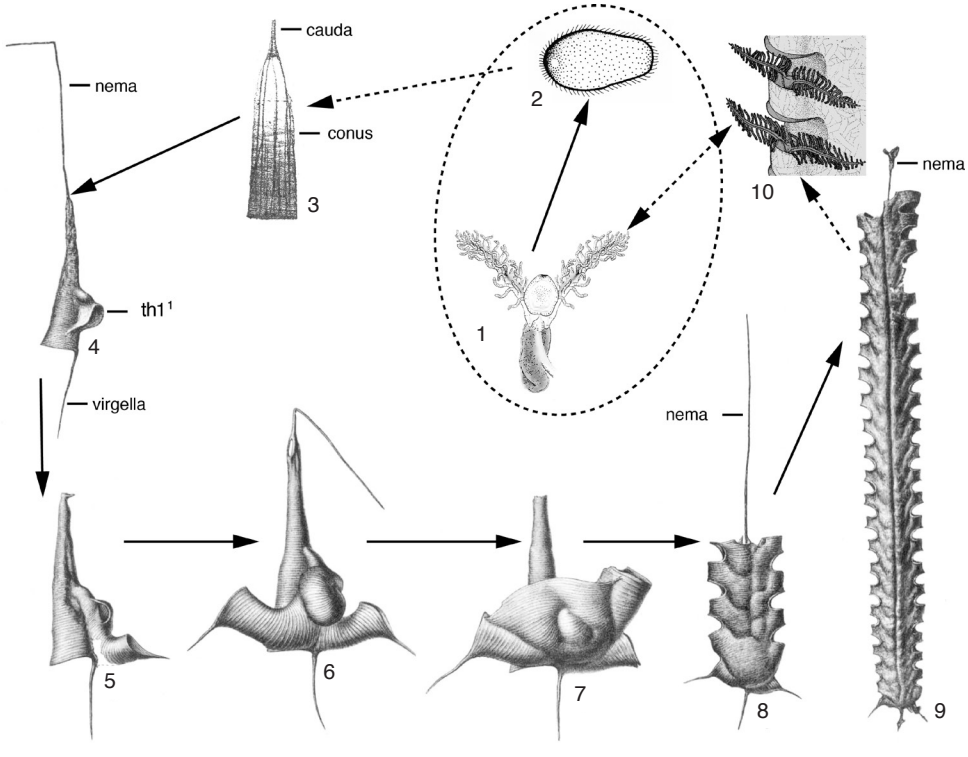


FIG. 14. Ontogeny (*1–3*) and astogeny (*4–10*) of the Graptolithina, based on the astogenetic series of tubaria of *Pseudamplexograptus distichus* (EICHWALD, 1840) (Maletz, 2015, fig. 6).

1970; RICKARDS, 1975; URBANEK, 1976), preferred the explanation that secretion of the graptolite tubarium occurs underneath a peridermal membrane. After a detailed investigation of the construction of the tubaria from fuselli and cortical tissues, CROWTHER and RICKARDS (1977), CROWTHER (1978), and ANDRES (1977, 1980) suggested a pterobranch-like zooid was responsible for the construction. BULMAN (1955, 1970) based his reconstruction of graptolite zooids on a rhabdopleurid type of zooid, and this analog has been used frequently (see ERDTMANN, 1982a; SUDBURY, 1991; UNDERWOOD, 1993; RIGBY & SUDBURY, 1995). Since the recognition of the extant genus *Rhabdopleura* as a living graptolite (MITCHELL & others, 2013), the debate has reached consensus that graptolite zooids are bilaterally symmetrical, small organisms, probably with a single pair of arms comparable to those of *Rhabdopleura*. Still, a certain variability should be considered likely for the anatomy of the zooids, although it cannot be proven from the fossil record.

LIFESTYLE

A number of researchers have observed and described the lifestyle and development of the extant Pterobranchia since the earlier appearance of works by SARS (1874), SCHEPOTIEFF (1906), BURDON-JONES (1954), and GILMOUR (1979), among others. The zooids of all pterobranchs are able to crawl out of their inhabited tubes and roam on the surface of the tubarium. Whereas the zooids of the unattached *Cephalodiscus* can glide freely inside and outside the tubaria, the zooids of *Rhabdopleura* are more restricted by their attachment to the stolon. However, the stolons can be stretched to allow considerable movement of the zooids. The zooids of *Rhabdopleura* can retract quickly into the

tubes when disturbed, but the subsequent extension is by slow, ciliary gliding. The zooids of *Cephalodiscus* and *Rhabdopleura* secrete external cortical bandages during the zooidal movements outside of the tubaria. The presence of external cortical bandages in extinct graptolite taxa indicates that this was also the case in these organisms.

Very little is known on the ecology of the various pterobranch species, even though living zooids have been observed a number of times (e.g., Andersson, 1907; Gilchrist, 1915; Rigby, 1993). Colonies of *Cephalodiscus* have been found at depths ranging from intertidal to ~650 m, attached to various substrates from remains of other organisms to rock surfaces. Species can be found from tropical to Arctic and Antarctic regions, but according to the sparse record (see Hyman, 1959, p. 177), such discoveries of cephalodiscids may be merely accidental and not indicative of their real biogeographical distribution. The zooids filter feed from the tips of their tubaria (Lester, 1985), but their dietary needs are unknown.

Rhabdopleura has been found at depths ranging from shore facies to 550 m deep (Dilly & Ryland, 1985) but appear to be most common at depths between 100–300 m from tropical to Arctic and Antarctic regions. The taxon appears to be worldwide in distribution but has rarely been found due to its small size and, therefore, may easily be overlooked. For example, only in relatively recent times, have rhabdopleurids been discovered in the Mediterranean Sea (Laubier, 1964, 1966). Specimens are usually attached to rocks, corals (*Lophelia*), or other living or dead remains of organisms, but they can also hide under empty shells, as is often the case with *Rhabdopleura compacta* (Stebbing, 1970b).

THE FOSSIL RECORD

The fossil record of the Pterobranchia relies completely on the presence of the sclerotized tubaria, as the tiny zooids are not preservable (Maletz, 2014a; Maletz & Steiner, 2015). It is known from observing modern pterobranchs that the zooids are unrecognizable after only a few days of decay (Briggs & others, 1995). The poor fossil record of putative pterobranch zooids indicates some lumps of diagenetic minerals in the regions where zooids may be expected (e.g. Bjerreskov, 1978; Rickards & Stait, 1984; Loydell, Orr, & Kearns, 2004), but no definite details of the animals' anatomy. However, Durman and Sennikov (1993, fig. 3,*2*) and Sennikov (2016a, 2016b) described the remains of possible zooids from a middle Cambrian (Drumian) rhabdopleurid (*Sphenoecium obuti* Durman & Sennikov, 1993) as including an indication of arms and tentacles. The photos of the zooids in Sennikov (2016a, 2016b) and the interpretative drawings indicate some features, but are not entirely convincing. Zalasiewicz and others (2013, p. 143) described the "polymorphic organization in a planktonic graptoloid," based on a strongly tectonized, single tubarium of *Dicranograptus* sp. No evidence of zooidal development was found, and the interpretation of the specimen as most likely representing a stolon-like system is conjectural.

Few early fossil taxa have been compared to the Pterobranchia (Fig. 15). Among these is the genus *Herpetogaster* Caron, Conway Morris, & Shu, 2010, based on a number of well-preserved specimens from the middle Cambrian Burgess Shale of British Columbia (Caron, Conway Morris, & Shu, 2010). The suggested relationship of these specimens to the Pterobranchia was supported by the presence of a muscular stalk with an attachment disk and the presence of paired dendritic oral tentacles (Fig. 15.1). However, the presence of the tentacles on the anterior of the head, its dendritic construction, the size of the organism, and the attachment site of the stalk in the middle of the segmented body makes a relationship unlikely and suggests an independent evolution of this stalked organism.

Hou and others (2011) described *Galeaplumosus abilus* Hou & others, 2011, from the lower Cambrian of China, as the oldest, best-preserved, and largest pterobranch of

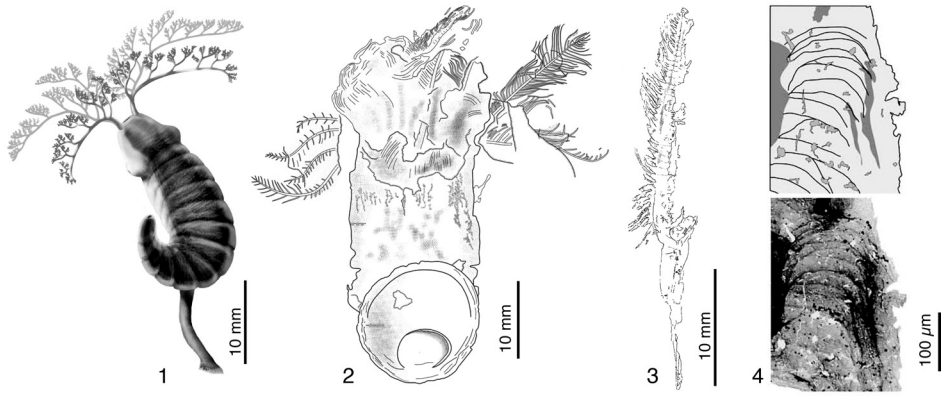


FIG. 15. Putative early pterobranchs. *1, Herpetogaster collinsi*, reconstruction (Caron, Conway Morris, & Shu, 2010); *2, Xianguangia* CHEN & ERDTMANN, 1991 (illustration drawn and used with permission by Qiang Ou, 2015); *3, Galeaplumosus abilus* HOU & others, 2011, holotype (Hou & others, 2011, fig. 2a); *4,* pterobranch fusellum (Harvey & others, 2012, fig. 4).

the fossil record, based on a single specimen (Fig. 15.3). The specimen consisted of arms (probably paired) with rows of paired tentacles, part of a body, and possible indications of a tube with a banding interpreted as fusellar. This specimen is highly fragmentary and a pterobranch relationship cannot be substantiated. OU and others (2017) assembled three Cambrian fossil taxa, including *Galeaplumosus abilus* into a single organism, now identified as the possible cnidarian *Xianguanxia* Chen & Erdtmann, 1991 (Fig. 15.2).

The specimens of *Ectocystis communis* NITECKI and SCHRAM, 1976 from nodules in the Carboniferous Mazon Creek biota of Illinois, are large (several cm long) and possibly represent colonial organisms. Apart from the general outline, details of the anatomy of this organism are not available. The outline vaguely resembles large pterobranch zooids. The arms are not differentiated into tentacles as in pterobranchs, and other characters cannot be compared with the known pterobranch anatomy. Thus, there is no compelling evidence to identify *Ectocystis* as a pterobranch.

HARVEY and others (2012) provided the oldest evidence of true Pterobranchia from a few fragments of fusellar wall material from the middle Cambrian Kaili Formation of China (Fig. 15.4), but it is unclear whether this fragmentary material can be referred to the Cephalodiscida or the Graptolithina. Early definite pterobranchs include *Sphenoecium mesocambricus* (ÖPIK, 1933) from the middle Cambrian of Sweden and Norway (ÖPIK, 1933; BENGSTON & URBANEK, 1986; MALETZ & STEINER, 2015). A number of specimens from the Wheeler Shale of Utah, USA, have been referred to *Sphenoecium wheelerensis* MALETZ & STEINER, 2015. A poorly illustrated specimen of *Dalyia annularoides* RESSER & HOWELL, 1938, from the Kinzers Formation of Pennsylvania may represent the genus *Sphenoecium;* and, thus, this specimen from the lower Cambrian *Olenellus* Zone would be the oldest recorded pterobranch fossil.

RICKARDS and DURMAN (2006) and MALETZ and STEINER (2015) discussed middle to upper Cambrian Graptolithina and provided a general analysis of the evolutionary relationships of the early taxa. Very little is known on the evolution of upper Cambrian pterobranch taxa until the sudden appearance of planktic graptolites close to the base of the Ordovician system. After the extinction of the planktic graptolites in the Lower Devonian (Emsian), the fossil record of the Graptolithina is very poor. Only a few specimens of rhabdopleurids and cephalodiscids are known from the Lower Ordovician to the Eocene (e.g., RICKARDS, CHAPMAN, & TEMPLE, 1984; MIERZEJEWSKI, 1986).

MORPHOLOGY OF THE PTEROBRANCH TUBARIUM

Jörg Maletz, Alfred C. Lenz, and Denis E. B. Bates

INTRODUCTION

The housing of the Pterobranchia, the tubarium, is a complexly organized organic structure with an extensive fossil record. However, the soft-bodied inhabitants of the tubarium are virtually unknown from the fossil record. Therefore, the anatomy of the Pterobranchia is based on the few extant members (*Atubaria* Sato, 1936; *Cephalodiscus* M'Intosh, 1882; *Rhabdopleura* Allman in Norman, 1869a). The variation and evolutionary changes of the tubarium through time are useful for the biostratigraphy in the planktic graptolites (Graptoloidea). A detailed knowledge of the construction of the tubarium is also important for the understanding of graptolite taxonomy. Basic terminology for the pterobranch tubarium is introduced herein (also see *Glossary of the Hemichordata,* p. 165–180), with special features of individual groups discussed in more detail in the taxonomic chapters.

Nearly all known Pterobranchia produce a housing structure from an organic material (Fig. 16), secreted in modern pterobranchs largely by the cephalic shield of the individual zooids and produced in distinct increments called the fuselli. The poorly known extant cephalodiscid *Atubaria* appears to be the only taxon that does not produce a tubarium. The initial part of some benthic colonies (e.g., *Rhabdopleura; Epigraptus* Eisenack, 1941a), the sicula, was secreted by dermal glands of a larval organism prior to the development of the preoral shield of the mature zooid (see Lester, 1988b). All subsequent housing development is by secretion from the preoral shield of the zooids. This housing was termed a tubarium by Lankester (1884) in the extant *Rhabdopleura,* and Hyman (1959) referred to it as the coenecium in modern Pterobranchia. Törnquist (1890) termed the homologous construction of the fossil groups of the graptolites the rhabdosome. This unique organic development has often been identified as an exoskeleton, but it represents a secreted housing for the pterobranch zooids and, thus, the term skeleton is inappropriate.

The pterobranch tubarium originally may have been highly translucent, as in modern *Rhabdopleura* and *Cephalodiscus,* either colorless or slightly brownish or yellowish in color. Sometimes organic and sediment particles are incorporated in the construction of the tubes and the interconnecting tissue, especially in *Cephalodiscus* tubaria (e.g., *Cephalodiscus agglutinans* Harmer & Ridewood, 1913). The organic material of the tubaria appears to darken with time, and Paleozoic material in general is dark brown to black in color. Sometimes the fossil tubaria are still partly translucent, as, for example, shown by Maletz (1994a) in *Pterograptus* Holm, 1881a, in which most specimens are not artificially bleached. It is not clear, however, whether this translucency is an effect of weathering of the sample.

TUBARIUM CONSTRUCTION

The pterobranch tubarium consists of variably developed independent chambers or communal living compartments for the individual zooids or of interconnected tubes. The two groups of the Pterobranchia, the Cephalodiscida and the Graptolithina, produce similarly developed tubaria, but those of the Cephalodiscida do not have the interconnection and seriality of the tubes in the colonial Graptolithina. The individual zooidal tubes of the tubarium are termed thecae (singular, theca) in fossil graptolites (Fig. 16.1). The term is also used herein for the individual tubes of extant pterobranchs (Fig. 16.2, Fig. 17.6).

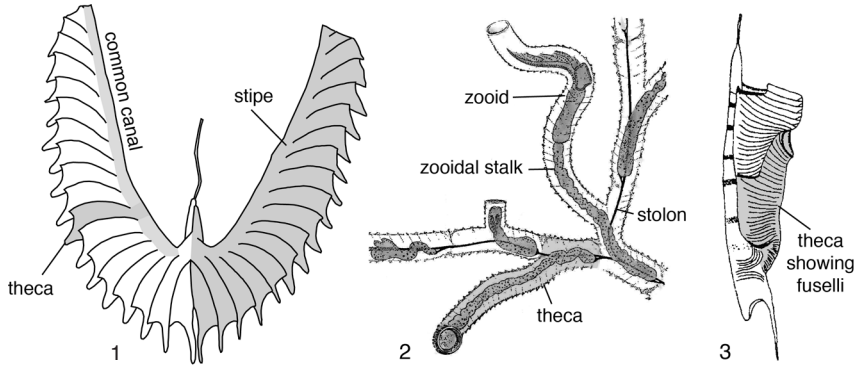


FIG. 16. The structure of the tubarium. *1, Isograptus mobergi* MALETZ, 2011a, tubarium showing two reclined stipes formed from numerous overlapping thecae; common canal indicates colonial organization (adapted from Maletz, Carlucci, & Mitchell, 2009, fig. 5E); *2, Rhabdopleura normani* ALLMAN in NORMAN, 1869a, part of extant tubarium, showing thecal tubes and interconnected zooids, with one thecal tube in *gray* (adapted from Ridewood, 1907, fig. 7a); *3, Heisograptus micropoma* (JAEKEL, 1889), small tubarium showing fusellar construction (adapted from Maletz, 1999a).

The tubaria of the Cephalodiscida (Fig. 17.1–17.2) differ in a number of aspects from those of the derived colonial Pterobranchia. They are quite variable in development, ranging from completely separate, proximally closed tubes for the individual zooids with their developing buds to an array of interconnected structures with a common internal cavity inhabited by the zooids. In forms with individual tubes, these are usually embedded in a coarse cortical mass or are laterally in contact, at least for part of their length. In one subgenus (*Acoelothecia* JOHN, 1931), the housing consists of a network of branched spines and bars without a common cavity. Because the tubaria of *Cephalodiscus* are formed from social groups of clonally developing organisms, they, unlike the Graptolithina, do not possess a recognizably differentiated housing tube for the founder of the colony. A dome or a sicula, as in the derived colonial Pterobranchia, does not exist (MITCHELL & others, 2013).

The thecal tubes of all Graptolithina are interconnected and form a communicating housing system through the common canal (Fig. 16.1). The tubes of *Rhabdopleura,* the only extant genus of the Graptolithina and interpreted as a fairly ancient and primitive taxon, are formed from creeping parts with a dorsal zigzag suture and an erect part with fusellar full rings (Fig. 17.5–17.6). The erect parts of each tube originate through a lateral resorption foramen from the creeping tubes (LANKESTER, 1884); thus, tube building differs considerably from tube growth in more derived graptolithines, in which an initial, primary opening is left for the emergence of the zooids. The development and differentiation of thecae is not well known in most dendroid graptolites, as tips of stipes with growing ends are difficult to obtain. In many benthic graptolites and in the planktic Anisograptidae, the thecae are bundled into triads with lateral origin of new autothecae and bithecae.

COLONY SHAPES

The shapes of pterobranch colonies vary considerably, based on numerous factors (some genetically controlled, others due to ecological interactions of the organisms with their environments). Ecophenotypic variation most frequently develops in benthic forms in both encrusting and erect taxa. Planktic taxa are less strongly affected by environmental conditions and, thus, generally have a lower amount of ecologically controlled variation. Instead, they possess more highly symmetrical colony shapes, presumably useful for maintaining a stable position in the water column. The main factor determining colony shape is the number of stipes in multiramous colonies.

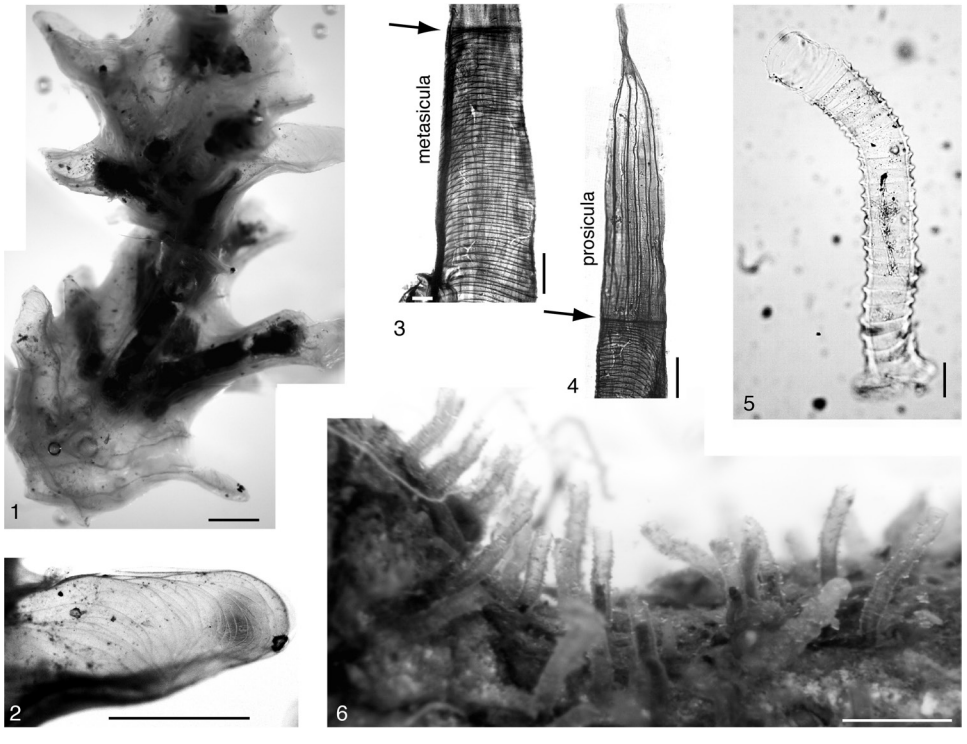


FIG. 17. Colony form and structure in the Pterobranchia. *1–2, Cephalodiscus (Idiothecia) levinseni* HARMER, 1905, origin unknown, extant, SMF 75728; *1,* fragment of a tubarium showing isolated tubes inhabited by zooids (darker matter); *2,* enlarged view of aperture of thecal tube showing irregular fuselli (adapted from Mitchell & others, 2013, fig. 3); *3–4,* isolated and bleached prosicula and metasicula of the Graptoloidea, *arrows* mark boundary between prosicula and metasicula (adapted from Palmer & Rickards, 1991, pl. 13–14); *5–6, Rhabdopleura normani* ALLMAN in NORMAN, 1869a; *5,* individual erect tube showing fuselli, extant (new); *6,* MB.G. 1122, Jaeger collection, Museum für Naturkunde, Berlin; large colony growing on coral, extant, Heltjefjord near Bergen, Norway, ~100 m depth (new). Scale bars, 1 mm (*1–2, 6*); 0.1 mm (*3–5*).

Graptolithines can produce two-dimensional (sheetlike) and three-dimensional (bushy) colonies. Sheetlike colonies can develop secondary three-dimensional shapes, from curved fans to conical colonies, in erect benthic forms and in planktic colonies.

BENTHIC ENCRUSTING COLONIES

Encrusting colonies can form only two-dimensional shapes (Fig. 17.6), but the amount of variation may still be high, depending on the shape of the overgrown surface. Thigmophilic colonies form dense masses of zooidal tubes connected to hardground or other hard surfaces, be it rocks, shells of bivalves and brachiopods, or the corallites of corals. The individual tubes grow in close contact to each other and do not leave any vacant space between them. The extant *Rhabdopleura compacta* HINCKS, 1880a is a good example of this thigmophilic colony shape, but many other benthic pterobranchs possess a similar growth form (see KOZŁOWSKI, 1949). Another common benthic colony form is the runner-type colony of the extant *Rhabdopleura normani* or the Upper Ordovician *Bulmanicrusta*? sp. (MITCHELL, WILSON, & ST. JOHN, 1993), which loosely and quickly covers large areas, though not completely. The individual zooids keep a certain distance from each other and, thus, the stipes never touch. Through their repetitious branching, the colonies can become extremely large.

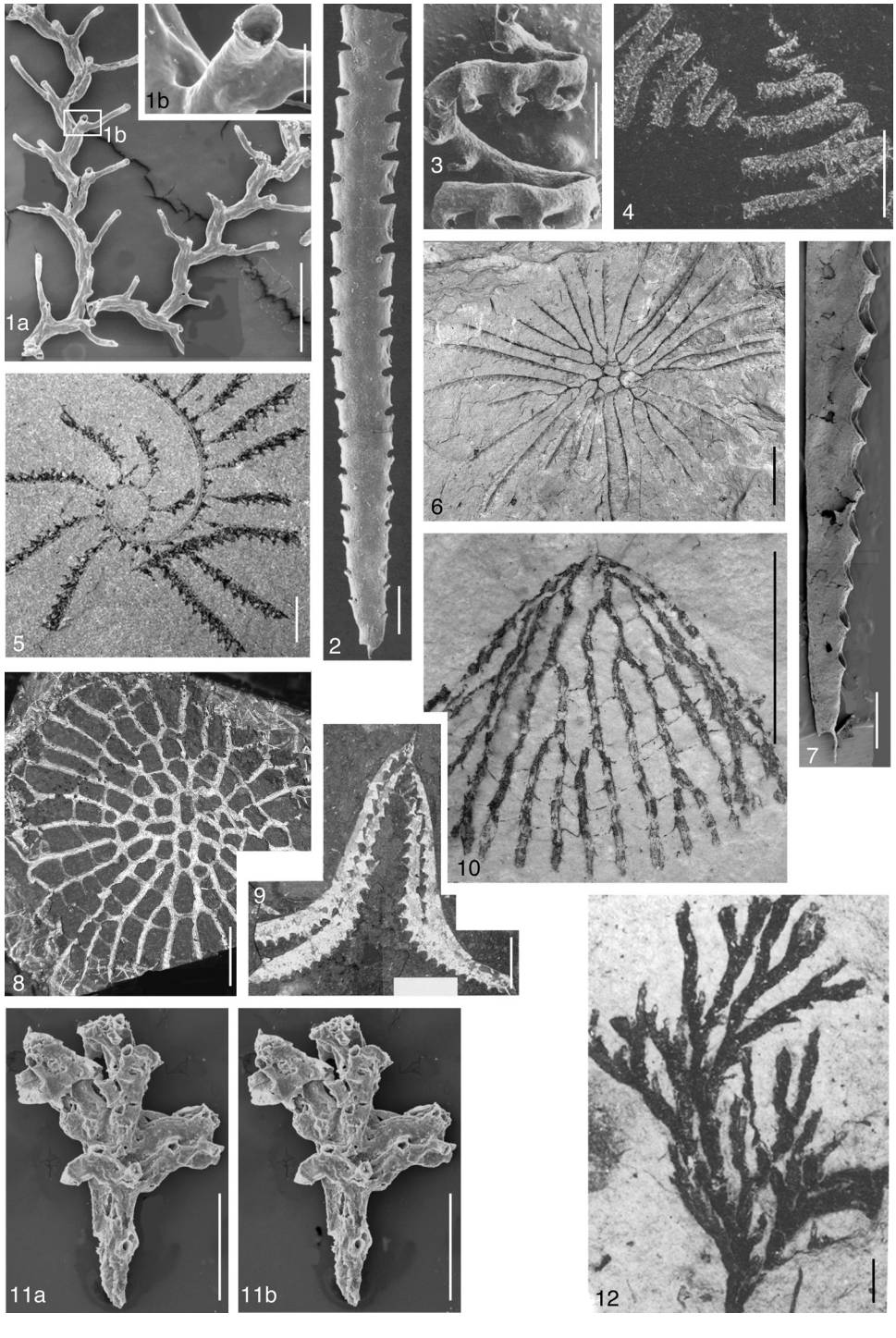


FIG. 18. *For explanation, see facing page.*

BENTHIC ERECT COLONIES

Erect benthic taxa do not develop into thigmophilic shapes, but usually branch at variable distances and form conical, as in planktic *Rhabdinopora* Eichwald, 1855 (Fig. 18.10), fan-shaped, or bushy (Fig. 18.12) colonies. In conical colonies, the thecae have their openings on the inside of the cone, as evidenced from the few, available, well-preserved specimens (Bulman, 1933a). In fan-shaped colonies, all openings are oriented in the same direction, whereas in bushy forms, thecal openings can be variably oriented and the colonies are truly three-dimensional. However, in the Dendrograptidae, even in the bushy forms, the thecae appear to be oriented in the same direction on the individual stipes in a serial arrangement. The development of the stipes and the orientation of the thecal openings may be more complex in the Callograptidae, in which individual stipes are formed from a number of overlapping thecal tubes and thecal openings may point in various directions (Fig. 18.1).

PLANKTIC COLONIES

The colony shapes of planktic taxa are generally more symmetrical, due to the need for balance and orientation in the water column. Most multibranched, planktic graptolites grew into an essentially two-dimensional, planar shape (Fig. 18.6). This shape, however, could be transformed either into umbrella-shaped (Fig. 18.8) or strongly conical (Fig. 18.3–18.4, Fig.18.10) colonies. Their three-dimensionality is based on the modification of this original conical arrangement of the stipes in the early planktic genus *Rhabdinopora* (Fig. 18.10). A truly three-dimensional colony growth with highly irregular branching (as, for example, in benthic *Dendrograptus* Hall, 1858 species) has not been recognized in any planktic form. Thus, there are no bushy planktic colonies, as there are in benthic colonies (Fig. 18.11–18.12). Three-dimensional shapes developed in coiled (Fig. 18.3–18.4) and cladial-bearing monograptids (Fig. 18.5) in the Silurian and Lower Devonian, but three-dimensional, spiral colonies were also present in Ordovician dicellograptids and dicranograptids.

THECAL WALL FORMATION

The tubes, or thecae, form housing structures for the individual members of the colony. They have a characteristic and simple construction in the form of fusellar half rings and full rings. The shape of these tubes may vary considerably and is used for taxonomic and phylogenetic interpretations. Isolated, erect tubes may be round in cross section, but creeping tubes are more often flattened on the ventral side. In complex colony structures, they may be shaped irregularly,

Fig. 18. General shapes of graptolite colonies. *1a–b, Acanthograptus* sp. fragment, branching, Silurian (upper Wenlock), Canadian Arctic, scale bar, 1 mm; *1b,* enlarged view of *1a,* showing bitheca and autotheca, scale bar, 0.1 mm (Lenz & Kozłowska-Dawidziuk, 2001, pl. 1,12); *2, Clinoclimacograptus barriei* (Zalasiewicz & Tunnicliff, 1994), straight, biserial development, Silurian (middle Llandovery), Canadian Arctic, scale bar, 1 mm (Melchin, 1998, pl. 1, fig. 13); *3, Spirograptus guerichi* Loydell, Štorch, & Melchin, 1993, narrow, conical spiral, Silurian (upper Llandovery), Sweden (Dalarna), scale bar, 1 mm (Loydell, Štorch, & Melchin, 1993, fig. 3B); *4, Spirograptus turriculatus* Barrande, 1850, narrow, conical spiral, Silurian (upper Llandovery), Czech Republic, scale bar, 5 mm (Loydell, Štorch, & Melchin, 1993, fig. 3A); *5, Cyrtograptus mehnerti* Hundt, 1949a, broad, low, conical spiral, Silurian (lower Wenlock, Sheinwoodian), Canadian Arctic, scale bar, 5 mm (Lenz & others, 2012, pl. 22, fig. 1); *6, Praegoniograptus clonograptoides* (Harris & Thomas, 1939), holotype, planar to umbrella shaped, Lower Ordovician, Victoria, Australia, scale bar, 10 mm (new); *7, Pristiograptus dubius* (Suess, 1851), uniserial, Silurian (middle Wenlock), Canadian Arctic, scale bar, 1 mm (Lenz & others, 2012, pl. 11, fig. 8); *8, Sagenograptus macgillivrayi* (T. S. Hall, 1899), umbrella shaped, Ordovician (Tremadocian), Victoria, Australia, scale bar, 10 mm (new); *9, Tshallograptus fruticosus* (Hall, 1865), pendent, bell shaped, Lower Ordovician (Floian), Canada (northern Yukon), scale bar, 5 mm (Jackson & Lenz, 2006, fig. 6D); *10, Rhabdinopora campanulatum* Harris & Keble, 1928, cone shaped, Lower Ordovician (Tremadocian), Dayangcha, China, scale bar, 5 mm (new); *11a–b, Thallograptus* sp., bushy, stereopair, Silurian (Ludlow), Canada, scale bars, 1 mm (Lenz & Kozłowska-Dawidziuk, 2004, fig. 2,12); *12, Callograptus huckriedei* Rickards, Hamedi, & Wright, 2001, bushy, Lower Ordovician (Floian), Iran, scale bar, 1 mm (Rickards, Hamedi, & Wright, 2001, fig. 2D).

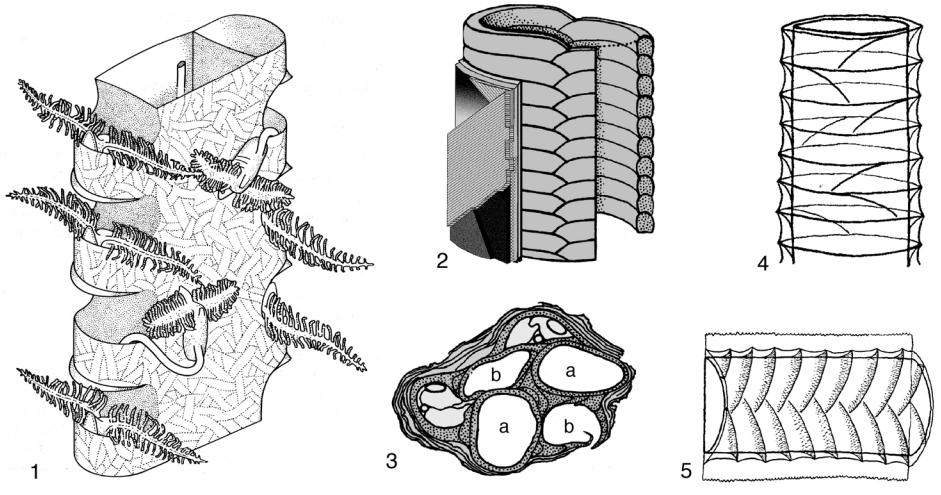


FIG. 19. Thecal construction in the Pterobranchia; illustrations of fusellar and cortical layers. *1,* Part of axonophoran colony with reconstructed zooids and cortical bandaged surface (adapted from Crowther & Rickards, 1977, fig. 3); *2,* zigzag fusellar structure and the outer crisscrossing cortical bandages (adapted from Bulman, 1970, fig. 5,1, and Kozłowski, 1938, fig. 2); *3,* cross section through stipe of dendroid showing autothecae (*a*), bithecae (*b*), fusellum and ectocortex (adapted from Bulman, 1955, fig. 6,2); *4–5, Rhabdopleura* sp.; *4,* portion of erect tube with fusellar full rings and irregular sutures; *5,* portion of creeping tube with fusellar half rings and zigzag sutures (Andres, 1977, fig. 4).

depending on the attachment sides and connection between the tubes.

The two, basic constructional features of the thecae are the fusellum (fusellar layer) and the cortex (cortical layer) (KOZŁOWSKI, 1949). These two layers together (Fig. 19.2) have been termed the periderm in the past (WIMAN, 1895), but it is now understood that these layers are formed by a special gland on the cephalic disk of the zooids and are not a dermal layer. As a result, the term periderm is inappropriate.

THE FUSELLUM

Each tube is secreted in individual, narrow increments, the fuselli (singular, fusellus). Numerous fuselli (collectively the fusellum of KÜHNE, 1955) are stacked one on another with some lateral overlap (Fig. 19.2), forming a distally open tube for the individual housing of each zooid. Each fusellus possesses at least one oblique suture (Fig. 19.4), indicating the method of secretion as a strip of material around the circumference of the tube. The zooid of an extant pterobranch starts at one point and secretes the fusellus while moving its oral disk in a circle around the thecal aperture. In full fusellar rings, a single oblique suture defines the position at which the zooid started and finished the secretion of the individual fusellar ring. In fusellar half rings, two separate fuselli form a full ring of the thecal tube, producing a dorsal and a ventral suture (Fig. 19.2). The fuselli are, thus, growth segments laid down by the zooids in a highly regular and highly symmetrical fashion.

In early members of the Pterobranchia, the fuselli are full rings with irregularly placed sutures (Fig. 17.5, Fig. 19.4); during the evolution of the group, these sutures become more regular and are replaced by fusellar half rings (Fig. 19.5) with a much higher degree of symmetry. Regular fusellar half rings are laid down alternately right and left and produce the dorsal and ventral zigzag sutures of the tubes (Fig. 19.2, Fig. 19.5). Full rings and half rings can, however, occur in the colonies of the extant *Rhabdo-*

pleura. Creeping parts of *Rhabdopleura* colonies possess a distinct zigzag pattern on the dorsal side of the creeping tubes (Fig. 19.5), whereas erect tubes have fusellar full rings with a distinct collar structure (Fig. 19.4). The thickness of the fuselli (and, therefore, the fusellar layer) is usually uniform along the colony, but the height of the individual fuselli may vary considerably, depending on the position in the thecal tube and the ontogeny of the secreting zooid. Early fuselli of a theca are usually of a lesser height than distal or apertural fuselli (Walker, 1953), but a lesser height may also be present at thecal apertures (Bates, 1987a, pl. 1).

REDUCTION OF FUSELLAR THICKNESS

Fuselli possess an interior part made of fibrils and a thin, denser wall made of the same construction material (see discussion of ultrastructure, p. 36). The amount of material used to form the fuselli varies considerably among groups, and a reduction in wall thickness and density is observable in a number of taxa. The Ordovician genera *Parisograptus* Chen & Zhang, 1996, and *Cryptograptus* Lapworth, 1880a, possess fairly thin thecal walls, visible often as translucent thecae with clearly observable fusellar structure, whereas associated graptolites on the same sedimentary surface have only thick, dark films of organic material (e.g., Williams & Stevens, 1988). In a further reduction of the fusellar wall material, it appears as if the taxa do not possess thecal walls at all, as the wall material is so thin that it rarely survives the fossilization process. For example, the remains of thecal walls may be observable in ragged edges preserved in the cortical bandages of the retiolitids (e.g., Bates & Kirk, 1992, 1997). A considerable reduction may be present only in part of the colonies, but it can also affect the whole colony and may be counteracted by the development of secondary cortical covers. In stratigraphically younger taxa of the genus *Cryptograptus,* for example, the sicula and the first two thecae are so weakly sclerotized that they have not been found in isolated material. Some authors (e.g., Bulman, 1945; Maletz & Mitchell, 1996) have suggested that because cortical bandages on these structures have not been recognized in isolated material, they were never present.

Thin thecal walls, seldom preserved, and development of lists are traits in all Retiolitidae, most Lasiograptidae, some members of the Abrograptidae (Mu, 1958), and as an exception in other taxa. Thecal walls in retiolitids are rarely preserved, even though it exists in isolated material that they were originally present (Lenz, 1994a, fig. 14,*3*, fig.14,*7–9*; Lenz & Kozłowska-Dawidziuk, 2002a, fig. 15) on both the thecal framework and ancora sleeve. Based on very rare preservation of thecal framework walls (Lenz & Thorsteinsson, 1997) as well as scars and shards in isolated material (Bates, 1987a), it is clear that the thecal framework was comprised of successive layers of fusellar bands. It is not clear, however, in what manner the ancora sleeve layer was constructed, because there appears to be no indication of fusellar laminae (see discussion of the ancora sleeve, p. 75). In other, unrelated groups (e.g., *Retiograptus* Hall, 1865; *Rectograptus* Přibyl, 1949), a reduction of the thickness and, ultimately, loss of thecal walls appears to have originated independently.

CORTEX

The cortex, cortical tissue, or cortical bandages are formed in extant pterobranchs in the same way as the fuselli, by the preoral lobe of the zooids. However, the cortical material differs considerably in the way in which it is laid down in the pterobranch colony. It can form thick masses of loose or spongy material around the individual tubes of a *Cephalodiscus* colony or thin layers of material surrounding and covering the surface of thecal tubes in planktic graptolites. In general, a differentiation of ectocortex and endocortex can be made (Crowther, 1981; Urbanek & Mierzejewski, 1984). Endocortex is made of

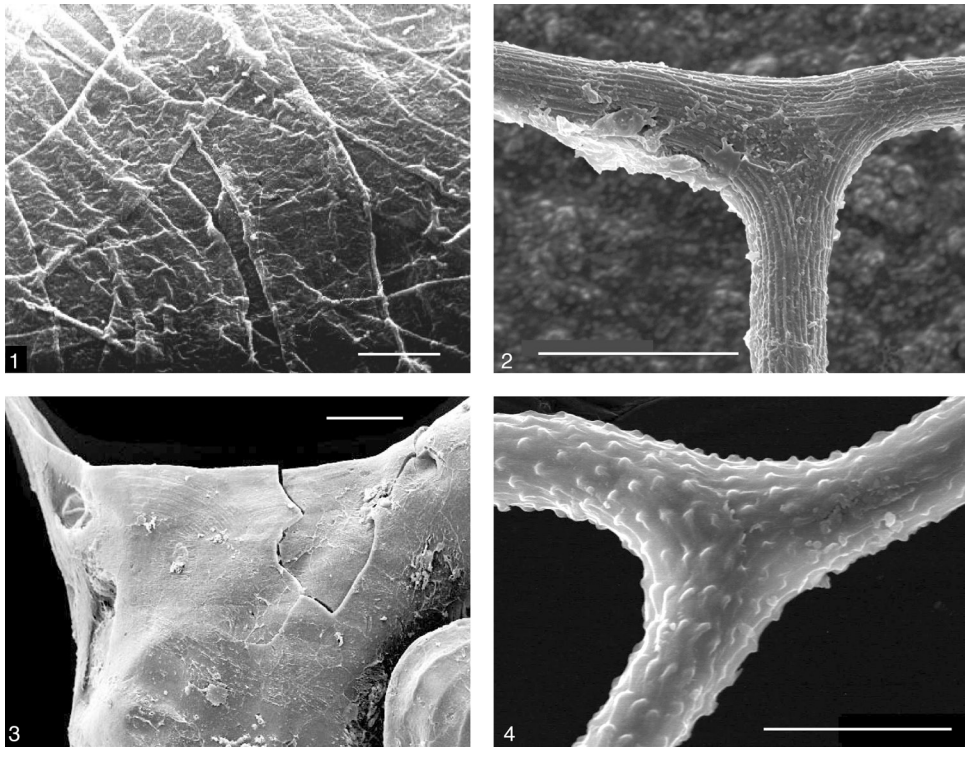


FIG. 20. Cortical bandages. *1, Rectograptus gracilis* (ROEMER, 1861), bandages with distinct raised rims (new, courtesy of Piotr Mierzejewski); *2, Rotaretiolites* sp., showing cortical tissue of strong, parallel, ridgelike bandaging, Silurian (upper Telychian, Llandovery), Canadian Arctic (new); *3, Paramonoclimacis sidjachenkoi* (OBUT & SOBOLEVSKAYA, 1965), Canadian Arctic, showing thin application of cortical material at growing end of colony (new); *4, Plectograptus macilentus* (TÖRNQUIST, 1887), pustulose surface of a plectograptine retiolitid, Silurian (Ludlow), glacial boulder, northern Germany (new). All scale bars, 50 µm.

cortical bandages laid down on the inside of the thecal tubes and is commonly found in some pterobranchs (ANDRES, 1977). It is also present in dendroids (e.g., *Dendrograptus*? sp. in BATES, 1997, pl. 4,*1*). CROWTHER (1981, pl. 16) indicated its presence even in monograptids. Ectocortex (Fig. 19.1–19.4) is much more generally distributed in the Pterobranchia and appears on the outside of colonies.

The cortex is typically secreted in the form of distinct bands or bandages (CROWTHER & RICKARDS, 1977) on the outer surface of planktic graptolite colonies (Fig. 20) and is also present in similar form in benthic colonies (BATES & others, 2011). The precise development of the ectocortex and its distribution in the various groups of Paleozoic graptolites is little understood. Differences in the development are apparent, as some graptolites possess cortical bandages with distinct lateral ridges (Fig. 20.1). Cortical bandages can also be quite indistinct, as in many monograptids, and appear similar to faint brush strokes (Fig. 20.3). In the Silurian retiolitids, there are two kinds of ornamentation on the cortical bandage surfaces: linear striae and pustules (Fig. 20.2, Fig. 20.4).

ULTRASTRUCTURE

DENIS E. B. BATES

The ultrastructure of the fusellar tissue is a complex secretion of the wall material. It can be differentiated into sheet fabric and fusellar fabric (Fig. 21). The details of this construction are visible only under the Scanning Electron Microscope (SEM) and Transmission Electron Microscope (TEM).

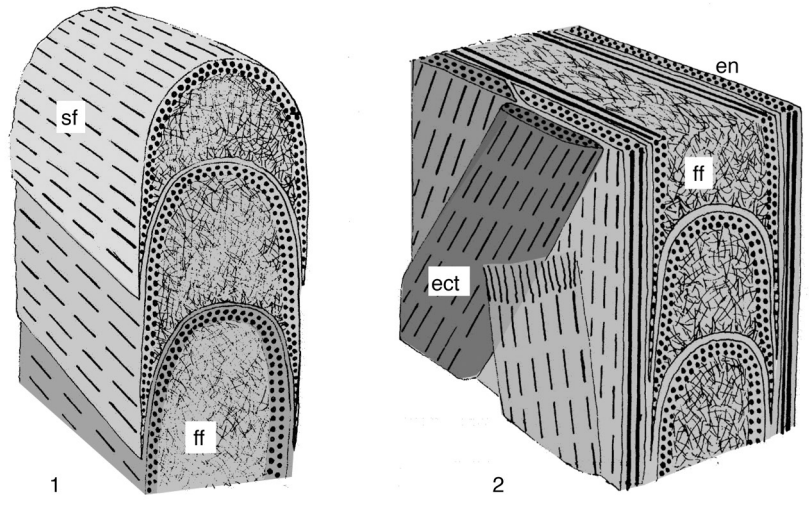


Fig. 21. Ultrastructure of the tubarium wall. *1,* Three stacked fuselli, showing sheet fabric (*sf*) and fusellar fabric (*ff*); *2,* tubarium wall structure with fuselli (*ff*), ectocortex (*ect*), and endocortex (*en*); ectocortex formed as separate bandages (adapted from Bates & Kirk, 1986, fig. 1).

FUSELLI

Each fusellus begins with the deposition of a sheet of granular fabric on the head of the previous fusellus (Bates & Kirk, 1986; Bates & others, 1988). This is succeeded by a three-dimensional meshwork of fibrils, the fusellar fabric (Fig. 21.1–21.2). Generally, these have a random orientation, but variations may be noted. They may start with clumps of fibrils springing up from the base of the fusellus, rather like the roots of mangrove trees or trabeculae. They also tend to become denser toward the arch of the increment. Fibril diameter ranges from 20 nm to 70 nm, with a tendency to increase in diameter toward the bounding sheet of a fusellus. Clockwise spiral striae appear to be present in some taxa (Fig. 22.5, Fig. 22.10).

Each arch is bounded by a sheet, which appears to be finely granular in form. This sheet may contain larger pustules, giving it a knobby surface (Fig. 22.6), the granular sheet fabric *sensu* Crowther and Rickards (1977). Oval vesicles are also characteristic of this bounding layer; they may be roofed over to give slight swellings, suggesting that there may be two layers to this bounding sheet, or they may appear as unroofed depressions (Fig. 22.6). Beneath the bounding sheet, there are usually fibrils intermingled with the fusellar fabric, parallel to one another and to the head of the incremental arch (Fig. 22.4).

CORTICAL BANDAGES

Cortical bandages vary in dimensions and ornament and also in the number of fabrics comprising them. In a typical bandage, the lowest layer is a thin sheet, again formed of a finely granular fabric. Occasionally, this is succeeded by random fibrils, especially where a bandage is laid down over an uneven surface (e.g., where it crosses the edge of a previous bandage). The bulk of the bandage is made of closely packed, parallel fibrils, the unit being from one to several fibrils thick, and varying in diameter from 80 nm to 400 nm (Fig. 22.4, Fig. 23.1). Most taxa have an ornament of striae that spirals clockwise (Fig. 22.5).

Interconnecting rods are smaller fibrils, which run perpendicular to the cortical fibrils of the cortex, observed in some genera. They are best developed in *Dictyonema,* in which they are ~27 nm in diameter and are regularly spaced at intervals of ~80 nm (Fig. 22.4–22.5).

The sheet layer covering the bandages is identical to that described for the fuselli (Fig. 22.6). In some taxa, the edges of the bandages are thickened (Crowther, 1981);

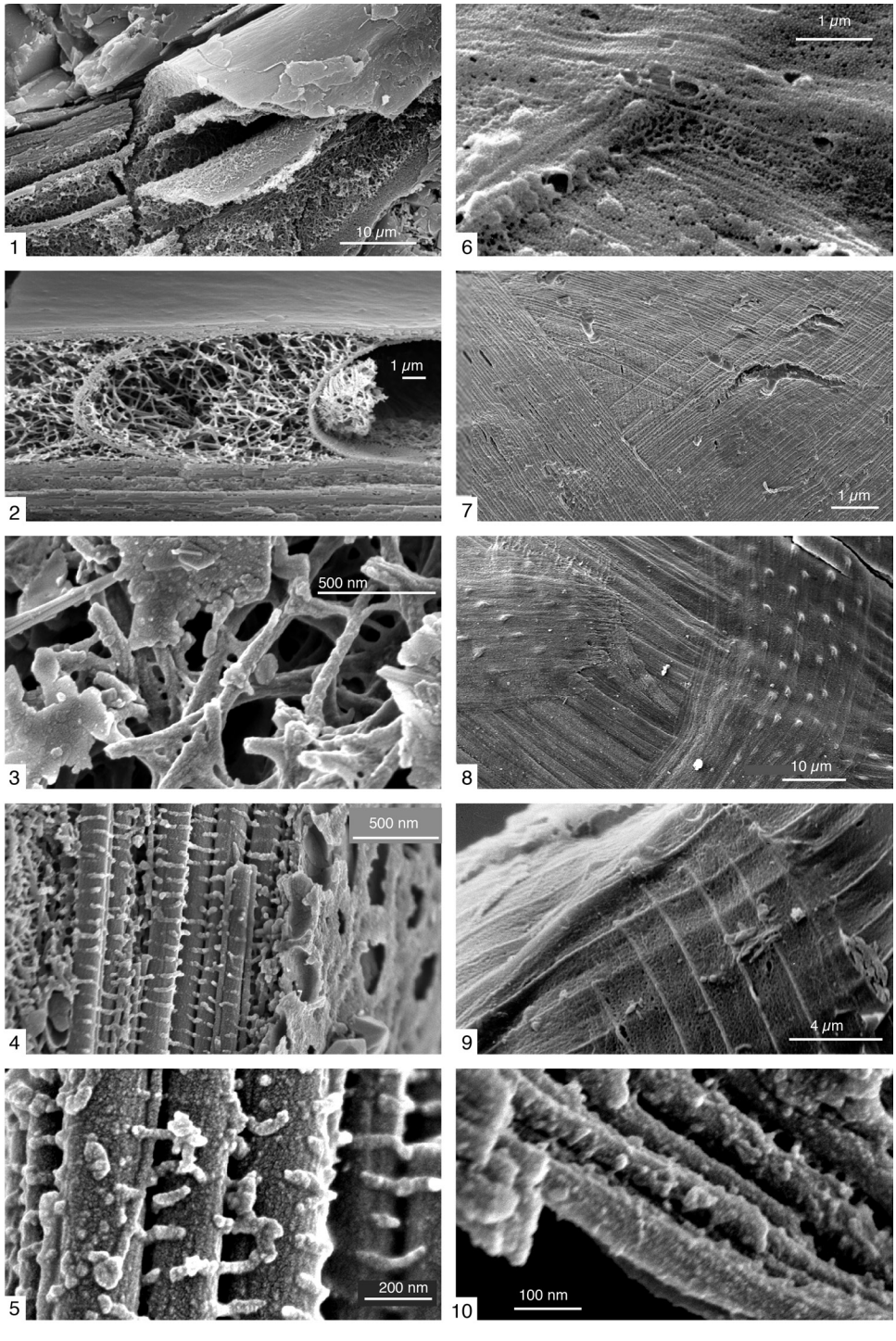


FIG. 22. *For explanation, see facing page.*

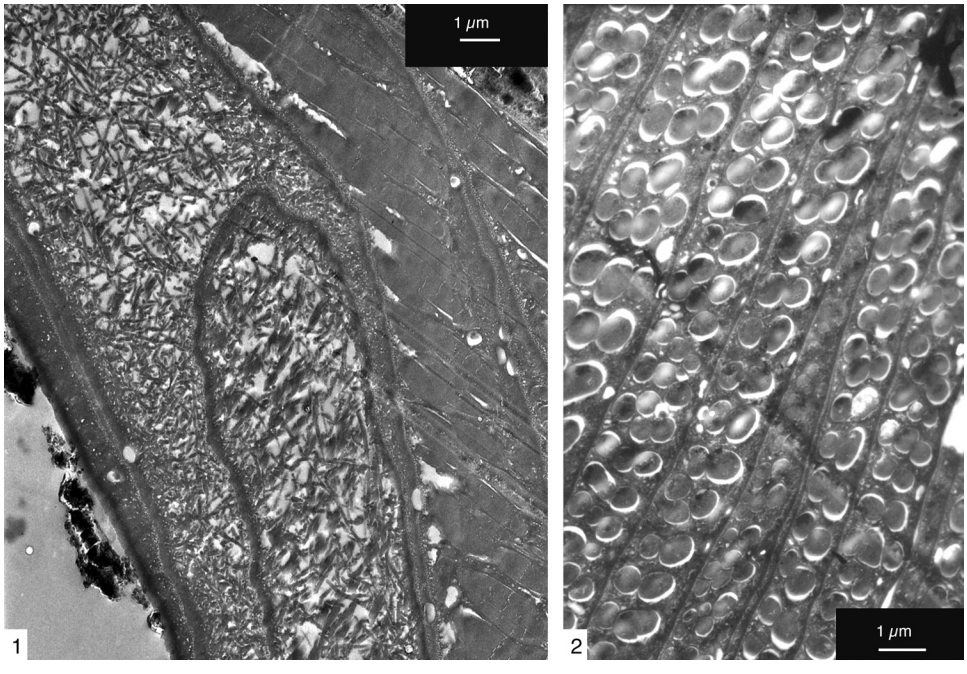


FIG. 23. TEM sections of tubarium wall construction. *1*, *Dendrograptus*? sp., two fuselli and bandages of the ectocortex, Gotland, Sweden; *2*, *Dendrograptus*? sp., cortical bandages, Gotland, Sweden (Bates, 1997, pl. 5).

in others, the bandage is covered by a series of prominent, equally spaced ridges across the bandage (Fig. 22.9). To date, it has not been possible to determine whether these ridges are formed from parallel fibrils or from thickenings of the covering sheet layer. Some Silurian retiolitids have another type of bandage ornament that bears a pattern of blunt tubercles or spines (Fig. 22.8). Internal bandaging (inner cortex) is much more rare. Commonly, internal bandages are much thinner (usually only one fibril thick) than external ones, and they lack the sheet covering (Fig. 22.7).

CHEMICAL COMPOSITION OF THE TUBARIUM

Pterobranch tubaria consist of organic material, as can easily be recognized from their brownish to black color and their reaction to tectonism within a rock, resulting in the surrounding pressure-shadow minerals (UNDERWOOD, 1992). Specimens weather out as dark films of material that may be

Fig. 22. SEM photographs. *1,6, Geniculograptus typicalis* (HALL, 1865), Viola Springs Limestone, Upper Ordovician (Katian), Oklahoma, USA; *1,* fractured fuselli (new); *2, Desmograptus micronematodes* (SPENCER, 1884), fuselli, with thicker ectocortex below and thinner endocortex above, Racine Dolomite, Silurian (Wenlock), Illinois, USA (new); *3,10, Acanthograptus*? sp., erratic boulder, Middle Ordovician, Mochty, Poland; *3,* fusellar fibrils with spiral striae (new); *4–5, Dictyonema* sp., erratic boulder, Upper Ordovician, Orłowo, Poland; *4,* section through cortical unit with cortical fibrils and interconnecting rods, base of unit on the left, sheet fabric of surface with vesicles on the right (new); *5,* cortical fibrils with spiral striae (new); *6,* bandages with sheet fabric forming their surfaces, both roofed and unroofed vesicles are shown (new); *7, Cyrtograptus lundgreni* (TULLBERG, 1883), internal bandages, one fibril thick and without any sheet fabric, Kolka Borehole, Silurian (Wenlock), Latvia (new); *8, Gothograptus nassa* (HOLM, 1890), bandages on genicular hood with pustules, Mulde Marl, Silurian (Wenlock) Gotland, Sweden (new); 9*, Reteograptus geinitzianus* (HALL, 1865), bandages with regularly spaced ridges, Athens Shale, Upper Ordovician (Sandbian), Alabama, USA (new); *10,* cortical fibrils with transverse ridges superimposed on spiraling striae (new).

attacked by bacteria and fungi in the laboratory. Early investigation suggested a material similar to chitin, but neither chitin nor cellulose was proven to be present (Foucart & others, 1965; Florkin, 1969). Instead, the presence of amino acids in three samples of Ordovician and Silurian age showed that they were comprised of proteinaceous substances (e.g., Kozłowski, 1966a). Towe and Urbanek (1972), Crowther and Rickards (1977), and Runnegar (1986), among others, interpreted the graptolite tubaria to be collagenous in composition, based largely on the observation of the banded fibrils in the cortical and fusellar material. The material of the fossil graptolite tubarium consists of an aliphatic polymer and does not contain any protein, even though the structure and analysis of the housing material of modern *Rhabdopleura* (Armstrong, Dilly, & Urbanek, 1984; Bustin, Link, & Goodarzi, 1989; Gupta, Briggs, & Pancost, 2006) indicated that the building material in fossil graptolites was originally collagen. Even the most recent investigation was unable to define the composition of the building material more precisely (Sewera, 2011).

ONTOGENY AND ASTOGENY

The Graptolithina have a complex pattern of sexual and asexual reproduction, the most conspicuous aspect of which is the asexual budding of the clonal, colonial zooids. Thus, the ontogenetic development of the individual zooids and their tubes needs to be differentiated from the astogenetic growth of the colony as a whole. The sexually produced founder zooid of the colony is usually easily differentiated from the later zooids. It inhabits (and produces) the sicula, the first theca of the colony.

A new benthic colony starts with the settling of a sexually produced larva and the secretion of the initial part of the sicula. In the extant *Rhabdopleura,* this is accomplished by a ciliated larva. The larva settles on a suitable surface and forms a cocoon or dome (Fig. 24.1–24.3), in which it morphs into the first zooid (Lester, 1988b). In derived benthic graptolites (e.g., *Dendrograptus*), the larval stage included a prosicula as the housing for the sicular zooid (Kozłowski, 1971). The shape of the prosicula of benthic taxa varies considerably but is known from only a very few species. In planktic graptolites, the prosicula always possesses a nema, inferred to indicate a planktic development and life mode.

SICULAR ONTOGENY

A sicula is present in all Graptolithina but not in the Cephalodiscida. It represents the housing of the sexually produced founder zooid of the colony, comparable to the ancestrula of the Bryozoa. Its construction and the construction of the early thecal tubes can be regarded as the most important characters for a specific determination of graptolite taxa.

ATTACHMENT DISK AND NEMA

The attachment of the prosicula to the substrate in benthic encrusting and bushy dendroid forms is poorly known, as mostly only fragments are available and specimens in life orientation often possess considerable cortical overgrowth covering the initial attachment site. Erect, bushy taxa may possess a dendritic holdfast structure to anchor them to a substrate (e.g., *Dictyonema cavernosum* Wiman, 1896a). There is no credible evidence of any so-called root system in benthic graptolites extending into the sediment, and it has to be assumed that the attachment is invariably produced as cortical tissue by the zooids of the colony fixing the colony to a hard substrate. One extant species of *Rhabdopleura* is known to live in sandy areas and does not depend on attachment to a hard surface (e.g., bivalve shell, coral, or other organism) or hardground.

INITIAL PART OF THE COLONY

The initial part of the colony, represented by the prosicula or dome, has a number of characters that help to identify its development and the phylogenetic relationships of taxa. The dome in extant *Rhabdopleura* (Fig.

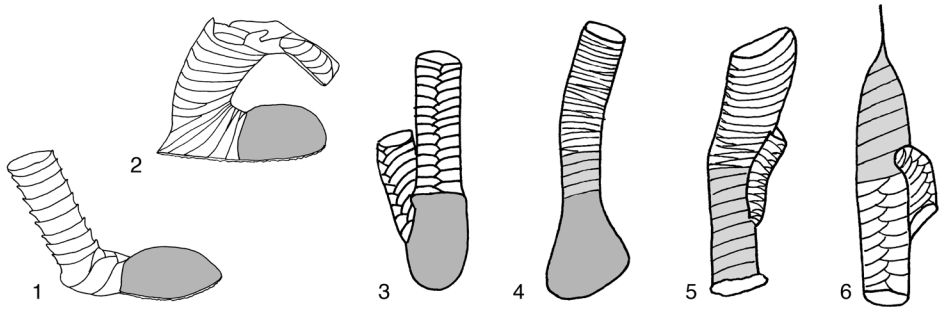


FIG. 24. Prosicular development and comparison with rhabdopleurid dome. *1, Rhabdopleura compacta* HINCKS, 1880*a*, lateral view of juvenile with dome and initial (sicular) tube (adapted from Stebbing, 1970b, fig. 3); *2, Epigraptus* sp., juvenile with dome and initial tube (adapted from Kozłowski, 1971, fig. 1); *3, Rhabdopleura* sp., dorsal view of tubarium with initial part of first post-sicular tube (new); *4, Dendrotubus* sp., with distal helical line in the prosicula (adapted from Kozłowski, 1971, fig. 5); *5, Dendrograptus communis* KOZŁOWSKI, 1971, tubelike prosicula with helical line (adapted from Kozłowski, 1949, fig. 1); *6,* nematophorous sicula with helical line (adapted from Maletz, Steiner, & Fatka, 2005, fig. 2). *Darker gray,* dome and possible equivalents; *lighter gray,* prosicula with helical line.

24.1, Fig. 24.3) is the only form of initial development known from modern pterobranchs, and it differs considerably from the prosicula of most graptolites. KOZŁOWSKI (1971) differentiated the discophorous sicula (Fig. 24.5) of the benthic taxa from the nematophorous sicula of the planktic forms (Fig. 24.6), based on the presence or absence of a free nema.

DOME AND PROSICULA

The prosiculae in *Rhabdopleura normani* and in *Rhabdopleura compacta* are known as a dome (Fig. 24.1, Fig. 24.3). They are formed as a featureless membrane encasing the developing or metamorphosing sicular zooid and are constructed by glands in the ventral epidermis of the larva (LESTER, 1988b). In *Cephalodiscus* (*Orthoecus*) *densus* ANDERSSON, 1907, a possibly comparable structure, a cocoon, is formed around developing larvae and is protected on the outside with sand grains (SCHIAPARELLI, CATTANEO-VIETTI, & MIERZEJEWSKI, 2004). The details of the construction of the dome or the cocoon are unclear. In *Rhabdopleura,* the sicular zooid produces a resorption foramen to hatch from the cocoon and starts to form the initial thecal tube (LESTER, 1988b). The development of a dome in place of a prosicula has been documented for the Ordovician genus *Epigraptus* (KOZŁOWSKI, 1971; ANDRES, 1977) but is otherwise unknown in the Graptolithina (Fig. 24.2).

KOZŁOWSKI (1971) described the prosicula of the benthic *Dendrotubus* KOZŁOWSKI, 1949 (Fig. 24.4) as bottle-shaped, erect, with a helical line in the distal part, homologous to the helical line in the prosicula of planktic graptolites (Fig. 24.6). In contrast to the dome of the rhabdopleurids, the prosicula of *Dendrotubus* is provided with a primary opening, an aperture through which the sicular zooid emerged and started to secrete the metasicular fuselli. This record represents the only evidence of a transition from the dome of the rhabdopleurids to the conical erect or nematophorous prosicula of derived taxa. *Dendrograptus communis* KOZŁOWSKI, 1971 (Fig. 24.5) is the only benthic dendroid known to have a tubelike sicula with an attachment and typical helical line in the prosicula.

The nematophorous prosicula of the planktic Graptoloidea is known from many species, and its detailed development was described first by KRAFT (1926) for *Rectograptus gracilis* (ROEMER, 1861), even though WIMAN (1893a, 1893b, 1895) already described and illustrated many of the features from his isolated material. The prosicula is a conical structure with a distinct helical line (Fig. 25.1–25.3), indicating its secretion as a continuous band of fusellar tissue, as is shown by unwound specimens

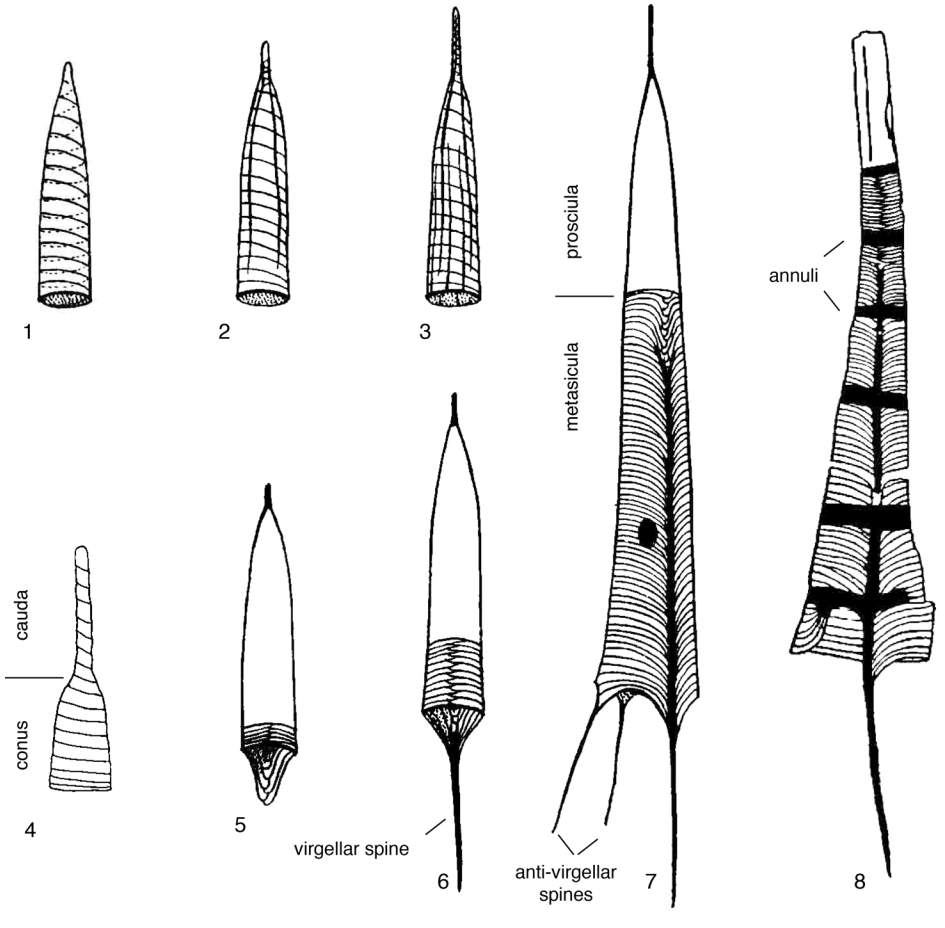


FIG. 25. Sicular development. *1,* Early prosicula with spiral line, cauda incomplete; *2,* prosicula with few longitudinal rods; *3,* mature prosicula with many longitudinal rods (*1–3* adapted from Bulman, 1955, fig. 36); *4,* conus and cauda differentiation in Anisograptidae (Hutt, 1974a, fig. 1); *5,* early metasicula with few fusellar half rings and rutellum; *6,* development of virgellar spine in axonophorans; *7,* complete axonophoran sicula with paired antivirgellar spines and resorption foramen for th1[1] in metasicula (*5–7* adapted from Bulman, 1955, fig. 36); *8,* monograptid sicula with sinus stage and sicular annuli (adapted from Walker, 1953, fig. 1H).

(KOZŁOWSKI, 1971). HUTT (1974a) differentiated the prosicula into the conus and cauda (Fig. 25.4), based on the strong constriction at the tip of the conus. The cauda merges into the nema, but it still preserves traces of the helical line, which is not present in the nema. The presence of the helical line can be interpreted to indicate that the conus and cauda were formed together from a juvenile zooid or larval stage. The helical line of the prosicula may be right- or left-handed, but there is no information on quantities and distribution of right- and left-handed specimens and the development in relation to right- and left-handed growth of the remainder of the colonies. A diaphragm (Fig. 26) has been recognized in the upper part of the conus of many species (KRAFT, 1926; HUTT, 1974a; BATES, 1996; WILLIAMS & CLARKE, 1999).

In a second stage of development, in many species, the prosicula may add a number of longitudinal rods on the outside (Fig. 25.2–25.3). The longitudinal rods do not,

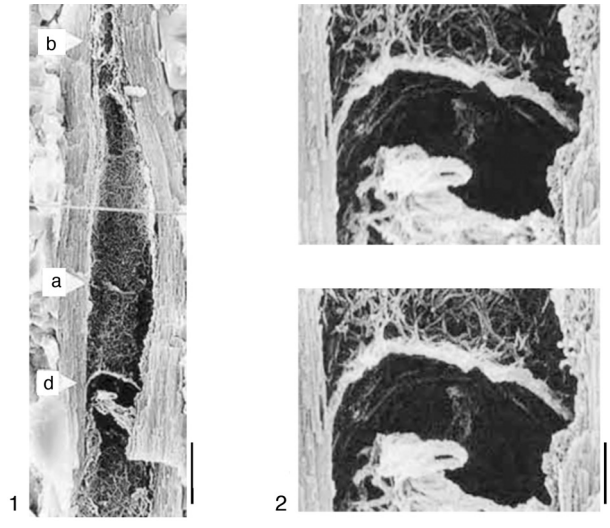


FIG. 26. SEM photograph of prosicular structure. *1*, Top of cauda, below diaphragm (*d*), proximal part of nema (*a*), wider part of nema, and beginning of narrow part of nema (*b*); *2,* stereopair (rotated vertically) showing diaphragm (adapted from Bates, 1996). Scale bars, 1 µm.

in general, encroach onto the metasicula. Thus, they were formed at some later stage during the ontogenetic growth of the prosicula before the metasicular fuselli were added (KRAFT, 1926). In *Diplacanthograptus spiniferus* (RUEDEMANN, 1912) and a number of related Upper Ordovician taxa, one or two thickened strengthening rods remain of the prosicular construction, as the complete prosicula is not recognizable (or perhaps not preserved) in the fossil specimens. This is also occasionally observable in a number of Silurian (Llandovery) retiolitinids. The reason for the presence of the longitudinal rods is uncertain, but it may be noted that a number of early planktic forms lacked the longitudinal rods, whereas they were consistently present in later Ordovician taxa (WILLIAMS & CLARKE, 1999) and were still present in Silurian to Lower Devonian monograptids (JAEGER, 1991; URBANEK, 1997a).

METASICULA

The metasicula is invariably formed as a distally open tube from fusellar half rings that have a dorsal and ventral zigzag suture, but fuselli may be irregular in dendroid siculae (Fig. 24.4–24.5). It differs considerably from the prosicula in its development and is usually easily differentiated (Fig. 25). The fuselli may be more densely spaced in the proximal part and more widely spaced close to the aperture. In early planktic forms, the differentiation was less prominent, as the helical line may be difficult to separate from the fuselli of the metasicula. KOZŁOWSKI (1954) stated that the zigzag sutures in a species of *Didymograptus* M'COY in SEDGWICK & M'COY, 1851–1855, s. str. (*Didymograptus artus* group) start only at some distance from the origin of the metasicula, and earlier fuselli were regularly developed.

MALETZ (1992, 2010a) used the origin of the first theca to define the ventral side of the sicula. The sicula is often adorned with a rutellum on this side, or with a spine, the ventral virgella (in most axonophorans). The rutellum is a rounded lip on the sicular aperture, formed by a downward extension and broadening of the fuselli at the ventral zigzag suture (Fig. 25.5). Its shape can be quite variable, and stongly elongated rutelli exist. The rutellum is usually broad and short, but it can develop into a distinct spoonlike feature as in *Kinnegraptus* (SKOGLUND, 1961). A dorsal rutellum is present in some genera and

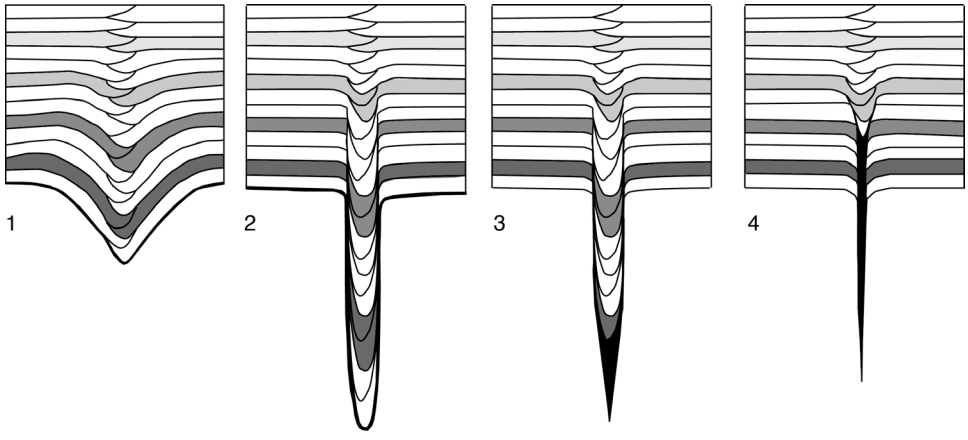


FIG. 27. The stages of development of the virgella. *1,* Rutellum; *2,* lamelliform rutellum; *3,* lanceolate virgella; *4,* virgella (adapted from Maletz, 2010a, fig. 2).

species, especially in the monograptids (e.g., JAEGER, 1978a, fig. 3; LENZ, 2013, fig. 9).

Beginning at the junction of the prosicula and metasicula in graptoloids, distinct, internal, thickened parallel rings, known as sicular annuli (KOZŁOWSKI, 1949) (Fig. 25.8), are present in many graptoloids. In many younger graptoloids, and commonly in the monograptids, such as those from the middle and upper Silurian (LENZ & KOZŁOWSKA-DAWIDZIUK, 1998), one or more annuli were formed on the inside walls of the metasicula (WALKER, 1953). Unlike the fusellar bands, the annuli are distinct, electron-dense, ringlike structures lying parallel to each other but typically at an oblique angle to the fusellar half rings on the dorsal and ventral sides of the sicula. The number and position of sicular annuli may be fixed in many upper Silurian taxa (URBANEK, 1997a). The function of annuli remains unknown, as does why they generally occur more frequently higher up the stratigraphic column. (URBANEK & others, 2012).

THE VIRGELLA

The metasicula may have a virgella or virgellar spine (Fig. 25.6–25.8, Fig. 27), developing from a prominent rutellum on either the dorsal or ventral side (MALETZ, 2010a). Its development can be differentiated into four stages (Fig. 27), often recognizable even in derived virgellate graptoloids. It starts with a rounded process, the rutellum, formed from the distal extension and widening of alternating fuselli on the ventral or dorsal side of the sicula. In a second stage, the rutellum is laterally restricted, and a thickened rim forms around it. At this stage, it is called a lamelliform rutellum (Fig. 27.2). In a third stage, a spine is added at the tip of the lamelliform rutellum, forming the lanceolate virgella (Fig. 27.3). A reduction of the lamelliform rutellum stage in the ontogeny of the virgella forms the true virgella (Fig. 27.4) in the last stage.

The virgella is now known to have originated independently in a number of Early to Middle Ordovician graptoloids (MALETZ, 2010a), as was suggested by BULMAN (1963a). A dorsal and a ventral virgella are differentiated, based on the position on the sicula (MALETZ, 2010a). The ventral virgella is positioned on the side of the origin of the first post-sicular theca with a dorsal virgella on the opposite side of the origin of the first theca.

The sicular aperture can bear a number of additional apertural modifications, other than the rutellum or the virgella (e.g., MITCHELL, 1987). A dorsal notch is present in many axonophorans, often associated with

paired antivirgellar spines (e.g., in the Lasiograptidae). The Dicranograptidae possess lateral lobes and paired notches on the sides of the virgellar spine. The Monograptidae bear various apertural modifications; and, whereas there are moderate variations within each pattern, many are species specific, for example, the tonguelike, ventrally curved, dorsal rutellum was a very common development among many single-stipe monograptids of the Lower Devonian (e.g., JAEGER, 1979; LENZ, 2013).

THE NEMA

The nema is a thin rod of material growing from the prosicula (cauda) in planktic graptolites, and the presence of a nema is, accordingly, regarded as evidence of a planktic life style (KOZŁOWSKI, 1971; RICKARDS, 1996). The nema of the Monograptidae has long been named the virgula, but it is now recognized to represent a modified type of nema, forming a leading rod on the dorsal side of the stipes of all monograptids (except those with a pseudovirgula), to which the thecae adhere (BULMAN, 1970; URBANEK & TOWE, 1975). Many biserial graptolites include the nema in the center of the colony, and this is often attached to an interthecal septum. However, the nema may also be off-center or even embedded in the obverse wall of the tubarium (see discussion of the median septum on p. 61). The distal end of the nema always grew in advance of the thecae in the development of the axonophoran colony.

The Monograptidae incorporate the nema as a dorsal rod of their stipes, where it also extends beyond the growing end of the branches. The importance of the nema in monograptids can be inferred from the fact that colonies with cladial branching produce a secondary nema, or pseudovirgula, as 1) the leading rod for the cladial stipe from one of the lateral apertural spines in *Cyrtograptus* CARRUTHERS in MURCHISON, 1867a (see THORSTEINSSON, 1955) and 2) as a separate new structure in the genus *Linograptus* (URBANEK, 1963) and possibly in others. A small number of strongly coiled Silurian monograptids over time abandoned the original nema, which was free at the isolated tip of the prosicula, and fabricated a pseudovirgula (Fig. 28) along which the stipe grew. This development was first recognized in *Cochlograptus veles* (RICHTER, 1871) by LOYDELL and CAVE (1994) and MALETZ (2001a) and was later also found in the late Wenlock *Testograptus testis* (BARRANDE, 1850) by LENZ and MELCHIN (2008).

In retiolitid taxa without a fully preserved prosicula, the nema is connected to the virgella by the virga (BATES, KOZŁOWSKA, & LENZ, 2005), a list secreted on the surface of the prosicula. It has a flat or grooved inner surface and a convex outer one. In the absence of a preserved prosicula, the length of the virgal groove serves as a proxy for the site and length of the prosicula. Toward (or at) the apex of the prosicula, the virga changes into a full concentric construction, marking the beginning of the nema.

THE INITIAL FORAMEN

The genus *Rhabdopleura* has a resorption foramen, an opening for the emergence of the sicular zooid from the dome, and a second resorption foramen for the origin of the first post-sicular zooid (STEBBING, 1970a). All subsequent zooids resorb a foramen into their compartment of the tube of the growing branch. The presence of a continual terminal zooid indicates a monopodial growth of the colony (URBANEK & DILLY, 2000). The derived taxa of the Graptolithina are an example of a sympodial growth in which each new zooid represents the temporary terminal zooid (URBANEK, 1986).

The origin of the first post-sicular zooid is through a foramen in the sicula. The position and type of this foramen have considerable implications for the higher-level taxonomy of the graptoloids. Initially, it was a resorption foramen, known from a few benthic specimens and most early planktic taxa. It is positioned in the middle to upper (distal) part of the erect tubular prosicula in *Dendrograptus communis* (KOZŁOWSKI,

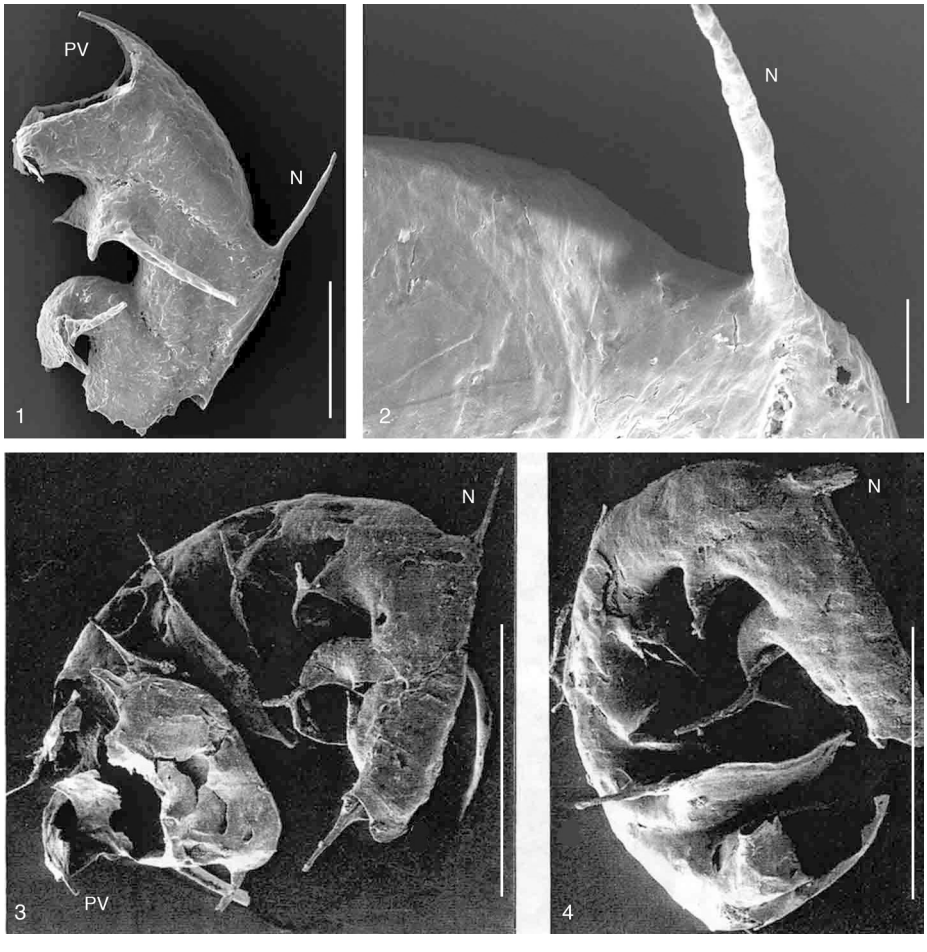


Fig. 28. SEM photographs of pseudovirgula. *1–2, Testograptus testis* (Barrande, 1850), Silurian (upper Wenlock), Canadian Arctic; *1,* tubarium fragment, scale bar, 0.5 mm; *2,* enlargement of pseudovirgula, scale bar, 0.2 mm (Lenz & Melchin, 2008, fig. 4A1–4A2); *3–4, Cochlograptus veles* (Richter, 1871), Silurian (upper Llandovery), Dalarna, Sweden, complete specimen with well-developed pseudovirgula, scale bars, 1 mm (Maletz, 2001a, fig. 3). *N*, nema, *PV*, pseudovirgula.

1971). Legrand (1964a) and Hutt (1974a) described the resorption foramen in the middle part of the conus in the upper Tremadocian *Adelograptus* Bulman, 1941, but it is unknown whether this position was typical of all Anisograptidae. A similar position occurred in the basal Tremadocian *Rhabdinopora* (Legrand, 1974). The foramen was located in the middle part of the conical prosicula in species of the upper Floian *Didymograptellus* Cooper & Fortey, 1982, but it was in the lowermost (distal) part of the prosicula in the closely related *Yutagraptus* Riva, 1994 and *Xiphograptus* Cooper & Fortey, 1982 (Maletz, 2010a). In most dichograptids, the origin of the first theca was in the lowermost part of the prosicula (Williams & Stevens, 1988; Williams & Clarke, 1999). The resorption foramen appeared in the metasicula in the axonophorans (Mitchell, 1987), mostly lying on the right side of the virgellar axis (Fig. 29.1), although sometimes the foramen developed precisely along the virgellar axis, before the origin of the virgellar spine (Loxton & others, 2011).

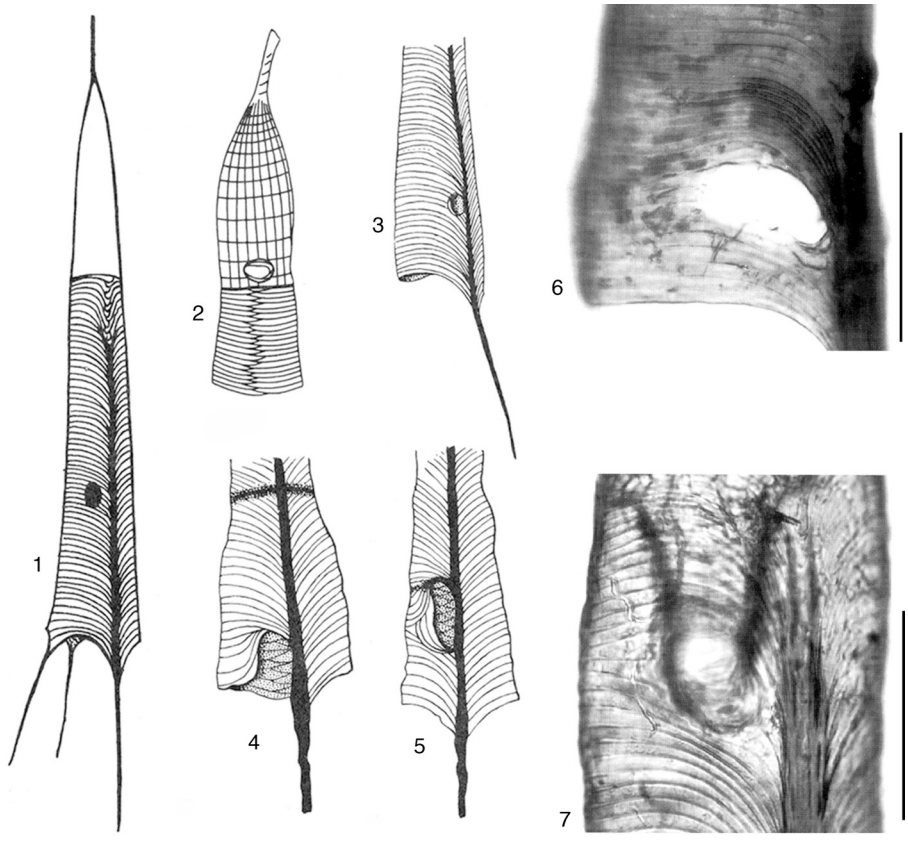


FIG. 29. Foramen development. *1, 3,* Resorption foramen in metasicula, typical of biserial graptolites; *2,* resorption foramen in lower part of prosicula as found in early dichograptids; *4–5,* sinus (*4*) and lacuna (*5*) stages, forming the primary opening for the first theca and developed only in monograptines; *6–7,* lenticular foramen in *Monograptus* sp. cf. *M. arciformis* CHEN & LIN, 1978, Silurian (lower Llandovery), scale bars, 0.1 mm (Dawson & Melchin, 2007, pl. 1).

At some point, a change occurred in the Monograptidae (Fig. 29.4–29.7). Previously, the foramen in the monograptids was considered to be a primary foramen left as an initial opening during the growth of the sicula through the sinus and lacuna stages (EISENACK, 1942). Isolated material indicates that early monograptids (e.g., *Atavograptus* RICKARDS, 1974; *Pribylograptus* OBUT & SOBOLEVSKAYA, 1966; *Coronograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968; and *Lagarograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968) possessed a resorption foramen (LUKASIK & MELCHIN, 1994, 1997). A modified resorption foramen with additional fusellar deflection developed in a number of *Monograptus* s.l. species (MELCHIN & KOREN', 2001). DAWSON and MELCHIN (2007) recognized the lenticular foramen (Fig. 29.6–29.7) as the first primary type of foramen, in which an opening for the emergence of the first post-sicular zooid is left in the metasicula. The originally described primary foramen of the younger monograptids with its typical sinus and lacuna stages (Fig. 29.4–29.5) was widely distributed in the greater portion of the Silurian and Devonian monograptids.

THECAL ONTOGENIES

The thecae of the Graptolithina are simple tubes, formed by repetitive clonal constructions, either with identical constructional mode or following a gradual change along

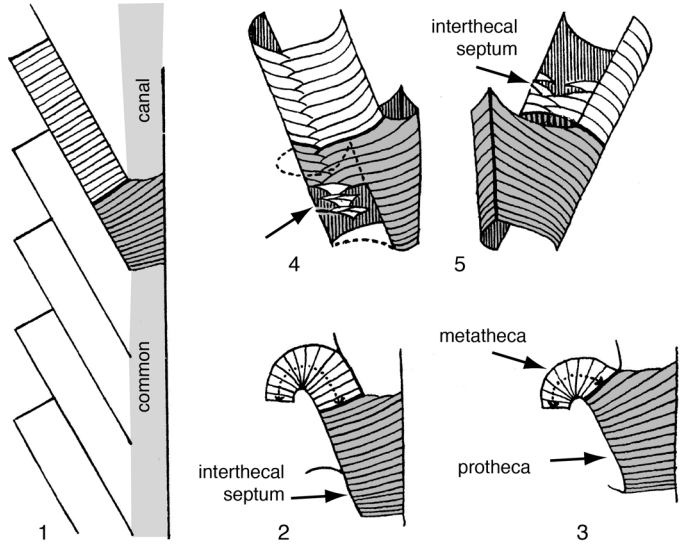


FIG. 30. Generalized shape and terminology of thecae. *1*, Lateral view of simple dichograptid (or pristiograptid) stipe with serially arranged thecae; *2–3*, lateral views of hooked thecae; *4*, oblique dorsal view showing development of interthecal septum; *5*, oblique ventral view showing development of interthecal septum (adapted from Bulman, 1955, fig. 30). *Light gray,* common canal; *dark gray,* prothecae.

the stipes (URBANEK, 1973). Fairly abrupt changes in the morphology of the thecae along a stipe occur in some species. The tubes in the Cephalodiscida, however, are formed as independent, not interconnected assemblages and are simple, round tubes when possessing an isolated aperture, sometimes provided with a distinct, perhaps ventral, rutellum, as in *Cephalodiscus* (*Idiothecia*) *nigrescens* HARMER, 1905. Even though modern pterobranchs, such as the extant *Rhabdopleura,* may possess separate male and female zooids, this differentiation is not expressed in the secretion of the housing tubes and interpretation is impossible from the fossil record.

The thecae, the housing structures for individual zooids, are the main building blocks of the graptolite colonies and define their construction and shapes. Individual thecae are interconnected through an opening in the Graptolithina, through which the next bud emerged to form its own thecal tube. The combined initial parts of the thecal tubes of a stipe are generally referred to as the common canal (Fig. 30.1) to emphasize the interconnection of the clonal, colonial development of the colonies; its existence, in fact, provides the evidence for a truly colonial organism. The common canal can be quite variable in size, depending on the geometry of the tubes and the shape of the prothecal parts of the thecae.

The thecae generally have a distinct thecal overlap, with the wall common to two overlapping thecae called an interthecal septum or internal septum (Fig. 30.5). The interthecal septum was secreted either by the first-formed thecal zooid or, in case of concurrent growth, as a combined effort of both thecal individuals (WALKER, 1953; URBANEK, 1958).

The degree of thecal overlap is quite variable and can reach high values (FORTEY, 1983). It is generally measured as a percentage of thecal length. Among the monograptids, a number of genera (e.g., *Campograptus* OBUT, 1949; *Rastrites* BARRANDE, 1850; and *Streptograptus* YIN, 1937) have little or no thecal overlap. Distally increasing thecal overlap is typical in many groups (e.g., *Didymograptellus* COOPER & FORTEY, 1982; *Expansograptus* BOUČEK & PŘIBYL, 1952a; *Nichol-*

sonograptus BOUČEK & PŘIBYL, 1952a; and certain monograptids including *Monograptus* s. str.) and commonly leads to extremely wide and robust distal stipes. Differences in the amount of thecal overlap can be used for taxonomic purposes, as in *Didymograptellus bifidus* (HALL,1865) by WILLIAMS and STEVENS (1988). (See discussion of thecal gradients on p. 54.)

The free ventral wall is the portion of the ventral theca margin that extends beyond the aperture of the preceding theca. The length of the free ventral thecal wall depends on the growth patterns of the thecae and is used for taxonomic differentiation in certain groups. It tends to be greater in thecae with low inclination.

The differentiation of the protheca and metatheca (Fig. 30) can be problematic, as a distinct break in the fusellar growth is not present in most thecae. The protheca may be recognized as the part of a theca before the insertion of an interthecal septum, but this varies from species to species. In taxa without an interthecal septum, the point at which the theca becomes a complete tube (for example, when the foramen of the daughter theca is closed) can be defined as the start of the metatheca (Fig. 30.3). This definition follows the distinction advocated in BULMAN (1955, 1970). MÜNCH (1938) discussed the common canal in monograptid thecae in some detail and suggested the terms semitubus, metatubus (protheca), and thecatubus (metatheca) to differentiate parts of the thecae, although these differ little from protheca and metatheca.

AUTOTHECAE AND BITHECAE

Two main thecal types can be differentiated: the autothecae and the bithecae (COOPER & FORTEY, 1983). Many benthic graptoloids, and even a few early planktic forms, possessed this distinct differentiation of their thecal tubes, with larger tubes identified as autothecae and smaller ones as bithecae. The reason for this differentiation is unknown, although a sexual differentiation has been suggested (e.g., HUTT in PALMER & RICKARDS, 1991). Alternatively, KIRK (1973) suggested that the smaller bithecae may have housed cleaning individuals.

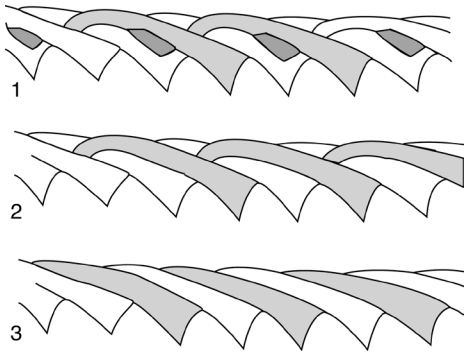


FIG. 31. Triad budding and plaited thecal overlap. *1,* Bithecate stipe in lateral view with lateral originating, alternating autothecae (*light gray*) and bithecae (*dark gray*), same construction would be seen on the other side of the stipe; *2,* non-bithecate stipe with plaited thecal overlap and lateral thecal origination; *3,* non-bithecate stipe with dorsal origins of autothecae (adapted from Lindholm, 1991, fig. 4).

Autothecae and bithecae (Fig. 31) are arranged in a consistent and highly geometrical pattern in most bithecate colonies. Each autotheca is connected to a bitheca, except at branching points, where the bitheca is replaced by a second autotheca. Normally, the bithecae occur alternately on both sides of the stipes, but irregularities are common in some taxa. Several successive bithecae on one side of a stipe are present in *Kiaerograptus kiaeri* (MONSEN, 1925), for example (SPJELDNAES, 1963; LINDHOLM, 1991). Complex growth patterns of bithecae occur in many dendroid graptolites (e.g., BULMAN, 1955; RICKARDS & others, 2003).

A number of other thecal types have been described in the various benthic taxa. Conothecae, microthecae, and umbellate thecae occur in the Cyclograptidae BULMAN, 1938, while autothecae are modified into highly inflated camerae and erect columns in the Cysticamaridae BULMAN, 1955. The details are discussed in the various taxonomic sections.

THECAL MORPHOLOGY AND MODIFICATIONS

The thecae of the Graptolithina are highly variable (Fig. 32), and the simple tubes of early benthic taxa are considerably modified in later forms. Structural modifications are here differentiated by their position on the thecae and their development. In the past, thecal types have been differentiated and named after their characteristic genera. Thus, dichograptid (Fig. 32.9), climacograptid (Fig. 32.11, Fig. 32.15), diplograptid (Fig. 32.10), glyptograptid (Fig. 32.13), nemagraptid, leptograptid (Fig. 32.17), and other thecal types are commonly used in the descriptive terminology of graptoloid thecae (Bulman, 1970). Initially, differences in the thecal shapes originate from the variation of widening of the thecae, which may be gradual and persistent (e.g., simple dichograptid), or in increments, producing bulges or cupulae (e.g., in *Pseudostreptograptus* Loydell, 1991a, and *Streptograptus* Yin, 1937) on the dorsal sides of thecae (Fig. 32.4, Fig. 32.8). In others, the thecae widen considerably from an initial width and then continue parallel sided (e.g., in climacograptids) or even decrease in width distally (e.g., *Dicranograptus* Hall, 1865, and some climacograptids).

The geniculum (Fig. 32.11, Fig. 32.15) is a distinct angular feature on the ventral side of the theca and quite common in the biserial groups as well as in some monograptids. It is often enhanced by hoodlike genicular flanges (Fig. 32.6, Fig. 32.2); but spines, lobed additions, and other enhancements may be present. The geniculum can also be rounded, but it invariably involves an abrupt change in inclination of the ventral thecal wall. Geniculate thecae are common in graptolites of all groups, from the dichograptids (*Aulograptus* Skevington, 1965) to axonophorans (*Climacograptus* Hall, 1865; *Archiclimacograptus* Mitchell, 1987; *Dicellograptus* Hopkinson, 1871; Fig. 32.17), to monograptids (*Monoclimacis* Frech, 1897), and retiolitinids (Fig. 32.7). The geniculum in all these graptolites is structurally homologous, but evolutionarily analogous, as is evidenced by its independent origination in many groups.

Thecae with a distinct recurved thecal aperture are called hooked thecae. The thecal hook is formed from an isolated metatheca with continuous fuselli. A typical example is *Monograptus priodon* Bronn, 1849 (Fig. 32.5), in which the distal metathecae form an open hook. A lateral or transverse widening of the thecal apertures

Fig. 32. Thecal morphologies. *1, Proteograptus opimus* (Lenz & Melchin, 1991), Silurian (Wenlock, upper Sheinwoodian), Canadian Arctic, scale bar, 1 mm (Lenz & others, 2012, pl. 13); *2, Demirastrites triangulatus* (Harkness, 1851) Silurian (Llandovery), central Wales, scale bar, 1 mm (Palmer & Rickards, 1991, pl. 74); *3, Crinitograptus operculatus* (Münch, 1938), Silurian (lower Ludlow), Canadian Arctic, scale bar, 0.1 mm (Lenz & Kozłowska-Dawidziuk, 2004, pl. 30); *4, Pseudostreptograptus williamsi* Loydell, 1991a, Silurian (Llandovery, lower Telychian), Sweden, scale bar, 1 mm (Palmer & Rickards, 1991, pl. 76); *5, Monograptus priodon* (Bronn, 1849), Silurian (middle Wenlock), Canadian Arctic, scale bar, 1 mm (Lenz & others, 2012, pl. 8); *6, Okavites spiralis* (Geinitz, 1842), Silurian (Llandovery, upper Telychian), Canadian Arctic, scale bar, 1 mm (new); *7, Papiliograptus papilio* Lenz & Kozłowska-Dawidziuk, 2002a, Silurian (Wenlock, upper Homerian), Canadian Arctic, showing thecal geniculae with large, supragenicular hoods, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 11); *8, Streptogaptus galeus* Lenz & Kozłowska, 2006, Silurian (Wenlock, lower Homerian), Canadian Arctic, scale bar, 0.5 mm (Lenz & Kozłowska, 2006, fig. 12); *9, Expansograptus abditus* Williams & Stevens, 1988, Lower Ordovician (Floian), Newfoundland, Canada, with simple, tubelike thecae, cleared to show fusellar half rings, scale bar, 1 mm (Williams & Stevens, 1988, pl. 14); *10, Neodiplograptus sinuatus sinuatus* (Nicholson, 1869), Silurian (middle Llandovery), Canadian Arctic, with biform thecae, scale bar, 1 mm (Melchin, 1998, pl. 3); *11, Clinoclimacograptus barriei* (Zalasiewicz & Tunnicliff, 1994), Silurian (middle Llandovery), Canadian Arctic, with strong geniculae, scale bar, 1 mm (Melchin, 1998, pl. 1); *12, Chigraptus supinus* Jackson & Lenz, 2003, Lower Ordovician (Tremadocian), Canada (northern Yukon), scale bar, 1 mm (Jackson & Lenz, 2003, fig. 6a); *13, Glyptograptus elegans* ssp., Arctic Canada, scale bar, 1 mm (Melchin, 1998, pl. 3.13); *14, Lobograptus scanicus* (Tullberg, 1883), Silurian (lower Ludlow), Canadian Arctic, with large, lobelike thecal lappets, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2004, pl. 32); *15, Glyptograptus elegans* (s.l.) Packham, 1962, Silurian (Llandovery), Canadian Arctic, scale bar, 1 mm (Melchin, 1998, pl. 5); *16,* Lignigraptus *kinnegraptoides* (Erdtmann, Maletz, & Gutiérrez-Marco, 1987), Lower Ordovician (Floian), Canada (Yukon), scale bar, 1 mm (Jackson & Lenz, 2006, fig. 7n); 17*, Jiangxigraptus vagus* (Hadding, 1913), Middle Ordovican (upper Darriwilian), Scania, Sweden, scale bar, 1 mm (new).

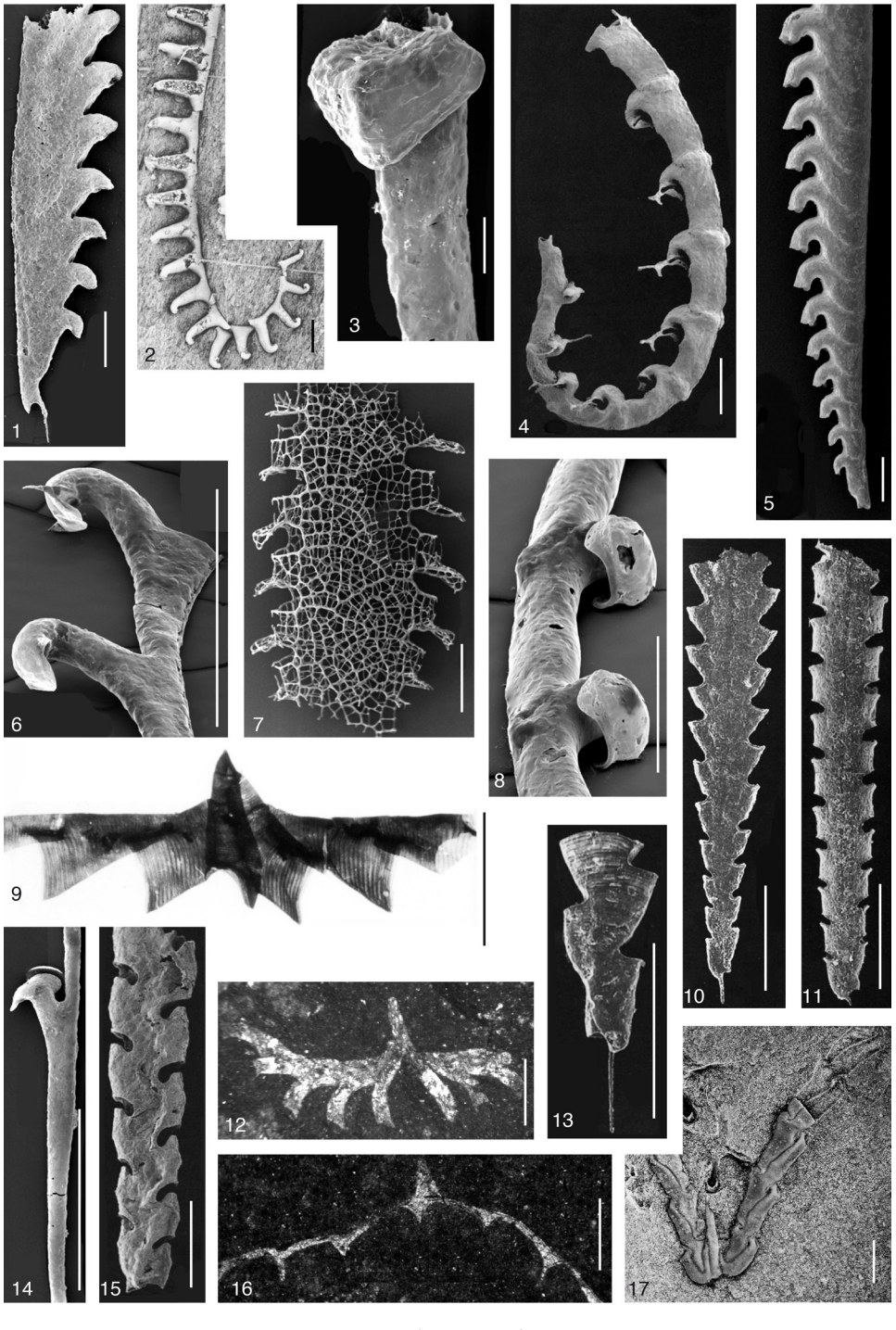


FIG 32. *For explanation, see facing page.*

may be associated with this thecal development, but restricted apertures may also be present. Hooked thecae may or may not have thecal overlap or even astogenetic variation in this character (e.g., *Stimulograptus* Přibyl & Štorch, 1983 and *Monograptus*). A special case of the hooked thecal aperture is identified as lobate (Bulman, 1970), in which the metatheca grows back on itself, e.g., *Campograptus lobiferus* (M'Coy, 1850) and *Lapworthograptus* Bouček & Přibyl, 1952b). Hooked thecae are most common in the Monograptidae, and more numerous and varying elaborations are present in these forms than in any other group.

A thecal development that may appear very similar to the hooked thecae has been identified as hooded thecae (Bulman, 1970). In this form, a thecal hood covers the thecal aperture (Fig. 32.3). The thecal hood is formed either as an extension of the dorsal wall of the theca or as a secondary, sometimes genicular addition to the thecal aperture. It is not comparable in development to the hooked theca, in which the development is completely formed by the dorsal and ventral thecal walls. Hooded and hooked thecae are very difficult to differentiate in flattened material. Isolated specimens possessing fusellar structure may be needed to recognize the precise development.

The thecae of the monograptids have the greatest variety—simple tubes, smoothly hooked (Fig. 32.5), tall, scarcely overlapping, elongated, distally hooked (Fig. 32.2, Fig. 32.4), bi- or multiform, or complex proximally to simpler distally (Fig. 32.1). They may have large thecal hoods that obscure the thecal aperture (Fig. 32.3), strongly hooked theca (sometimes with torsion), and/or various kinds of spines (Fig. 32.6), or have lobate and asymmetrical lappets (Fig. 32.14). On the other hand, thecae with fairly complex or unusual features were already present in a few Tremadocian and Floian taxa, such as *Paradelograptus* Erdtmann, Maletz, & Gutiérrez-Marco, 1987; *Psigraptus* Jackson, 1967; and *Chigraptus* Jackson & Lenz, 1999 (Fig. 32.12).

Thecal isolation is common in many graptolites. In the benthic Callograptidae and Acanthograptidae, the typical thecal tubes possess isolated apertures, but thecal overlap is present on the stipes. An isolation of thecal apertures occurs in many planktic graptoloids. The metathecae can be completely or only partially isolated. In taxa with complete metathecal isolation, there is no thecal overlap and, accordingly, no interthecal septum is present (Fig. 32.2).

Partial isolation is present in benthic taxa and also in many planktic forms. Partial isolation of the metatheca has been described in the Tremadocian genera *Chigraptus* (Fig. 32.12) and *Kiaerograptus* and is common in Silurian monograptids with thecal hooks (e.g., *Monograptus*, *Streptograptus*). Completely isolated metathecae are present in *Rastrites* Barrande, 1850; *Demirastrites* Eisel, 1912; *Lituigraptus* Ni, 1978; and a number of other monograptid genera, in which a gradual change in thecal shape is typically also present. The term triangulate has been used frequently for the thecal shapes in this group (Sudbury, 1958) (Fig. 32.2).

The orientation of the thecal aperture ranges from introverted through perpendicular to everted, unless hooks modify the apertural orientation. This orientation can also be affected by apertural modifications, which are common in graptolites and often used for identification of both species and genera. Apertural modifications are highly variable and can be difficult to interpret in flattened material. Even the number and orientation of spines and flanges cannot be identified correctly without isolated, three-dimensionally preserved specimens. Apertural modifications are defined independent of the orientation of the aperture and may include a wide variety of spines (Fig. 32.4, Fig. 32.6), lobes, shelves, and selvages. These can be defined by their position on the theca as dorsal, ventral, or lateral.

Prothecal folds and intrathecal folds, termed recumbent folds by Cooper and Ni (1986), are features related to the origin of

the thecae in some Sinograptina and in the axonophorans and have not been recognized in benthic graptolites. Thecal folding is indicated through a change in growth direction of a thecal tube. The theca generally grows back on itself, forming a conspicuous bending of the tube. The growth direction is taken to differentiate prothecal and intrathecal folds (Fig. 33). The development of a prothecal fold forms around the base of an interthecal septum (Fig. 33.1), whereas in intrathecal folds, a secondary bar or septum forms from the dorsal side of the stipe (Fig. 33.2). The details of the development of prothecal and intrathecal folds are not known from isolated material.

Prothecal folds have been used to define the Sinograptidae (Mu, 1957) but are now known to be present in a number of independent groups of planktic graptoloids. The earliest example includes the dichograptid *Cymatograptus undulatus* (Törnquist, 1901) from the lower Floian of Scandinavia (Jaanusson, 1965), but bithecate taxa with apparent prothecal folding have also been described. Prothecal folds in the upper Tremadocian *Cymatograptus lauzonensis* Erdtmann, 1966, now *Kiaerograptus lauzonensis* (see Maletz & Egenhoff, 2001), are enhanced by the presence of bithecae with lateral thecal origins, the plaited thecal overlap of Lindholm (1991).

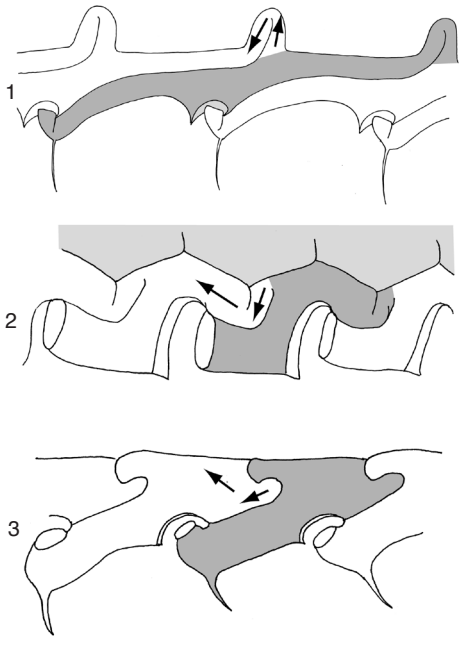


Fig. 33. Diagrams of prothecal and intrathecal folds. *1, Holmograptus* sp., with pronounced prothecal fold; *2, Haddingograptus* sp., intrathecal folds with bar originating from median septum, second thecal series in *light gray; 3, Dicellograptus* sp., intrathecal fold in relief specimen without fusellar structure; all reconstructions adapted from relief material, one theca indicated in *darker gray* in each illustration, arrows indicate growth direction (new).

SERIALITY OF THECAE

The zooids of *Rhabdopleura* bud from each other in a sequential manner, forming a serial succession. However, the secreted tubes of the individual zooids branch irregularly from this succession to both sides of the main axis (Fig. 16.2). The erect tubes in *Rhabdopleura normani,* for example, may originate on the left and right side of the central axis (Fig. 16.2), with no apparent regular organization (Lankester, 1884). Due to the clonal development of the colonies and the constructional mode of new tubes, a distinct regularity evolved and occurs in most derived graptolites. Irregularities are most pronounced in benthic encrusting colonies, probably recalling the original unordered development of the *Rhabdopleura* colonies. The Cyclograptidae retain some of the disorganization of their thecal tubes but develop a distinct internal regularity, fostered by their underlying budding system. The thecal tubes in these forms are round, with isolated apertures. A differentiation into a dorsal and ventral side is visible only through the presence of the zigzag sutures of the regularly organized fusellar half rings of the tubes.

Most dendroids and graptoloids developed a highly precise seriality of their thecal arrangements in which all thecal apertures on the stipe are precisely oriented in the same direction (Fig. 16.1, Fig. 30.1, Fig. 31). This arrangement has been retained by all planktic taxa, including the Silurian to

Lower Devonian monograptids (Fig. 32). The ventral rutellum and the development of thecae without complete apertural isolation were already present in such dendroid graptolites as *Dendrograptus* and *Dictyonema* (Wiman, 1896; Bulman, 1933a). This differentiation of the dorsal and ventral sides of the thecal tubes developed in all derived pterobranchs with serially arranged thecae.

THECAL GRADIENTS

Thecal gradients or astogenetic variation of thecae is an aspect of many planktic graptolites and has been studied in some detail (e.g., Bulman, 1963; Urbanek, 1973). Minor gradual change in size of thecae is most commonly observed in graptolites, especially in the dichograptids, typically associated with a distally increasing thecal overlap (see Cooper & Fortey, 1982; Williams & Stevens, 1988). Biform or multiform colonies are common in many axonophorans (biserials and monograptids), with different thecal styles at the proximal and distal ends (Fig. 34). Changes can be fairly gradual and include minor structural modifications of the apertures, but taxa with dramatic changes along the stipes are not uncommon, such as in *Paramonoclimacis sidjachenkoi* (Obut & Sobolevskaya, 1965) and *Monograptus limatulus* Törnquist, 1892. These changes may be dramatic enough that the stipe fragments could easily be referred to different genera. The modifications may be precisely located, and a distinct change may occur at a certain theca along the length of the colony (Fig. 34), but they can also be more variable.

THE WIMAN RULE AND TRIAD BUDDING MODEL

The Wiman rule originally described the interconnection of three thecal types and the branching of the thecal tubes, which is the external expression of the internal stolon system (Kozłowski, 1949). Initially, triad budding was understood as a branching in triads from a stolotheca, in which the stolotheca does not possess an apertural opening but is accompanied by a new autotheca and a bitheca. Kirk and Bates (in Kirk 1969) and Bulman (1970, p. 26) recognized the stolotheca as the "immature basal portion of the succeding autotheca." Thus, a separate stolothecal zooid does not exist, and the stolotheca and succeeding autotheca are now regarded as a single unit, the autotheca (Cooper & Fortey, 1983).

In a typical triad, each autotheca produces a new autotheca and a new bitheca (Fig. 35.1), effectively eliminating the need of the term stolotheca. The Wiman rule, in its revised meaning, essentially states that at each branching point a new autotheca is formed on one side of the stipe, while on the other side, a bitheca is developed at the same point. This development produces bithecae and autothecae, alternately, on the left and right side of the stipes (Fig. 31.1, Fig. 35). All thecal origins are lateral in these taxa, forming a structure that was termed plaited thecal overlap (Fig. 31.1) by Lindholm (1991), including taxa in which bithecae are absent (Fig. 31.2).

The number of bithecae of the planktic graptoloids became fewer over time, apparently in all lineages. By the end of the Tremadocian, they were scarce and were completely absent during the Floian. The details of these changes are still unclear, but a number of separately evolving lineages may have lost their bithecae and the plaited thecal overlap independently (Fortey & Cooper, 1986; Lindholm, 1991). In derived graptoloids, the thecal origins are on the dorsal side of the stipes, even though lateral thecal origins from a dicalycal theca may still occur at branching points.

THE DICALYCAL THECA

The structural details of the branching in graptolite colonies is known from specimens preserved in full relief and from isolated specimens. Dichotomous branching is invariably related to the presence of a dicalycal theca (Fig. 35), a theca that produces two autothecae instead of an autotheca and a bitheca (Maletz, 1992). In forms with triad budding, branching is achieved through

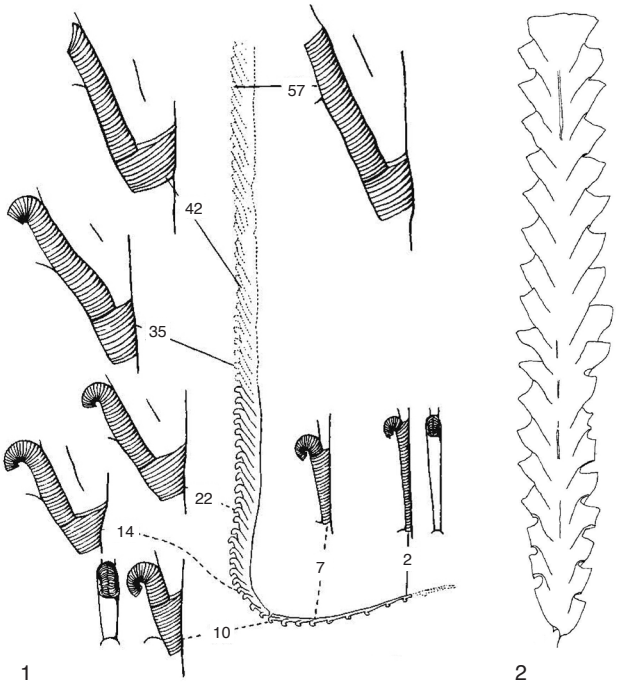


FIG. 34. Thecal gradients. *1, Pernerograptus argenteus* (NICHOLSON, 1869), thecal modifications along the stipes of a specimen; *numbers* indicate position of thecae along stipe (Bulman, 1955, fig. 29); *2, Neodiplograptus apographon* (ŠTORCH, 1983), thecal gradient (Loydell, 2007, fig. 10D).

the replacement of a bitheca with an autotheca at one of the triads. A bitheca, therefore, is missing at the branching point (Fig. 35.1–35.2). The previous autotheca curves distinctly in the direction of one of the new stipes, and the first new autotheca of this stipe grows along its back. The second theca produced by the dicalycal theca bends directly away to form the second stipe (Fig. 35.2).

Successive dicalycal thecae are present in early planktic graptolites (e.g., *Staurograptus* EMMONS, 1855; *Rhabdinopora* EICHWALD, 1855), but apparently a dicalycal theca can produce only one additonal dicalycal theca and one normal autotheca (MALETZ, 1992). In younger graptoloids, dicalycal thecae were separated by at least one normal monocalycal theca and, thus, were not successive.

In graptolithines without triad budding, the development differs slightly, but follows the same general rules described by MALETZ (1992). The main difference is that in non-bithecate taxa, autothecae can produce only a single new theca (an autotheca), whereas a dicalycal theca retains the ability to produce two new autothecae (Fig. *35.3).* Another difference occurs in the origination of daughter thecae, which are no longer paired, but originate at different levels on the mother theca (Fig. 35.3).

THECAL NOTATION

Thecal notation was introduced by ELLES (1897) for biserial colonies and was adopted and modified by BULMAN (1970). Its modern use is discussed by COOPER and FORTEY (1982) and is followed herein. It is easy for two-stiped colonies, in which the thecae of thecal series 1 (the primordial series of ELLES, 1897) are labeled $th1^1$, $th2^1$, $th3^1$, etc., and the thecae of thecal series 2 are labeled $th1^2$, $th2^2$, $th3^2$, etc. (Fig. 36). The thecal notation is a bit more complicated in taxa with a

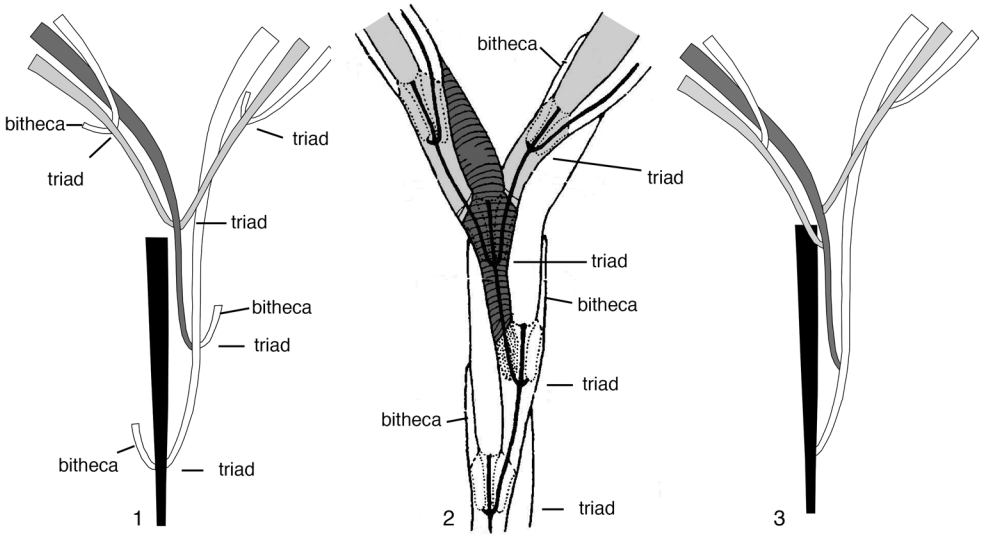


FIG. 35. Triad budding and dicalycal theca. *1,* Diagram of bithecate taxon showing the triad budding system (adapted from Cooper & Fortey, 1983, fig. 7); *2,* branching division of *Rhabdinopora flabelliformis* (EICHWALD, 1855), also showing the internal stolon system (adapted from Bulman, 1970, fig. 13.1); *3,* thecal diagram of non-bithecate form; note that the two daughter thecae originate at different levels on the dicalycal theca (adapted from Cooper & Fortey, 1983, fig. 7). *Dark gray,* dicalycal thecae; *light gray,* derived autothecae.

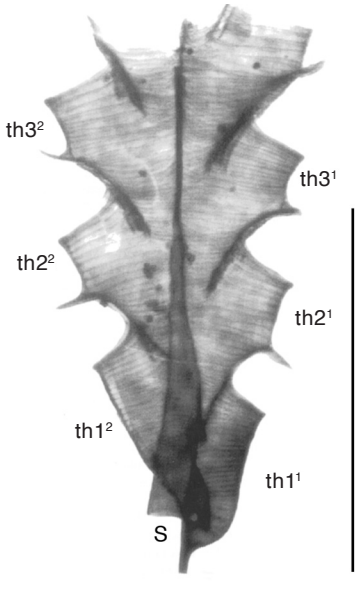


FIG. 36. Thecae labeling procedure on the scandent biserial *Paraclimacograptus exquisitus* RICKARDS, 1970; *S,* sicula; scale bar, 1 mm (adapted from Russell, Melchin, & Koren', 2000).

higher number of stipes, but it is rarely used. COOPER and FORTEY (1982, 1983) provided a useful system for such taxa and compared it with the system of BULMAN (1970). The system used by LEGRAND (1964a) is not supported here.

THE STOLON SYSTEM

An important aspect of the Graptolithina is the stolon system (Fig. 35.2, Fig. 37.1), which connects the individual zooids in the extant *Rhabdopleura* (URBANEK & DILLY, 2000), and is also known from fossil graptolites (e.g., KOZLOWSKI, 1949; HUTT, 1974a; BATES & URBANEK, 2002; SAUNDERS & others, 2009). The stolon system, which is not secreted by the cephalic shield, may represent the only preservable part of the actual organisms, the zooids. In the Cephalodiscida, the new zooids originate from the base of the zooidal stalk (originally called the peduncle or contractile stalk) and separate when mature. In the Graptolithina, a stolon system develops connecting the individual zooids for life as a true colony (LANKESTER,

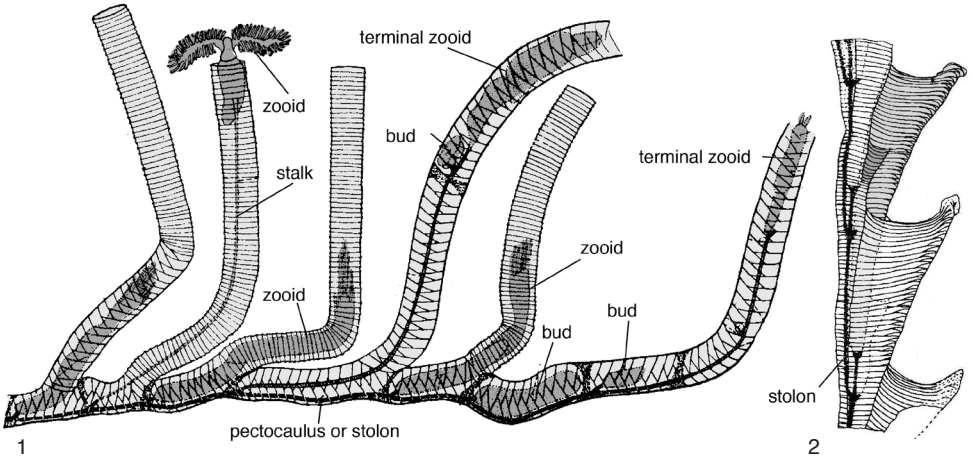


FIG. 37. The stolon system. *1,* Pectocaulus (stolon) in *Rhabdopleura* (adapted from Kozłowski, 1949, fig. 11, and Schepotieff, 1907b, pl. 22); *2,* stolon system (*black*) in stipe fragment of *Adelograptus tenellus* (LINNARSSON, 1871) (adapted from HUTT, 1974a, fig. 8).

1884; SCHEPOTIEFF, 1906). The zooidal stalk attaches the zooid to the stolon, the sclerotized and inflexible strand of organic matter connecting all zooids with each other (Fig. 37). Details of the stolon system are difficult to obtain and are unknown from most planktic graptoloids.

COLONIAL ASTOGENY

OBVERSE AND REVERSE SIDE

The two sides of the graptolite colonies may differ considerably in their appearance, especially when the proximal development on the reverse side of the tubarium is complex. This is clearly present in all Graptoloidea, except for the single-stiped Monograptidae. The initial portions of the first few thecae, the crossing canals, grow across the sicula and cover it in part on one side of the tubarium. This side is generally identified as the reverse side. The only part of the sicula visible on the reverse side of a biserial colony is the aperture and the virgella (Fig. 38.5), but on the obverse side, at least part of the sicula is visible (Fig. 38.6). In nonbiserial taxa, the complete sicula is visible on the obverse side (Fig. 38.2). The genera *Pseudisograptus* (Fig. 38.1) and *Arienigraptus* cover a larger part of the sicula on the reverse side of the colony, where the complex construction of the manubrium takes place.

DEXTRAL AND SINISTRAL DEVELOPMENT

The proximal geometry, structure, and development types of the major groups of the Graptoloidea were redefined by COOPER and FORTEY (1982, 1983), and dextral and sinistral developments were differentiated (Fig 39). Dextral and sinistral growth types have been illustrated from various anisograptid and dichograptid specimens, but the frequency of the dextral and sinistral development types is unknown, due to the very limited number of specimens available (MALETZ, 2021). The dextral and sinistral development of the proximal end may not be connected to the dextral and sinistral development of the helical line of the prosicula. Most authors (e.g., BULMAN, 1936a; LEGRAND, 1964a; HUTT, 1974a) agree that the proximal development in anisograptids can be either dextral or sinistral. SPJELDNAES (1963) discussed the dextral and sinistral development of the late Tremadocian genera *Bryograptus* LAPWORTH, 1880a; *Kiaerograptus* SPJELDNAES, 1963; and *Ancoragraptus* JACKSON & LENZ, 2003 in some detail and provided illustrations of both types

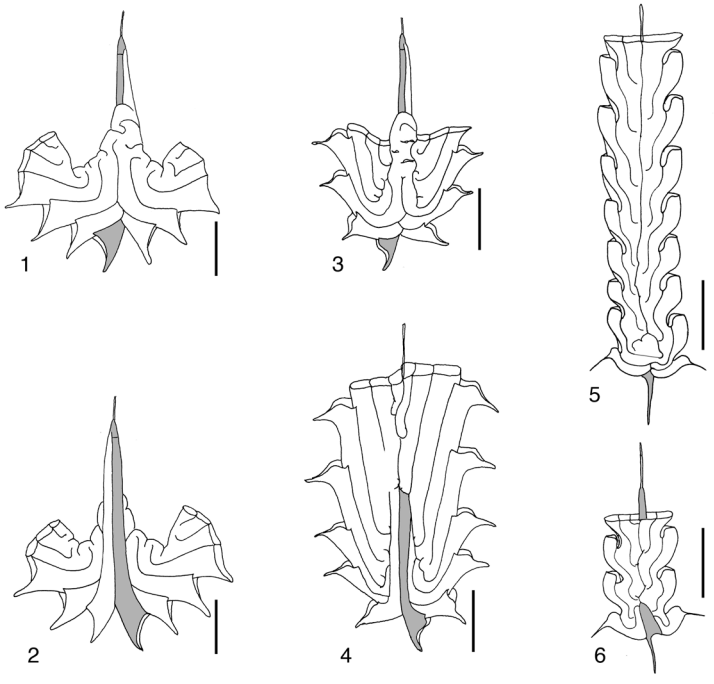


FIG. 38. Obverse and reverse sides of colonies. *1–2, Pseudisograptus bellulus* COOPER & NI, 1986, in reverse (*1*) and obverse (*2*) views; *3–4, Exigraptus uniformis* MU in MU & others, 1979, reverse (*3*) and obverse (*4*) views; *5–6, Levisograptus austrodentatus* (HARRIS & KEBLE, 1932) reverse (*5*) and obverse (*6*) views; sicula shaded to highlight the differences of obverse and reverse sides, scale bars, 1 mm (new).

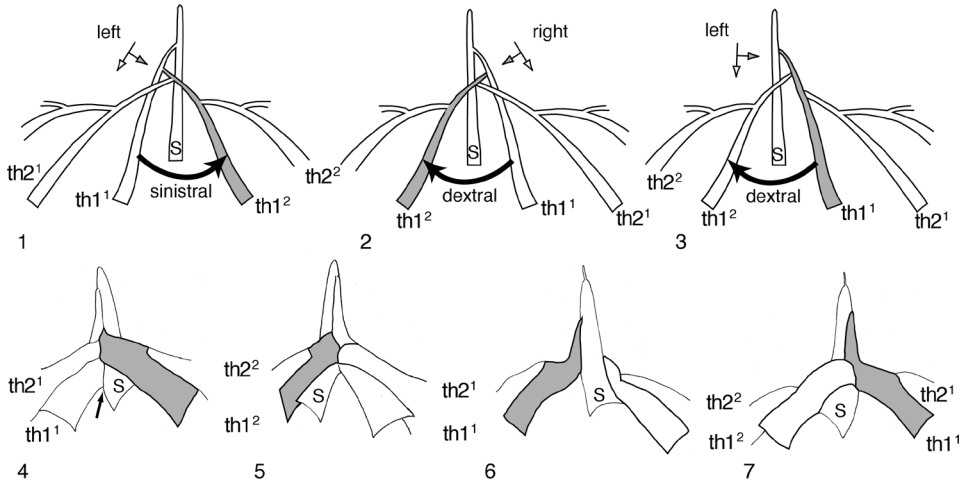


FIG. 39. Dextral and sinistral development and the proximal development types in Dichograptacea (with thecal notation). *1–3,* Thecal diagrams; *1,* isograptid-type, sinistral development; *2,* isograptid-type development, dextral; *3,* artus-type development, dextral; *4–7,* reconstructions of proximal developments; *4–5,* isograptid-type development in *Cymatograptus* sp., sinistral (*4*) and dextral (*5*) style; *6–7,* dextral, artus-type development in *Cymatograptus bidextro* TORO & MALETZ, 2008, obverse (*6*) and reverse (*7*) views (Toro & Maletz, 2008, fig. 6).

in his relief specimens from the uppermost Alum Shale Formation of Norway. Toro and Maletz (2008) described dextral and sinistral specimens of *Cymatograptus bidextro* Toro & Maletz, 2008 from the middle Floian of Argentina, the youngest- known taxon in which dextral and sinistral development is present. The dextral development is the standard in younger graptoloids and a sinistral development is extremely rare (Cooper & Fortey, 1983).

THE PROXIMAL DEVELOPMENT

Stebbing (1970a) described the early astogeny of extant *Rhabdopleura compacta* zooids and the tubarium structure. The sicular zooid buds a new zooid from the base of the zooidal stalk, then forms a septum to separate a part of the dome as an initial housing for the first zooid. The first zooid subsequently resorbs a foramen into its part of the dome and starts secreting fuselli and a new tube alongside the tube produced by the founder zooid.

The development is similar in species with an erect or planktic prosicula. However, the zooids construct a tube much smaller than the initial tube of the first post-sicular zooid of *Rhabdopleura*. Growth is initially in the direction of the sicular aperture, and is related to a considerable widening of the tubes and an increasingly regular development of the fuselli. This initial growth pattern occurs in all graptoloids, including normalograptids, except the monograptids in which the first theca emerged and always grew in a direction opposite to that of the sicular aperture.

The most important aspect of the next step in the astogeny of the graptolite colony (other than uniserial taxa) is branching, and especially the branching of Early Ordovician forms, as it defined the shape of the emerging colony. Branching was accomplished by the development of a branching division, expressed as a dicalycal theca in the tubarium.

The proximal development has been the focus of numerous investigations, which provided the basis for the main taxonomic interpretations and classification of the graptoloids. Elles (1922) differentiated four types of proximal development: the dichograptid, leptograptid, diplograptid, and monograptid types. This early concept was elaborated on by a number of people, and more than 30 different proximal development types and subtypes are now differentiated (e.g., Mitchell, 1987, 1994; Melchin, 1998; Melchin & others, 2011).

The earliest proximal development type is called the isograptid type (Cooper & Fortey, 1983), with a first dicalycal theca at $th1^2$ (Fig. 40.1). The artus-type development (Fig. 40.2) differs mainly in the change to a first dicalycal theca at $th1^1$. It is interesting, however, to mention that almost all nonaxonophoran graptoloids have the isograptid-type development no matter what thecal style or stipe orientation the colonies possess. The only difference from the artus-type development is the position of the dicalycal theca (Cooper & Fortey, 1983). A finer differentiation of the proximal development types of the Dichograptina could otherwise easily lead to another plethora of proximal development types.

The majority of the described proximal development types are from the axonophorans with their complex, proximal-end structure. These types basically define the position of the initial dicalycal theca and the development of the crossing canals, but commonly include numerous independent characters of the sicula and thecae (Fig. 41). Cooper and Fortey (1983) differentiated the proximal-end construction into the proximal development type and the proximal structure, but this distinction was not adopted by axonophoran taxonomists.

Following Mitchell (1987), Melchin and Mitchell (1991), Melchin (1998), and Melchin and others (2011) defined a number of proximal development types in the axonophorans. These were based on increasingly smaller differences in the construction of the graptolite colonies. The main characters of these proximal developent patterns include the position of the dicalycal

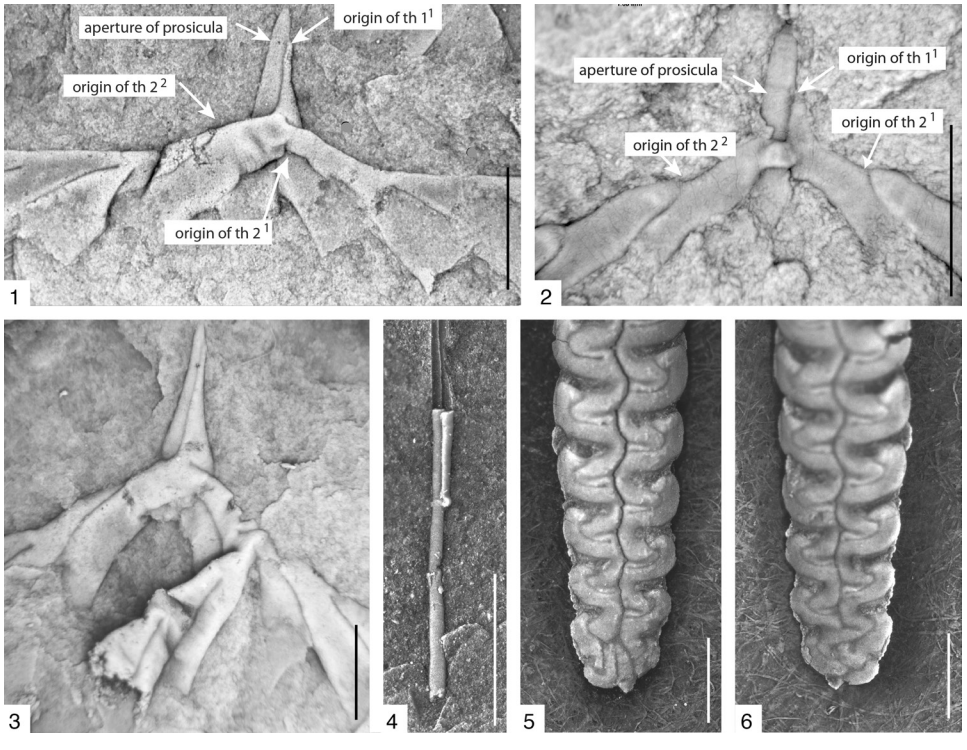


FIG. 40. Proximal development types. *1, Expansograptus holmi* (TÖRNQUIST, 1901), reverse side, isograptid-type development, latex cast (adapted from Toro & Maletz, 2008, fig. 5); *2, Cymatograptus bidextro* TORO & MALETZ, 2008, reverse side, artus-type development (adapted from Toro & Maletz, 2008, fig. 5); *3, Tetragraptus amii* ELLES & WOOD, 1902, reverse side, isograptid-type development, latex cast; *4, Huttagraptus* sp., pattern M astogeny, early monograptid development with long sicula, LO 11856t, (Maletz, Ahlberg, & others, 2014, fig. 1F); *5, Archiclimacograptus* sp., obverse side; *6, Archiclimacograptus* sp., reverse side, pattern C astogeny, LO 2413t (see Hadding, 1913, pl. 3.20); (*5–6,* new). All scale bars, 1 mm.

theca, the origin and growth direction of the primordial thecae, and the placement of the insertion of the median septum. Some of these patterns originated independently several times during the evolution of the axonophorans (MALETZ, 2011b).

The proximal development patterns are not known for many graptolites. Chemically isolated or, at least, relief specimens and growth series of juveniles are needed to establish the development. The interpretation of the proximal development types is difficult or impossible for flattened material (see also discussion in MITCHELL, 1987).

CONTINUED THECAL GROWTH

The number of thecae simultaneously growing at the tip of a stipe depends considerably on the length, overlap, and inclination of the thecae and is difficult to estimate. In slender sigmagraptines, a single theca may be growing at any time. However, in wide-stiped dichograptids, as well as in biserial colonies, a variable number of thecae may simultaneously grow at the tip of the stipe. WILLIAMS and STEVENS (1988) demonstrated the continued thecal growth in the growth series of *Didymograptellus bifidus* (HALL, 1865); *Expansograptus nitidus* (HALL, 1865); and *Expansograptus pennatulus* (HALL, 1865) from western Newfoundland. They concluded that, especially in *E. pennatulus,* numerous thecae continued growing intermittently during the astogeny of the colony, leading to a continuous widening of the stipes for quite some time and a consider-

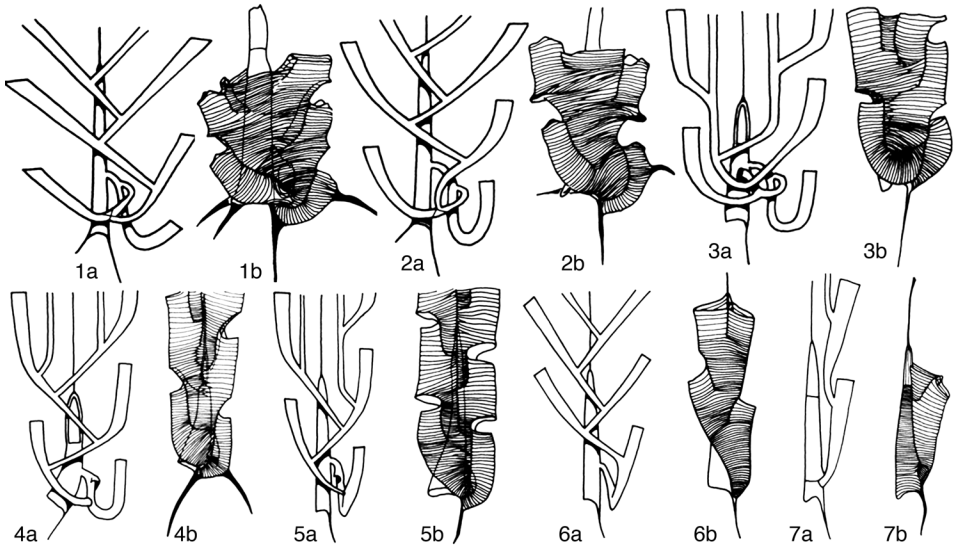


FIG. 41. Proximal development and proximal structure in axonophorans. *1a–b, Amplexograptus maxwelli* (DECKER, 1935a), pattern G; *2a–b, Anticostia lata* (ELLES & WOOD, 1906), pattern K; *3a–b, Styracograptus tubuliferus* (LAPWORTH, 1876a), pattern D; *4a–b, Diplacanthograptus spiniferus* (RUEDEMANN, 1912), pattern E; *5a–b, Normalograptus kuckersianus* (WIMAN, 1895), pattern H; *6a–b, Glyptograptus tamariscus* (NICHOLSON, 1868a), pattern I; *7a–b, Pristiograptus* sp., pattern M (all adapted from Melchin & Mitchell, 1991, fig. 1–2).

able changing of the tubarium shape during late-stage astogeny into the gerontomorph colony (Fig. 42).

THE MEDIAN SEPTUM

The development of the median septum in biserial axonophoran graptolites varies depending on the taxonomic group. The median septum is essentially the shared wall separating the two thecal series and is visible as the line separating the two thecal series in relief material (Fig. 43.1–43.2). There is little information on the detailed construction of the median septum in most graptolites, but some general information is available. BULMAN (1970) commented on the fact that there is no evidence that the median septum comprises more than a single layer of fuselli, following the description of URBANEK (1959) of the median septum of *Urbanekograptus retioloides* WIMAN, 1895, as a single-layered feature with numerous intercalating fuselli. Rare specimens of biserial graptolites can separate and rejoin the two thecal series temporarily as in *Cardiograptus amplus* HSÜ, 1947 (HAN & CHEN, 1994), suggesting that the median septum may be formed from two separate fusellar layers. The median septum can be complete (Fig. 43.1) or incomplete, and may begin at some distance from the proximal end (Fig. 43.3). URBANEK (1959) introduced the term cryptoseptate for *Gymnograptus linnarssoni* (MOBERG, 1896), in which the nema is attached to the tubarium walls by rods (adapertural ring) but lack a fusellar sheet.

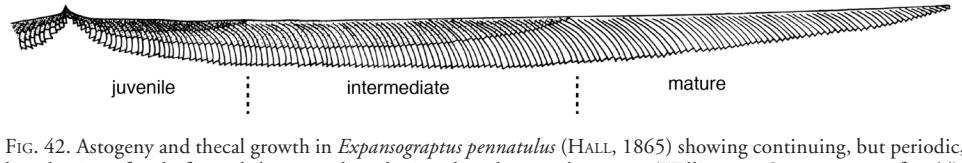


FIG. 42. Astogeny and thecal growth in *Expansograptus pennatulus* (HALL, 1865) showing continuing, but periodic, lengthening of early-formed thecae as the tubarium lengthens and matures (Williams & Stevens, 1988, fig. 44).

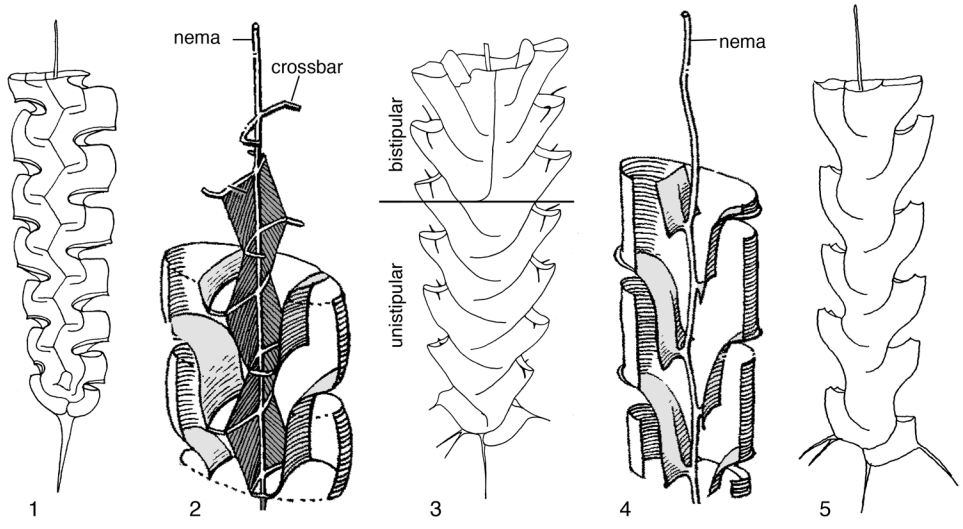


FIG. 43. Median septum. *1, Haddingograptus oliveri* (BOUČEK, 1973), bistipular colony with complete, strongly zigzag median septum, reverse view; *2,* the complete median septum (adapted from Bulman, 1955, fig. 34); *3, Orthograptus quadrimucronatus* (HALL, 1865), reverse view, showing unistipular and bistipular parts of colony; *4,* tubarium without median septum, nema connected centrally to interthecal septa (adapted from Bulman, 1955, fig. 34); *5, Anticostia macgregorae* (STEWART & MITCHELL, 1997), reverse view, unistipular colony with alternating thecae (reconstructions in *1, 3,* and *5,* from Maletz, 2014b). *Dark gray,* median septum; *light gray,* interthecal septa.

The median septum may be present on one side of the tubarium only, usually the obverse side, but not on the reverse side in many Silurian taxa, e.g., *Cephalograptus* HOPKINSON, 1869; *Petalolithus* SUESS, 1851 (BATES & KIRK, 1992, fig. 41). The embedded nema and base of the partial median septum always appear to be attached to the obverse wall in axonophorans (see examples in MELCHIN, 1998).

A median septum may be lacking completely (Fig. 43.5) in unistipular taxa in which the thecal origins develop alternately (e.g., *Amplexograptus* ELLES & WOOD, 1907; *Gymnograptus* BULMAN, 1953; and *Anticostia* STEWART & MITCHELL, 1997), or they could develop intermittently, as in *Skanegraptus* MALETZ, 2011b. A number of taxa delay the dicalycal theca and produce a unistipular proximal part without a median septum and a bistipular distal part of the colony with a delayed insertion of the median septum (Fig. 43.3).

A median septum is also present in tri- and quadriserial taxa (*Phyllograptus* HALL, 1858; *Pseudophyllograptus* COOPER & FORTEY, 1982; *Pseudotrigonograptus* MU & LEE, 1958), in which it is formed in a complex way through the dorsal sides of three or four connected thecal rows. In *Phyllograptus,* the dorsal thecal walls are largely lacking and the structure is represented only by the columnella supported by a complex network of struts and horizontal perforated plates (COOPER & FORTEY, 1982).

The monopleural taxa of the Glossograptidae do not possess a median septum. The two thecal series are attached laterally to each other and appear to have a double layer of fusellum, which is visible in relief specimens.

BRANCHING

Benthic and many planktic graptolites are able to produce multiramous colonies due to the branching of stipes in a number of different ways (Fig. 44). Theoretically, the number of stipes in pterobranch colonies is unlimited, and some benthic colonies are more than 50 cm in diameter and contain thousands of zooids on numerous branches. Planktic species (e.g., *Paratemnograptus magnificus* PRITCHARD, 1892), may have

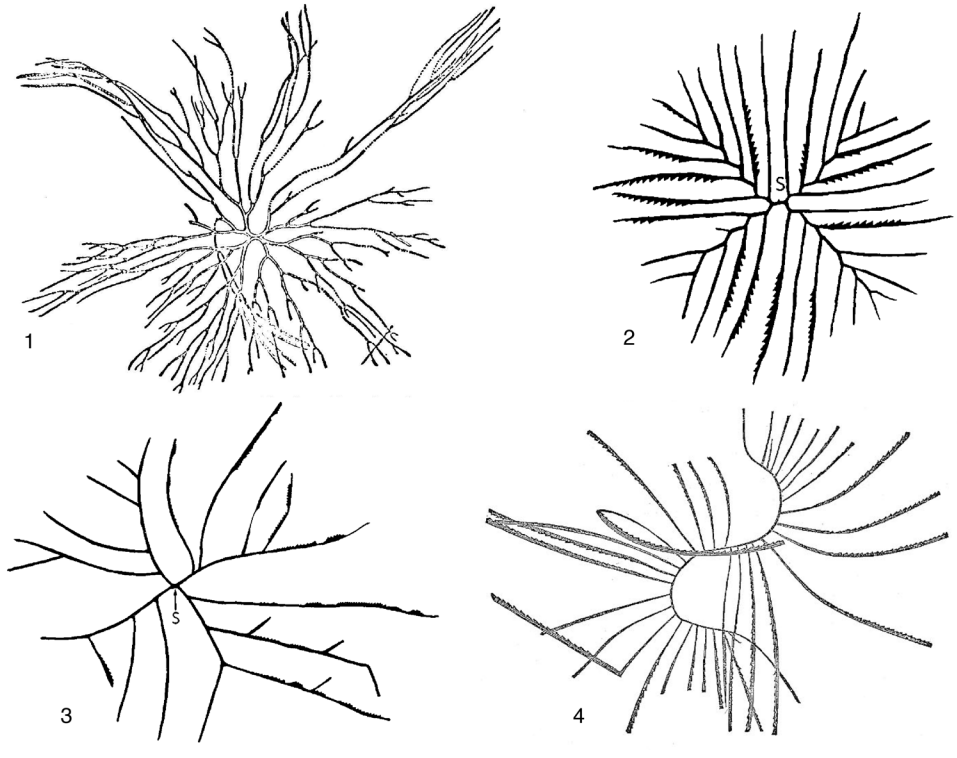


FIG. 44. Branching styles in multiramous colonies. *1, Clonograptus flexilis* (HALL, 1858), showing progressive dichotomous branching (Hall, 1865, fig. 8); *2, Goniograptus* sp., monoprogressive branching with four main stipes forming a zigzag line, *S*, sicula (Bulman 1970, fig. 77.1); *3, Schizograptus* sp., dichotomous lateral branching from four second-order stipes, *S*, sicula (Bulman, 1970, fig. 80.1); *4, Nemagraptus gracilis* (HALL, 1847), reconstruction, cladial branching at regular intervals on one side of the two main stipes (Hall, 1859a, fig. 10).

diameters as large as 100 cm. The longest monograptid has been measured at 1.45 m long and is still incompletely preserved (LOYDELL & LOVERIDGE, 2001). The exact development and differentiation of the stipes is often impossible to recognize, especially in flattened material, but the main features have been identified from chemically isolated specimens and can be referred to two structural types, dichotomous and cladial branching.

DICHOTOMOUS BRANCHING

Branching in earlier pterobranchs developed entirely and invariably at the tips of the stipes, the growing end, where new thecae are added to the colony (Fig. 44.1). This type of branching is identified as dichotomous branching, even though in some taxa, branching appears to be based on a lateral origination of the new stipes (Fig. 44.3). A secondary, later branching from an older part of the stipes cannot be produced by these colonies. The details of the branching structure are only recognizable in well-preserved, isolated material or in relief specimens.

In dichotomus branching, the two resulting stipes diverge at identical angles from the path of the previous branching division (Fig. 44.1, Fig. 45); thus, the original direction of the prebranching stipe is not continued (e.g., in *Adelograptus* BULMAN, 1941; *Clonograptus* NICHOLSON, 1873). In some species, one of the resulting stipes follows the original direction, whereas the second stipe grows at a distinct angle (e.g., *Schizograptus* NICHOLSON, 1876; *Trichograptus* NICHOLSON, 1876). In this development, it appears as if the second stipe is produced differently

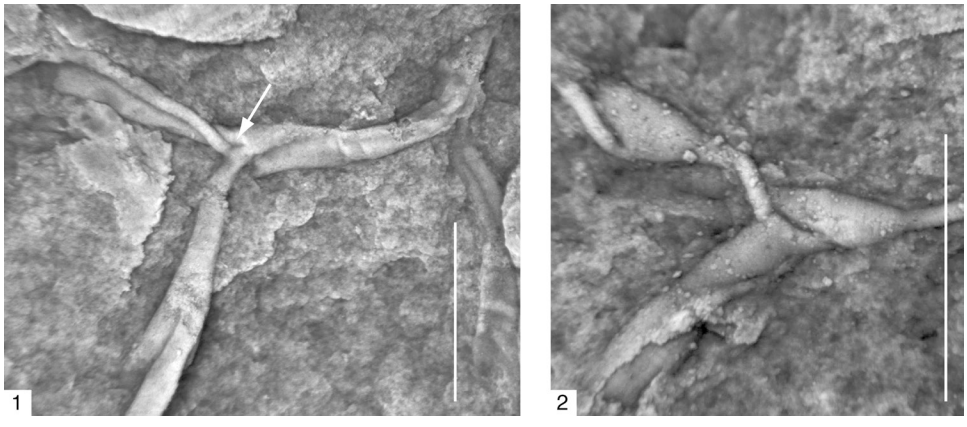


FIG. 45. Dichotomous branching. *1, Trichograptus dilaceratus* (HERRMANN, 1885), Lower Ordovician (lower Floian), DI 858, slightly curved main stipe with lateral branch growing downward in photo, note lateral origin of theca at branching point (*arrow*), latex cast; *2,* indeterminate dichograptid on slab with GSC 123228 (Jackson & Lenz, 2003, fig. 9m), Lower Ordovician (upper Tremadocian), showing thin prothecae and strongly widening metathecae, all thecae originate laterally, latex cast, scale bars, 1 mm (new).

and has a lateral origin (Fig. 44.3). Relief specimens indicate that this lateral branching is only an apparent difference: the construction of both the lateral and the dichotomous branching divisions is structurally identical. It is, however, observable that lateral branches often start growing later after the main stipe has already achieved a certain length. (Fig. 44.3).

The distances between branching divisions can be quite variable and increase distally along the colony in most species (Fig. 44.1). This progressive branching includes a highly variable number of thecae of each stipe division, and irregularities are common. A more regular type of branching appears in the monoprogressive branching of *Goniograptus* M'COY, 1876 (Fig. 44.2) and a few other genera, in which branching regularly develops after one or two thecae. The main stipe in these genera displays a distinct zigzag shape, with branches originating alternately on both sides, resulting in fewer distal branches. This type of branching is also present in a few benthic graptolites (e.g., *Ptilograptus* HALL, 1865).

CLADIAL BRANCHING

Cladial branching (Fig. 46) represents a special type of branching, which is quite different from the normal dichotomous branching at the tip of the colonies, but its precise construction is often impossible to recognize in flattened specimens (see *Nemagraptus,* Fig. 44.4). Cladial branching is secondarily produced by mature zooids, and branches originate from the aperture of its mother theca, not from the dorsal side of the stipe as in dichotomous branching.

Cladial branching is recognized when a thecal tube develops at the apertural opening of a previously formed theca and at some distance proximally from the growing end of the main stipe. At first, small flanges of fusellar material attached to the thecal aperture are produced by the daughter zooid of the mother thecae and subsequently develop into a thecal tube. The thecal shape may be identical to that of its mother theca, but can also be quite different. Cladial branching is best known from *Cyrtograptus* (see THORSTEINSSON, 1955) (Fig. 46.1, Fig. 46.4) but is also known in taxa such as *Linograptus* FRECH, 1897; *Diversograptus* MANCK, 1923; and *Neodiversograptus* URBANEK, 1963 (Fig. 46.2–46.3).

Theoretically, cladial branching may be present at any place in the colony, but it is usually restricted to certain positions in most genera and species. In the

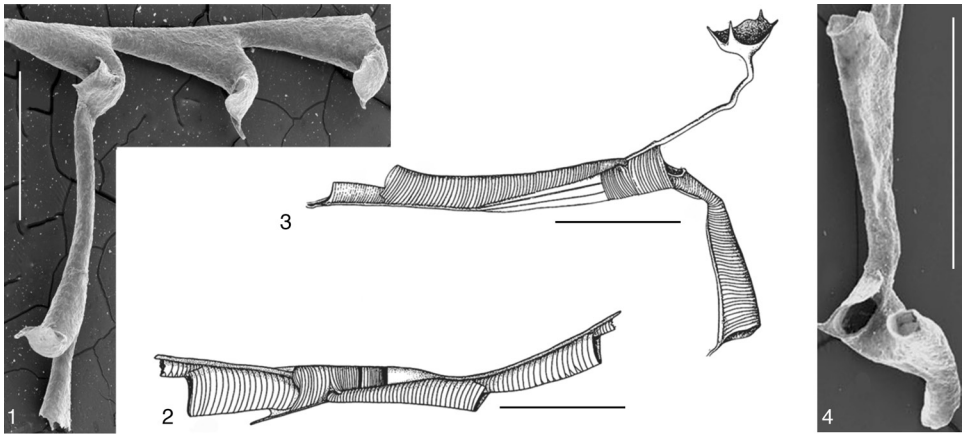


FIG. 46. Cladial branching in *Cyrtograptus, Linograptus, and Neodiversograptus. 1, Cyrtograptus perneri* BOUČEK, 1933, fragment with thecal cladium, Silurian (Wenlock, upper Sheinwoodian), Canadian Arctic (new); *2, Neodiversograptus nilssoni* (BARRANDE, 1850), specimen with wide, sicular cladium, Silurian (Ludlow, lower Gorstian) (Urbanek, 1997b, fig. 2B); *3, Linograptus posthumus* (RICHTER, 1875), reconstruction showing sicular cladium and idealized virgellarium attached to virgella, upper Silurian (Urbanek, 1997b, fig. 5D); *4, Cyrtograptus radians* BOUČEK, 1933, fragment with thecal cladium, Silurian (Wenlock, lower Homerian), Canadian Arctic (Lenz & Kozłowska, 2006, fig. 16.2). All scale bars, 1 mm.

genus *Cyrtograptus,* thecae produce cladial branching at regular distances, and the position of cladia can be important for the taxonomic identification of various species. Paired cladial branches and multiple cladial branches occurred in a small number of Ordovician to Lower Devonian genera and species (e.g., *Amphigraptus* LAPWORTH, 1873b; *Tangyagraptus* MU, 1963a; *Abiesgraptus* HUNDT, 1935a; *Linograptus* FRECH, 1897). Single and multiple cladial branches also appeared at the sicular aperture in upper Silurian and Lower Devonian monograptids (Fig. 46.2–46.3). Numerous cladia may have developed at the sicular aperture in *Linograptus* (URBANEK, 1963).

The oldest known cladial branching is documented from the Middle Ordovician (Darriwilian) genus *Pterograptus* (SKWARKO, 1974; MALETZ, 1994a). Cladial branching occurred in *Nemagraptus* and other dicranograptids (*Amphigraptus*, *Tangyagraptus*) but was most commonly developed in the Silurian to Lower Devonian monograptids (*Abiesgraptus, Cyrtograptus*, *Diversograptus*, *Linograptus*, *Sinodiversograptus* MU & CHEN, 1962a). The cladial branching appears to have originated independently numerous times throughout the evolution of the graptolites. Cladial branching in the monograptid genera invariably involved the development of a secondary nema along which the cladial branches grew. Such a structure is not present in the cladia of Ordovician dichograptid and dicranograptid specimens. Thus, Ordovician and Silurian taxa adopted a fundamentally different approach to the construction of cladia.

STIPE ORIENTATION

The colony shapes in planktic graptolites are quite variable, based on the development of the stipes. Generally, the orientation of the stipes is considered in relation to the sicula, although ELLES (1922, fig. 42) proposed the nema as the main defining character for the orientation of the colonies. In the standard orientation of the sicula with the aperture downward and the free nema directed upward, the stipe orientation is defined as pendent to scandent and all variations between (Fig. 47). This orientation may not represent the orientation of the living graptolite colonies, because very little can be known for certain about the orientation of graptolite colonies in the

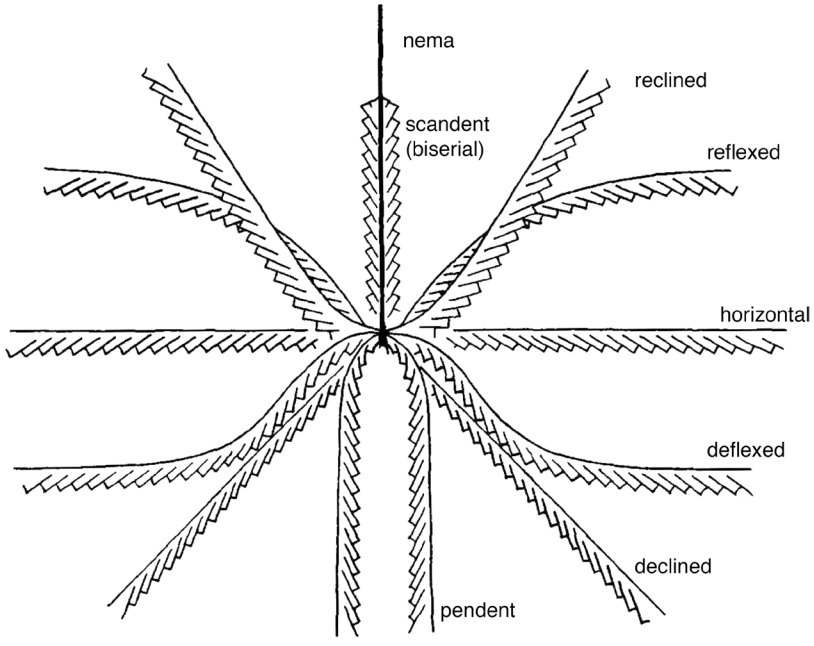


FIG. 47. Diagram illustrating the orientation of graptolite stipes to the nema and the terminology (Bulman, 1970, fig. 38).

water column. The colony shapes of many graptolite species vary considerably, but the general stipe orientation usually can easily be recognized. During the burial process, the highly flexible tubarium was commonly distorted, especially the longer, more mature stipes.

Scandent graptoloids can be constructed in two fundamentally different ways (JAANUSSON, 1960). These colonies usually have two or four stipes connected to each other. In biserial axonophoran colonies, the two stipes are connected back-to-back, a condition identified as scandent (Fig. 47) and dipleural (Fig. 48.4). Four-stiped scandent taxa include the Lower to Middle Ordovician genera *Phyllograptus, Pseudophyllograptus,* and *Pseudotrigonograptus,* in which the colony has a cross-shaped cross section (Fig. 48.5–48.6). Three-stiped scandent taxa are extremely rare. The only example known from well-preserved material is *Pseudotrigonograptus minor* MU & LEE, 1958 (FORTEY, 1971), a phyllograptid graptoloid.

The stipes are connected along their lateral margins in the glossograptids (e.g., *Glossograptus, Cryptograptus*), enclosing the sicula and the initial growth of the proximal thecae. This development is identified as a monopleural arrangement (Fig. 48.1–48.2). In monopleural colonies, the proximal structure is difficult to ascertain, because the details are only visible in juvenile specimens. Mature specimens encase the proximal structure by the later growth of the stipes and completely cover them. Partially monopleural development is present in a few taxa, most notably in *Kalpinograptus* JIAO, 1977 (Fig. 48.3). In *Kalpinograptus,* the proximal end is monopleural, but distally the stipes separate from each other; the outline of the genus is very similar to a typical reclined isograptid. The tubarium structure in taxa with a monopleural development appears to be identical on both sides, whereas in dipleural taxa the structure is different on the obverse and reverse sides.

STIPE CONNECTIONS

Pterobranch colonies are formed from a highly flexible material, and the interference of individual stipes might be common when

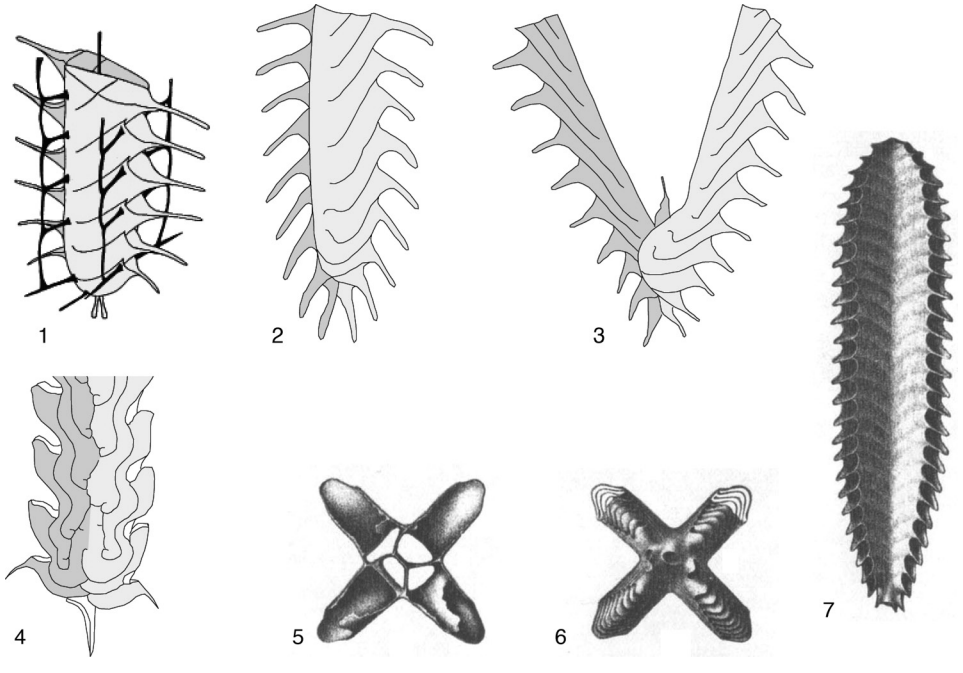


FIG. 48. Monopleural and dipleural development. *1, Paraglossograptus* sp., reconstruction of colony showing monopleural arrangement and development of lacinia from lateral apertural spines (new); *2, Glossograptus* sp., monopleural; *3, Kalpinograptus* sp., with initially monopleural and distally two-stiped colony; *4, Levisograptus austrodentatus* (HARRIS & KEBLE, 1932) dipleural, reverse view, (*1–4*) left and right sides in different *gray* shades (*2–4* adapted from Maletz, Carlucci, & Mitchell, 2009, fig. 5); *5–7, Pseudophyllograptus* sp., quadriserial colony, cross sections (*5–6*) and lateral view (*7*) (Holm, 1895, pl. 13).

overlapping. However, the stipes in multiramous erect and planktic colonies tend to keep a precisely defined, minimum distance between them. This distance might be a function of avoiding unintended interaction and competition during feeding and, thus, be defined by the size of the zooids and the feeding range of their arms (STARCHER & MCGHEE, Jr., 2003). Computer modeling by FORTEY and BELL (1987) added support to the proposal that the various stipe configurations in multiramous forms were designed for maximum feeding efficiency of stipes and minimum interference with their neighbors.

Dissepiments are the easiest, although uncommon, way of giving rigidity to the tubarium and keeping stipes from overlapping or interfering with each other. Dissepiments are thin bands of fusellar and cortical tissue connecting adjacent stipes (URBANEK & MIERZEJEWSKI, 2009). Dissepiments are developed in erect, benthic dendroid colonies (*Dictyonema* HALL, 1851; *Ptiograptus* RUEDEMANN, 1908) and are present in a few early planktic forms (*Rhabdinopora* EICHWALD, 1855; *Staurograptus* EMMONS, 1855; and *Sagenograptus* OBUT & SOBOLEVSKAYA, 1962) (Fig. 49.1). They appear to grow from two adjacent stipes, perhaps as a joint work of zooids from each stipe, and meet in the middle, where they are thinner. Dissepiments can be distributed irregularly along the stipes, depending on the need for separation. In many dissepimentous species, however, they form a highly regular mesh of stipe connections and the density of dissepiments has been used to identify taxa, especially within the genus *Rhabdinopora* (COOPER & others, 1998). This highly regular meshwork is reminiscent of colony development in some bryozoans (e.g., *Fenestella*), and these taxa may easily be confused if the construction material is not considered in fossil specimens. The bryozoans do not produce an organic

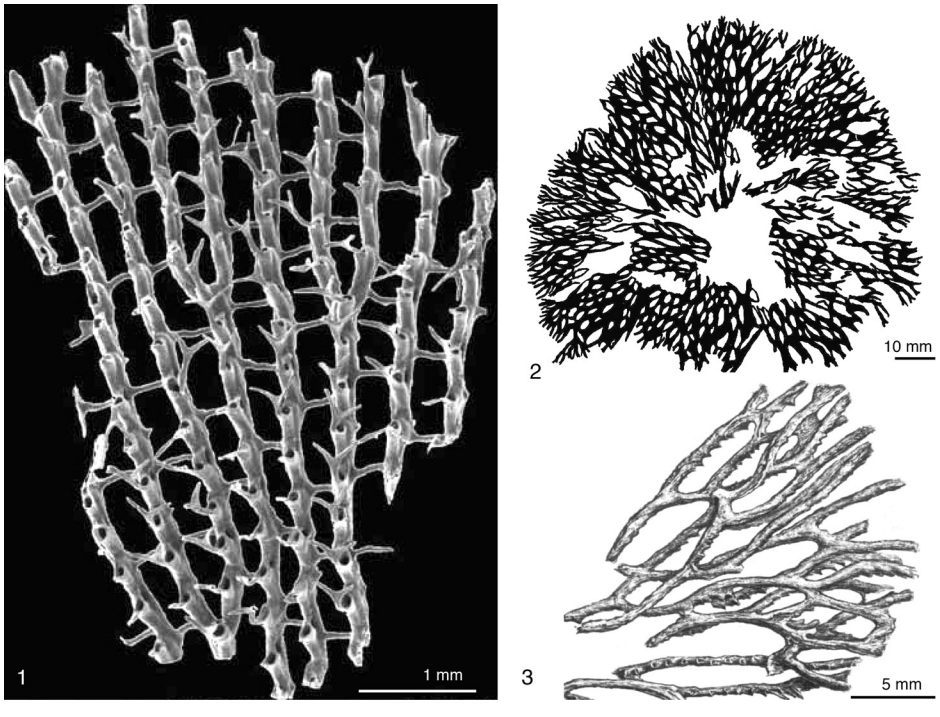


FIG. 49. Dissepiments and anastomosis. *1, Dictyonema* sp. cf. *Dictyonema cervicorne* HOLM, 1890, colony fragment showing well-developed dissepiments, Ordovician, glacial boulder, Poland (Urbanek & Mierzejewski, 2009, fig. 3); *2, Palaeodictyota anastomotica* (RINGUEBERG, 1888), showing anastomozing stipes, upper Silurian (Bulman, 1970, fig. 21,*3*); *3, Desmograptus idoneus* BULMAN, 1933a, fragment showing anastomosis with thecal transfer (Bulman, 1933a, pl. 4,*18)*.

housing; instead, they form their housing structures, the zooecium, as a calcified cuticle (LANKESTER, 1884).

HARMER (1905) discussed numerous bridges connecting adjacent branches in *Cephalodiscus dodecalophus* M'INTOSH, 1887. These bridges are structurally homologous to the dissepiments of benthic and planktic graptolites. *Cephalodiscus dodecalophus*, even though not a colonial pterobranch, forms branched, erect structures in a way similar to that of an erect colonial pterobranch.

ZALASIEWICZ (1993) described a rare occurrence of structures resembling dissepiments in *Spirograptus turriculatus* (BARRANDE, 1850), which formed as outgrowths from apertural thecal spines that connected to the dorsal side of the underlying stipe. These developments should not be designated dissepiments because their construction is based on previously secreted and subsequently elongated spines and are not independently developed features. However, they served the same (presumed) purpose of keeping the stipes separate and not overlapping.

Anastomosis includes the transfer of individual thecae or groups of thecae from one stipe to another or the temporary connection of two adjacent stipes (Fig. 49.2–49.3). It exists in the tubarium of a few, erect, benthic pterobranch genera, such as *Desmograptus* (Fig. 49.3); *Koremagraptus* BULMAN, 1927a; or *Palaeodictyota* WHITFIELD, 1902 (Fig. 49.2). This feature is not well understood. BULMAN (1945) described anastomosis in *Koremagraptus kozlowskii* BULMAN, 1945, from the Upper Ordovician of Britain, based on isolated, bleached material. RICKARDS and LANE (1997) differentiated pseudanastomosis as anastomosis with transfer of thecae, from anastomosis as a temporary connection of stipes without thecal transfer.

EXTRATHECAL DEVELOPMENTS

Many different extracolonial features can be recognized in the graptolites, especially in the planktic forms. They are differentiated herein, based upon their position in the colony and precise development.

NEMATULARIA

A short nema is present in most early (Tremadocian) planktic graptoloids, including the branched nemal tufts of some early *Rhabdinopora* specimens (Lin, 1988) (Fig. 50.7). Although the nema is typically short, a long nema and a considerable development of nematularia (Fig. 50) occurred in Lower Ordovician (Floian) species (e.g., *Pendeograptus* Bouček & Přibyl, 1952a; *Kinnegraptus* Skoglund, 1961; *Isograptus* Moberg, 1892a; and *Pseudisograptus* Beavis, 1972).

The nema is incorporated into the colonies of the axonophorans and evolved into the long, slender nemata typical of these taxa, commonly bearing nematularia at the tip (Fig. 50.10). The nema is either incorporated into the ventral thecal walls of the biserial colonies and connected to the thickened lists around the thecal origins or may be free inside unistipular tubaria with their alternating thecal origins. It generally extends far beyond the distal end of many axonophoran colonies (Fig. 50).

A number of extracolonial features are connected to the nema at the distal end of the colonies. These features have been called Schwimmblase (Dacqué, 1923; Münch 1938), floating device or Schwebeapparat (Müller & Schauer, 1969), or buoyancy mechanism (Bulman, 1970) and were termed—more neutrally—the nematularium by Müller (1975). Nematularia have been suggested to be gas-filled chambers used as flotation devices (e.g., Hundt, 1939; Bouček & Přibyl, 1941). However, recent studies have convincingly demonstrated that nematularia are solid, planar structures formed of successive layers of fusellar tissue (Urbanek, Koren', & Mierzejewski, 1982; Mitchell & Carle, 1986). Examples include two isolated, three-dimensional nematularia associated with *Normalograptus brevis* (Elles & Wood, 1906) in which one of the nematularia is clearly a solid, three-vaned structure (Bulman, 1947, pl. 9,*14–15*). In addition, a few three-dimensionally preserved, two-vaned, paddle-shaped, and three-vaned nematularia—all retaining original shapes and all solid—have been discovered in Silurian retiolitids from the Canadian Arctic (Lenz & Kozłowska-Dawidziuk, 2001) (see Fig. 50.1–50.2).

Størmer (1933) described a proximal organ in *Rhabdinopora flabelliformis* (Eichwald, 1840) and interpreted it as a possible disklike floating device. Harris and Keble (1928) described a similar structure in *R. campanulatum,* although the nematularium appears to be a bundle of fibers (Fig. 50.7). Possible small nematularia are present in the Lower Ordovician species—upper Tremadocian anisograptids (e.g., *Kiaerograptus*? *peelensis* Jackson, 1974) and the Floian dichograptid *Tshallograptus fruticosus* (Hall, 1858) (see Jackson & Lenz, 2006) (Fig. 50.6). However, nematularia are more common in Middle Ordovician to Silurian axonophorans. Slender, long, and slightly spiraled nematularia are present in the Dapingian isograptids (Moberg, 1892a) and appear to be typical for the Middle Ordovician glossograptid *Cryptograptus,* identified as *Tonograptus* by Williams (1992).

In many taxa, the nema broadens distally, gradually or abruptly, into a prominent nematularium that ranges from a slim to broad band that may be flat (Fig. 50.9), helically spiraled (Fig. 50.10–50.11), or three vaned, disklike, or heart shaped (Fig. 50.8), or it may develop as multipronged structures distal to the growing end of the tubarium (Fig. 50.3–50.4). The nema may be recognizable in the center of the structure or reach only to the base of the nematularium.

Generally, nematularia are partially or completely external to the main body of the tubarium, but some band-shaped, paddle-

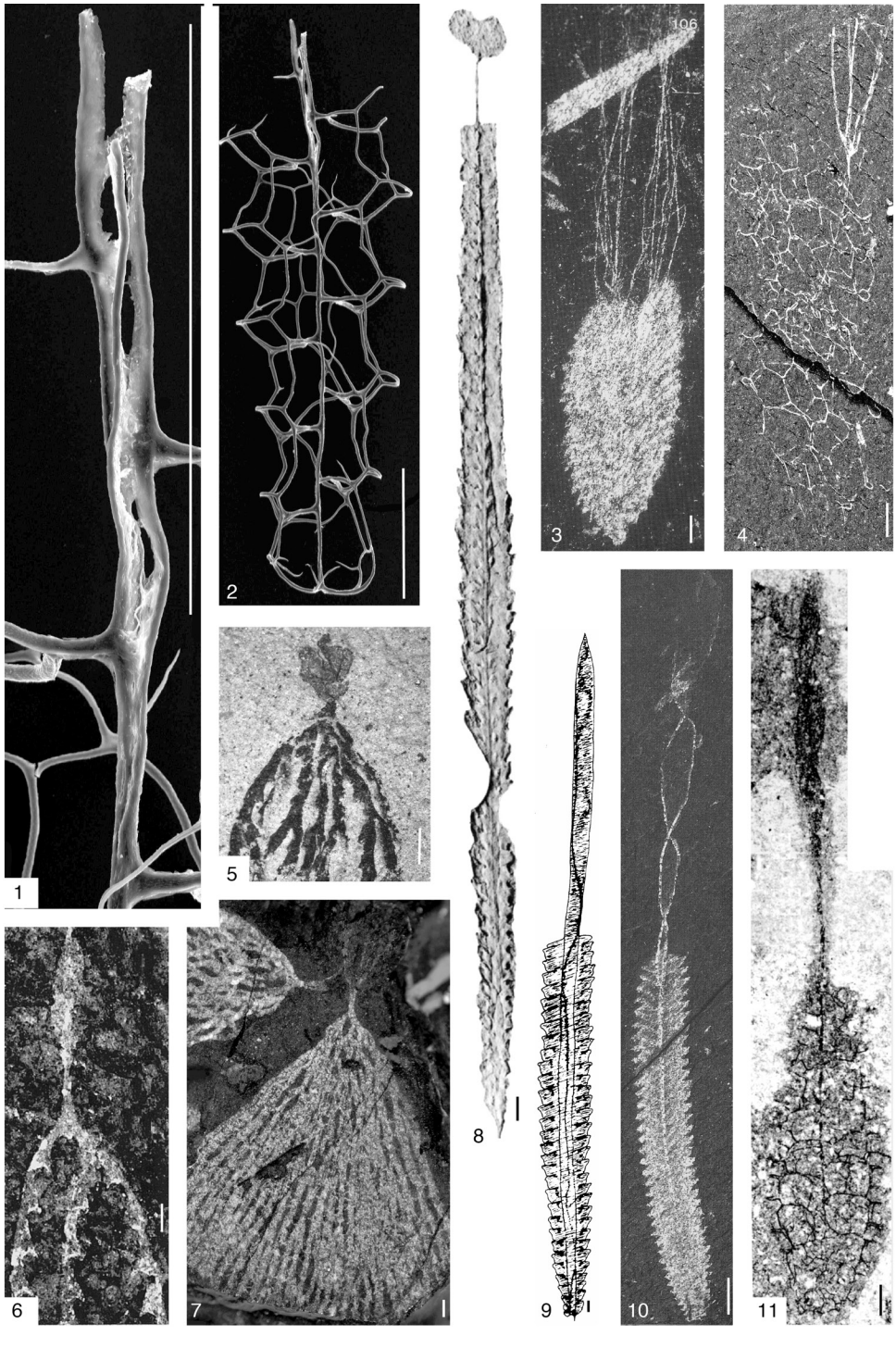


FIG 50. *For explanation, see facing page.*

shaped, two- or three-vaned nematularia, or multifurcating, thickened rods originate well within the (mature) tubarium and continue distal of the main tubarium (e.g., *Cystograptus* HUNDT, 1942) (JONES & RICKARDS, 1967) (see Fig. 50.9). This is particularly evident among the retiolitids, though also present in a number of other biserial graptoloids. As is well known in *Cystograptus vesiculosus* (NICHOLSON, 1868a) and *Archiclimacograptus decoratus* (HARRIS & THOMAS, 1935), the nematularia may have been constructed at the growing tip of the nema, far beyond the advancing zooidal tubes and overgrown during the later astogeny of the colonies (Fig. 50.8–50.9).

FINNEY (1985a) summarized the evidence for small, hollow spheres that are attached to the siculae or nemata of some planktonic dendroids and graptoloids, particularly during the very early life stage of the colony. From the relatively poor preservation, however, it is unclear whether these features are a normal feature of juvenile graptolite colonies or an artifact of preservation. They may, perhaps, even be acritarchs or other palynomorphs accidentally attached to the colonies.

PROXIMAL WEBS

Web structures are common in certain groups of graptolites, especially in multiramous Lower to Middle Ordovician dichograptids (Fig. 51). RUEDEMANN (1947) illustrated numerous dichograptids with web structures. They have been described from shale material, but are unknown from isolated specimens. Therefore, their construction is poorly understood. In a number of genera (e.g., *Dichograptus* SALTER, 1863a; *Loganograptus* HALL, 1868; and *Tetragraptus* SALTER, 1863a), these webs appear to be formed from fusellar material, considering that growth lines are sometimes recognizable (Fig. 51.2). They connect adjacent stipes and appear to start at the proximal end and grow outward as thin membranes. JAANUSSON (1960) described the pendent didymograptid *Didymograptus pakrianus* JAANUSSON, 1960, as having a considerable overgrowth of the proximal end, forming a large communal cavity for the proximal thecae.

A distinct, apparent, lateral thickening of the proximal stipes of the colonies is present in numerous multiramous Lower to Middle Ordovican dichograptids, such as *Adelograptus* BULMAN, 1941 (Fig. 51.3); *Clonograptus* NICHOLSON, 1873; and *Stellatograptus* ERDTMANN, 1967). Details of this development are uncertain, as isolated material is not available and specimens are flattened. In juvenile specimens of the same species, the stipes are much more slender and thecal apertures can be recognized. These stipe modifications could be interpreted as lateral web structures, similar to the proximal webs of other forms, but alternatively they could represent actual thickening of the stipes, which appears to be common in many dendroid graptolites as a gerontic feature.

FIG. 50. Nematularia and other extraneous structures. *1–2, Paraplectograptus* sp., Silurian (upper Wenlock), glacial boulder, Germany; *1,* enlargement showing triradiate cross section of nematularium; *2,* showing internal nematularium (new); *3, Dischidograptus regius* (HUNDT, 1957a), showing branched structures distally, Silurian (Llandovery), Germany (Palmer & Rickards, 1991, fig. 106, as *Petalograptus ovatoscopularus* SCHAUER, 1971); *4, Eiseligraptus eisenacki* (HUNDT, 1951a), with multifurcated nematularium, Silurian (upper Llandovery), Hohenleuben, Germany, (new); *5, Rhabdinopora proparabola* (LIN, 1986), showing lobate nematularium, Dayangcha, China (new); *6, Tshallograptus fruticosus* (HALL, 1858), showing ovate nema structure, Lower Ordovician (Floian), Canada (northern Yukon) (Jackson & Lenz, 2006); *7, Rhabdinopora campanulatum* (HARRIS & KEBLE, 1928), showing proximal end with tuft-like bundle of fibers, Lower Ordovician (Tremadocian), Victoria, Australia (new); *8, Archiclimacograptus decoratus* (HARRIS & THOMAS, 1935), with heart-shaped nematularium, Upper Ordovician, Nevada, USA (Ross & Berry, 1963); *9, Cystograptus vesiculosus* (NICHOLSON, 1868a), with long nematularium, Silurian (Llandovery), Germany (Schauer, 1971); *10, Parapetalolithus* sp., with a strongly spiraled nematularium, Silurian (Llandovery), Germany (Palmer & Rickards, 1991, fig. 38); *11, Hoffmanigraptus karlsteinensis* (KOZŁOWSKA-DAWIDZIUK, LENZ, & ŠTORCH, 2001), with spiraled nematularium, upper Silurian (Wenlock, upper Homerian), Czech Republic (Kozłowska-Dawidziuk, Lenz, & Štorch, 2001, fig. 6.1). All scale bars, 1 mm.

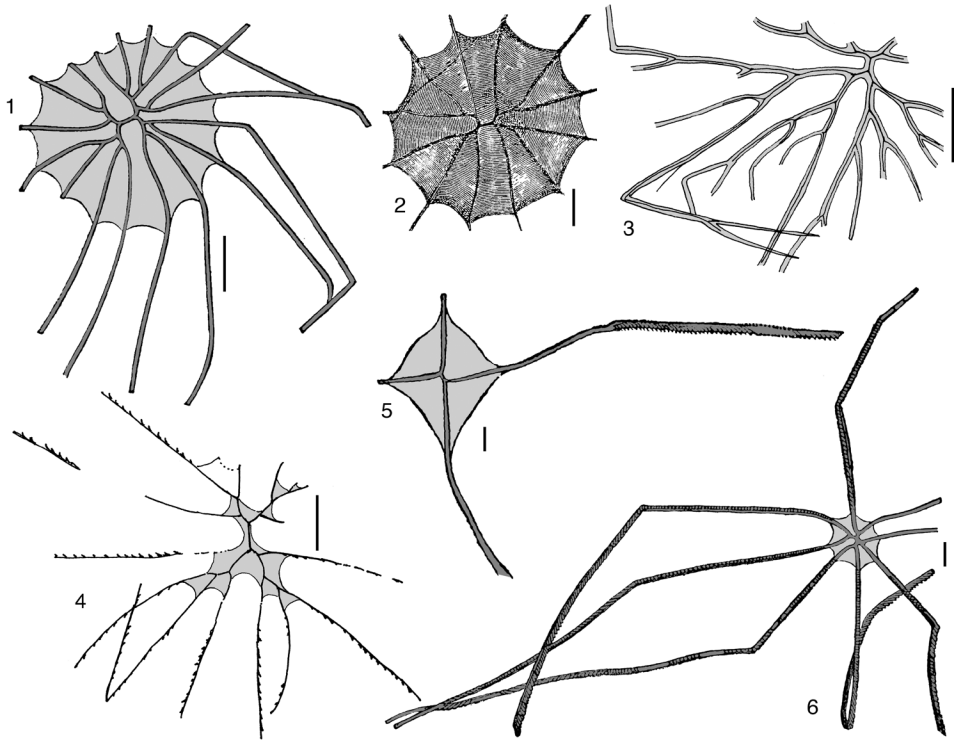


FIG. 51. Proximal webs or membranes. *1, Loganograptus logani* (HALL, 1865), extensive membrane development (adapted from Hall, 1865, fig. 6); *2, Loganograptus kjerulfi* (HERRMANN, 1885), proximal membrane (Herrmann, 1885, fig. 10); *3, Adelograptus tenellus* (LINNARSSON, 1871) showing extreme thickening of stipes, particularly in proximal regions (adapted from WESTERGÅRD, 1909, pl. 4,*8*); *4, Goniograptus palmatus* HARRIS & KEBLE, 1932, membranes between some of the branching divisions (adapted from Harris & Keble, 1932, pl. 6, fig. 5); *5, Tetragraptus headi* HALL, 1865, proximal membrane (adapted from Hall, 1865, fig. 4); *6, Dichograptus octobrachiatus* (HALL, 1858) (adapted from Hall, 1865, fig. 4). All scale bars, 10 mm.

Proximal webs may be present in the axils of Upper Ordovician *Dicellograptus*, where they cover and obscure the sicula (Fig. 52.2–52.3). In outline, these specimens may more closely resemble specimens of *Dicranograptus* HALL, 1865, with a short, wide, biserial proximal end, as, for example, in *Dicellograptus moffatensis* (CARRUTHERS, 1858); and *Dicellograptus ornatus* ELLES & WOOD, 1904 (WILLIAMS, 1982a).

Proximal webs and membrane-like features are extremely rare in monograptids. MOBERG (1893) described *Monograptus pala* MOBERG, 1893, with an apparent large, rounded proximal membrane. As MOBERG's illustrated specimens show the thecae in scalariform view (Fig. 53.8), a more precise identification is impossible and details of the membrane are not available.

A single *Cyrtograptus* specimen with an extensive proximal membrane has been discovered in the Canadian Arctic (LENZ, 1974). In this specimen, the membrane partly covers the thecal apertures of the proximal end of the specimen. It is, in part, a double membrane that extends along the initial spiral part of the colony. UNDERWOOD (1995) illustrated a similar and more completely preserved membrane in a flattened specimen of *Cyrtograptus murchisoni* CARRUTHERS in MURCHISON, 1867a (Fig. 52.1).

Bladderlike structures, or sacs, developed in a few Ordovician axonophorans, most typically apparent in *Archiclimacograptus*

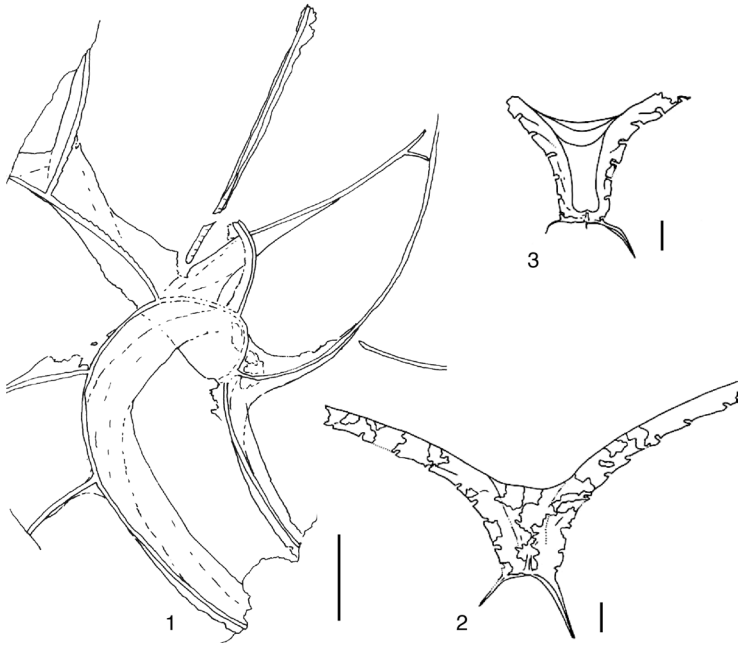


FIG. 52. Proximal membranes. *1, Cyrtograptus murchisoni* CARRUTHERS in MURCHISON, 1867a, with remnants of thin, multilayered membranes, mostly in the proximal region, Silurian (lowermost Wenlock), UK, scale bar 10 mm (adapted from Underwood, 1995, fig. 2c); *2–3, Dicellograptus turgidus* MU, 1963b, showing proximal membrane closing reclined stipes of proximal end, Upper Ordovician, Vinini Formation, Nevada, USA, scale bars, 1 mm (Štorch & others, 2011, fig. 10).

bursifer (ELLES & WOOD, 1906) (ELLES & WOOD, 1906, pl. 27,*6*). A possibly similar development is known from the Llandovery *Glyptograptus auritus* (BJERRESKOV, 1975). It is unclear whether they represent membranes or three-dimensional features. Proximal webs are also constructed in mature specimens of a number of climacograptids, where they grow upward from the dorsal side of the proximal spines in *Climacograptus bicornis* (HALL, 1847) (Fig. 53.2) and may reach the fourth or fifth thecal pair (RIVA, 1976, fig. 6). *Climacograptus*? *papilio* MU, 1963b (Fig. 53.5) may also construct considerable webs based on the proximal spines, but they are not attached to the sides of the colony.

SCOPULAE AND OTHER LATERAL AND PROXIMAL NEMAL DEVELOPMENTS

Scopulae are special developments on the sides of axonophoran colonies and form paddle-like structures (Fig. 53.4). They may originate from the nema, but the development is unclear for most taxa. Scopulae are usually bladelike with a thickened rim around a thin fusellar membrane (BATES, 1987a; BATES & KIRK, 1991). They are most common in the Upper Ordovician Lasiograptidae, but analogous features may be present in a few Silurian normalograptids (e.g., *Dittograptus* OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968; see KOREN' & RICKARDS, 1996).

The paired lateral spines of *Alulagraptus uncinatus* (KEBLE & HARRIS, 1934) (Fig. 53.9), are based on the nema and form during an early stage in the development of the colony (CARTER, 1972). After only a few millimeters of growth of the colony, the nema splits into two rods that grow subhorizontally outward. The nema stops growing, and the colony grows across this point unchallenged and without the production of a new nema. MU (1963b) described a similar development

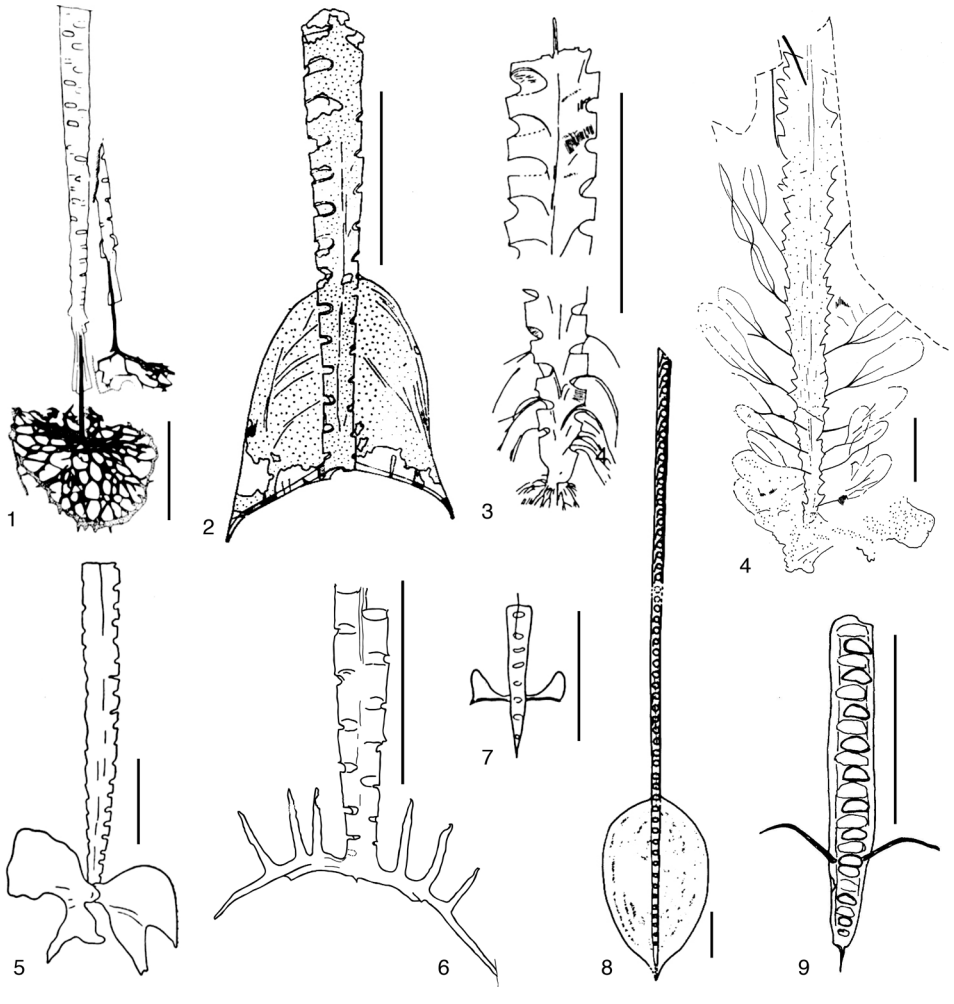


FIG. 53. Scopulae and other extraneous proximal structures. *1, Climacograptus*? *baragwanathi* HALL, 1906, Upper Ordovician (Katian), Australia (VandenBerg & Cooper, 1992, fig. 9D); *2, Climacograptus bicornis* (HALL, 1847), with large proximal membranes, Upper Ordovician (Sandbian), New York, USA (Riva, 1976, fig. 6N); *3, Comograptus comatus* OBUT & SOBOLEVEKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, Silurian (Llandovery), Norilsk region, Siberia, Russia (Koren' & Rickards, 1996, fig. 6G); *4, Dittograptus* sp., specimen with numerous scopulae, Silurian, Thuringia, Germany (Müller, 1977, fig. 11); *5, Climacograptus*? *papilio* MU, 1963b, with proximal membranes, Upper Ordovician, China (Mu, 1963b, fig. 11); *6, Appendispinograptus venustus* (HSÜ, 1959a) showing development of complex parathecae, Wufeng Formation, southwestern China (Mitchell, Chen, & Finney, 2007, fig. 1.4); *7, Alulagraptus ensiformis* (MU & ZHANG in MU & others, 1963), Upper Ordovician, China (Mu, 1963b, fig. 12); *8, Monograptus pala* MOBERG, 1893, with large proximal membranes (Bulman, 1970, fig. 70.15); *9, Alulagraptus uncinatus* (KEBLE & HARRIS, 1934), Upper Ordovician, Vinini Formation, Nevada, USA (Carter, 1972, fig. 2l). All scale bars, 5 mm.

from the poorly known *Alulagraptus ensiformis* (Fig. 53.7), but in this material a nema apparently continues through the colony.

VIRGELLARIA

In *Linograptus posthumus* (RICHTER, 1875), the virgellarium, a construction formed from the tip of the virgella, may represent the typical development of a virgella-related feature. Unfortunately, the details of its development are uncertain, as the isolated specimens do not preserve the remains of the fusellar structure. The virgellarium is formed from a membrane with four

petals, ending in fingerlike or umbrella-like outgrowths (URBANEK, 1963, 1997b) (Fig. 46.3). MÜLLER (1977) illustrated a number of virgellar features as virgellaria and suggested a detailed terminology of these features, but details are extremely rare. Virgellar extensions are limited to the extremely long virgellar spines in a number of biserial taxa (e.g., *Archiclimacograptus* MITCHELL, 1987; *Orthograptus* LAPWORTH, 1873b). Bifurcation of the virgella, as in *Normalograptus bifurcatus* LOYDELL, 2007, appears to be extremely rare (LOYDELL, 2007) and has not been found in other taxa. The development of the ancora umbrella and ancora sleeve in the Retiolitidae also belongs to the modifications of the virgella.

ANCORA SLEEVE

The ancora sleeve is a special development in the Retiolitidae. It consists of a secondary membrane surrounding the tubarium and its original thecal construction. Usually, the ancora sleeve is preserved as a more or less regularly developed system of lists, the reticulum, which developed from the distal extension and development of the virgellar structure, the ancora umbrella. It is comprised of seamed lists made up of cortical tissue and enlarged by concentric layering. This combination of the ancora sleeve forming the outer wall and the thecal framework forming the inner wall is unique among the graptolites. It is clear that the thecal framework was formed by the laying down of a succession of thin fusellar sheets, but the origin of the sheets in the ancora sleeve is unclear (e.g., BATES, 1987; BATES & KIRK, 1992). In the vast majority of specimens, the fusellar layer is too thin to be preserved in the fossil record. It is most commonly recognized through the presence of fusellar shards (Fig. 54.6) in the seams of the list structures (BATES & KIRK, 1992) and, especially the very rare, complete preservation of fusellar sheet layers (LENZ, 1994a; LENZ & THORSTEINSSON, 1997).

Because the lacinia in the Lasiograptidae develops quite differently from the clathrium and reticulum (ancora sleeve) of the Retiolitidae, they may be treated as analogs rather than homologs. Whereas the lacinia lists of the lasiograptids and glossograptids are without list seams, both the clathrial lists (generally the equivalent of the thecal framework; Fig. 54, *white arrows*) and the reticulum (the finer meshwork, mainly related to the ancora sleeve; Fig. 54, *gray arrows*) invariably bear seams that were probably occupied by very thin fusellar bands. Fusellar shards appear only in the seams of the thecal framework lists (Fig. 54.6), whereas the seams of the ancora sleeve are apparently devoid of fusellar shards.

LACINIA

The lacinia is typically a development of a meshwork of rods originating as thecal spines with a concentric core. It produces a complex, three-dimensional, meshwork structure around the entire colony in some Lasiograptidae (Fig. 55.1–55.2). The spines and bars are formed from fusellar material, typically covered and thickened by cortical overgrowth (BATES & KIRK, 1991). At the same time, the fusellar structure of the archiretiolitid colonies is reduced, and generally only thin bars remain outlining the thecal framework (Fig. 55.1). These lists have distinct seams, indicating their origination on the fusellar surfaces of the thecae (BATES & KIRK, 1991). In early lasiograptids, the fusellum is more complete, and the difference from the encasing lacinia is easily recognizable (Fig. 55.2).

A small amount of lacinia appears to develop in the Glossograptidae. Species of the genus *Paraglossograptus* MU in MU & others, 1962, possess lateral thecal spines that are interconnected with vertical bars. Four ladderlike structures are formed in *P. proteus* (HARRIS & THOMAS, 1935) (WHITTINGTON & RICKARDS, 1969), but a more complex meshwork is present in *P. tentaculatus* (HALL, 1865) (Fig. 55.3–55.4). This type of a lacinia is not homologous to the lacinia in the Lasiograptidae. Details of its construction are not available.

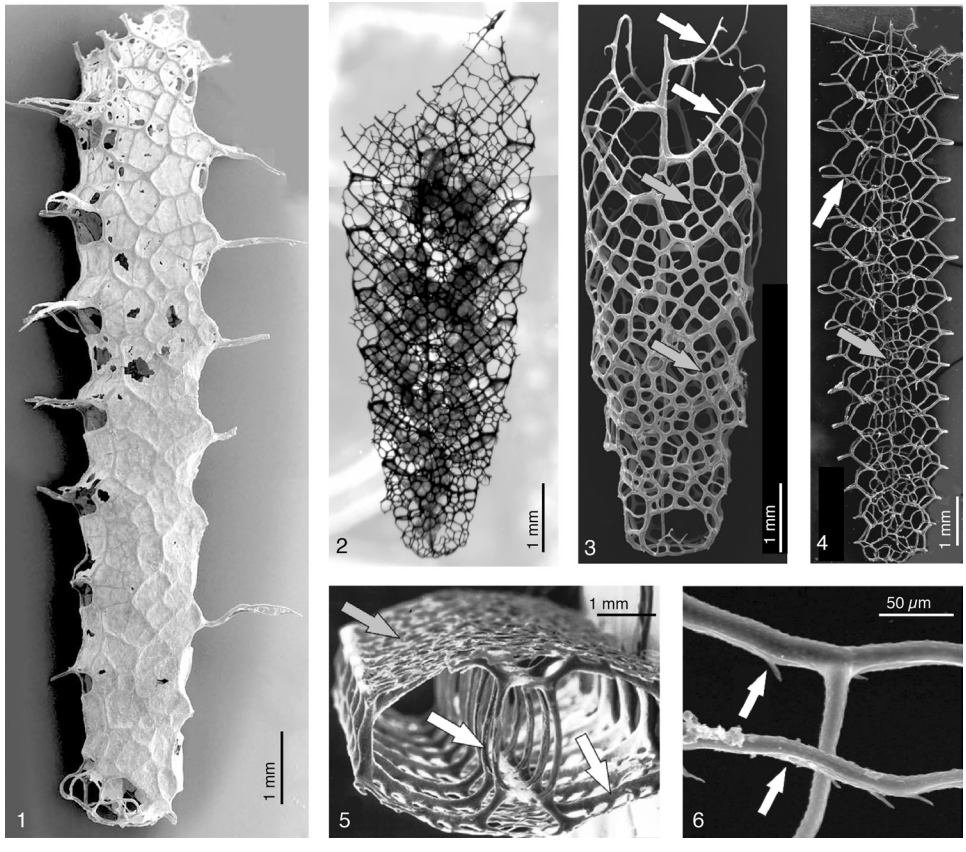


FIG. 54. Clathrium and reticulum. *1, Spinograptus clathrospinosus* (EISENACK, 1951), with preserved ancora sleeve membranes (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 14,*7*); *2, Retiolites geinitzianus* BARRANDE, 1850, showing partial preservation of thecae (Maletz, 2008, fig. 1a); *3, Retiolites* sp., longitudinal view, SEM photograph (new); *4, Paraplectograptus simplex* (KOZŁOWSKA-DAWIDZIUK, 1995), (Lenz & others, 2012, pl. 2); *5, Retiolites* sp., cross section (new); *6, Paraplectograptus eiseli* (MANCK, 1918), enlarged view, showing seams and remains of fuselli in the thecal framework lists (new). *White arrows,* clathrium (*3–4*); *gray arrows,* reticulum (*3–5*); *arrows*, remains of fuselli (*6*).

LATE-STAGE AND GERONTIC MODIFICATIONS

A number of late-stage and gerontic modifications observable in the colonies can considerably change the colony shape and easily lead to misidentifications. They appear in large, supposedly mature tubaria and have never been found in juveniles. These features include the excessive development of cortical tissues in many benthic and a few planktic graptolites and also the resorption of structural details in mature colonies. The parasicula and parathecae or the strongly elongated proximal thecal spines of certain biserial graptolites may also be examples of gerontic development. The elongation of proximal spines and the virgella, although common in many biserial graptolites, does not add any new features to the tubaria and, thus, is not considered herein.

PARASICULA AND PARATHECAE

A colony feature first introduced in some early biserials is the parasicula (VANDENBERG, 1990), an apertural elongation of the sicula that forms a tube of various lengths, as illustrated by BULMAN (1947) in *Pseudoclimacograptus scharenbergi* (ELLES & WOOD, 1906). Based on the observations by LOXTON and others (2011) of an isolated specimen of *Appendispinograptus supernus* (ELLES &

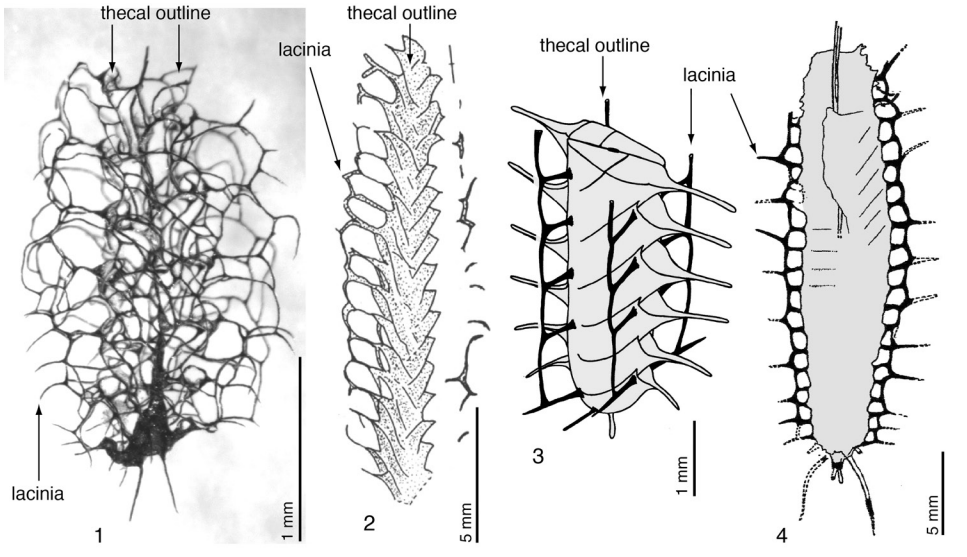


FIG. 55. The lacinia. *1, Pipiograptus* sp., specimen showing a vague thecal outline and the extensive lacinia, sicula, and first theca completely sclerotized, Viola Limestone, Oklahoma, USA (new, photograph provided by Daniel Goldman); *2, Neurograptus margaritatus* (LAPWORTH, 1876a), specimen with sclerotized tubarium and lacinia (Williams & Bruton, 1983, fig. 24a); *3, Paraglossograptus* sp., reconstruction showing lacinia (new); *4, Paraglossograptus tentaculatus* (HALL, 1865), GSC 950b, syntype showing lacinia development and connection to lateral apertural thecal spines (adapted from Rickards, 1972, fig. 1a).

WOOD, 1906), the parasicula is comprised of narrow fuselli. The parasicular tube grows along the elongating virgella and may twist around it. A number of climacograptid species develop the parasicula as a species-specific character. MITCHELL, CHEN, and FINNEY (2007) recognized similar tubular extensions of the proximal thecal pairs and termed them parathecae (Fig. 53.6, Fig. 56). MITCHELL, CHEN, and FINNEY (2007) and, more extensively, VANDENBERG (1990) described the development of parasiculae and parathecae in a number of species of *Appendispinograptus* LI & LI, 1985 (Fig. 56.1–56.2, Fig. 56.4). The parasiculae and parathecae originated as tubular outgrowths along the virgella and the proximal thecae, respectively. In some species, these structures progressively grew into very long and robust spinelike structures as the colony matured. The earliest parasicula known is from the lower Darriwilian in the genus *Archiclimacograptus* MITCHELL, 1987 (MALETZ, 1997a).

A number of Lower Ordovician anisograptids (especially the Tremadocian genera *Ancoragraptus* and *Chigraptus*), certain Middle Ordovician sigmagraptines (*Perissograptus* WILLIAMS & STEVENS, 1988; *Maeandrograptus* MOBERG, 1892a), and Middle to Upper Ordovician nemagraptids, such as *Nemagraptus gracilis* (HALL, 1847), possess a long, free portion of the apertural part of the sicula that extends well below the lowest level of the thecae (Fig. 56.3). These bear some resemblance to the parasiculae of Ordovician biserials. However, in these taxa, the siculae are completely formed before the development of the stipes; and the free, projecting parts are not a late-stage addition to the colonies. These are not homologous constructions so should not be identified as parasiculae.

Other basal structures, which were probably progressively enlarged as the tubarium matured, include the large meshwork in *Climacograptus*? *baragwanathi* T. S. HALL, 1906 (Fig. 53.1); this is apparently an extension of the virgella and, thus, may be constructionally comparable to the ancora sleeve of the retiolitids. Another example of progressive proximal development is the

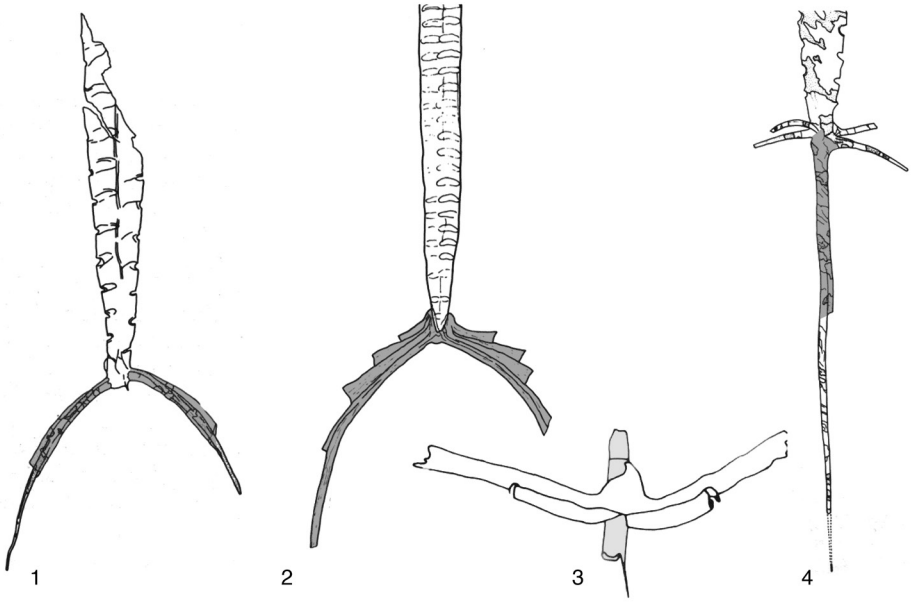


FIG. 56. Parasicula and parathecae. *1–2, Appendispinograptus longispinus* (HALL, 1902); *1,* with at least one pair of parathecae; *2,* mature tubarium with multiples of parathecae and long spine pairs (adapted from Riva, 1974a, fig. 4d); *3, Nemagraptus gracilis* (HALL, 1847), with sicula proximal region extending well below thecal level, and moderately long virgella (adapted from Finney, 1985a, fig. 12–11); *4, Climacograptus hastatus* (HALL, 1902) with multiples of spines, a very long virgella, and long parasicula (Riva & Ketner, 1989, fig. 9b). *Dark gray,* parasiculae and parathecae; *light gray,* sicula in *Nemagraptus.*

numerous spines at the sicula and the early thecae in *Comograptus comatus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968 (Fig. 53.3). The development of the bulbous construction at the proximal end of *Climacograptus wilsoni* LAPWORTH, 1876a (WILLIAMS, 1994) appears to start from a short parasicula, but details are unknown. The round shape in most specimens suggests a vesicle of some kind.

CORTICAL OVERGROWTH

A thick cover of cortical tissue (Fig. 57) may cover important structural details in dendroid graptolites and is occasionally present in planktic taxa (BATES & others, 2011). Cortical overgrowth can be excessive in certain taxa and can completely occlude thecal apertures. In general, the cortical overgrowth is more pronounced in the proximal regions of the colonies and, thus, can be regarded as a late-stage or gerontomorph addition, but its secretion may start early during the astogeny of the graptolite colony. The thecal development and form are completely obliterated in extreme cases, and only a vague outline of the colony shape remains. Therefore, the cortical overgrowth may influence considerably the appearance of the graptolites and provide problems for taxonomic identifications.

RESORPTION

Large parts of the siculae are lacking in mature stages of the colonies of a few species of planktic graptolites. This has been interpreted as a resorption of part or even all of the sicula or other parts of the colonies. One of the most impressive examples was represented by the lack of a visible sicula in the genus *Janograptus* TULLBERG, 1880a. However, ALBANI and others (2001) argued that isolated specimens from the Table Head Group of western Newfoundland are actually regenerated stipes of extensiform dichograptids, and the genus *Janograptus* is

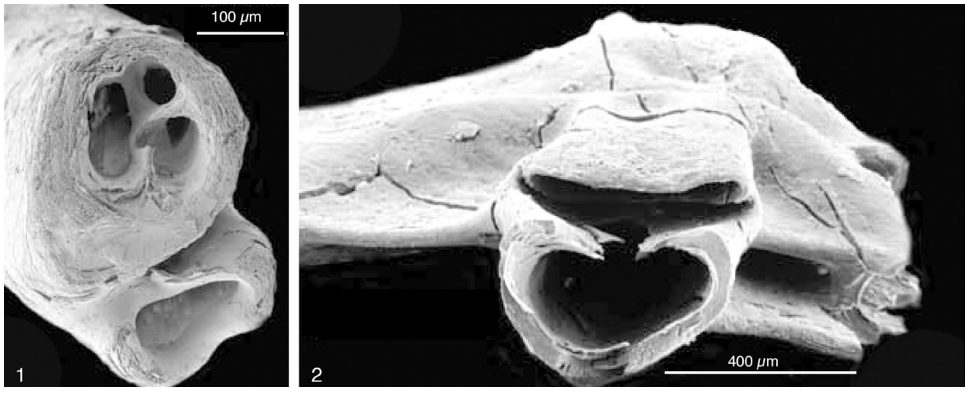


Fig. 57. Cortical overgrowth. *1, Dendrograptus* sp., broken end of stipe showing thecal cavities and excessive cortex development; *2, Amphigraptus* sp., view into thecal opening with thick cortical cover (Bates & others, 2011).

based on regeneration of stipes, a feature that becomes common only in slender Silurian monograptids (see discussion of regeneration and pseudocladia to follow).

A clear effect of resorption is the lack of a visible supradorsal part of the sicula in *Dicellograptus jonstrupi* Hadding, 1915a and related Upper Ordovician taxa (Williams, 1982a). Juveniles invariably had a complete sicula prominently exposed in the axil of the colony (Fig. 58.1), but the sicula is no longer visible in mature specimens (Fig. 58.2); moreover, the axil may show a slight bump in the horizontal, proximal part of the stipes only. Resorption of the apex of the sicula has also occurred in *Pleurograptus lui* Mu, 1950a, from the Upper Ordovician of Nevada (Štorch & others, 2011).

REGENERATION

Graptolite colonies, as all colonial organisms, possess a considerable capacity for regeneration of their damaged tissues and secreted housing structures (Fig. 59). Even though the regeneration of the soft tissue in fossil specimens is not preserved, the tubaria may convey considerable evidence of this capacity (Kraft, 1926; Bulman, 1932a; Eisenack, 1941b; Urbanek, 1958; Rigby, 1994a). In isolated material, damage and repair is evident from unconformities of fusellar structures. Repair is common in juvenile siculae. Many have experienced damage; regeneration of nemata and partly missing prosiculae are common. Where damage occurred at a growing end of a colony (e.g., through breakage of part of the stipe), the zooids were able to regenerate and begin secreting new fuselli without changing the design of the colony. If the damage occurred in older parts of the colonies, cortical tissue was used to repair the tubarium, but normal fusellar tissue no longer developed. The repaired section was instead formed of a structureless film of material (Bulman, 1970).

Malformation is also visible in graptolites. Biserials can lack the second stipe, as demonstrated from a specimen of *Dicaulograptus hystrix* (Bulman, 1932a) in which the second stipe is abandoned after a single theca, whereas the first stipe continued to grow a number of thecae (Bulman, 1932a, pl. 9,*9*). Others develop a third stipe, as described in *Orthoretiolites hami* Whittington, 1954 (Bates & Kirk, 1991). Maletz (2003) described an isolated specimen of *Normalograptus scalaris* (Hisinger, 1837) with a typical biserial proximal end and a distal portion lacking a second stipe. In this specimen, a thick covering of cortical material covers the ventral and lateral sides of the uniserial part. The dorsal part does not have a cortical cover and is broken, suggesting a genetically determined control of the deposition of cortical material. Malformation is also apparent in the accidental development

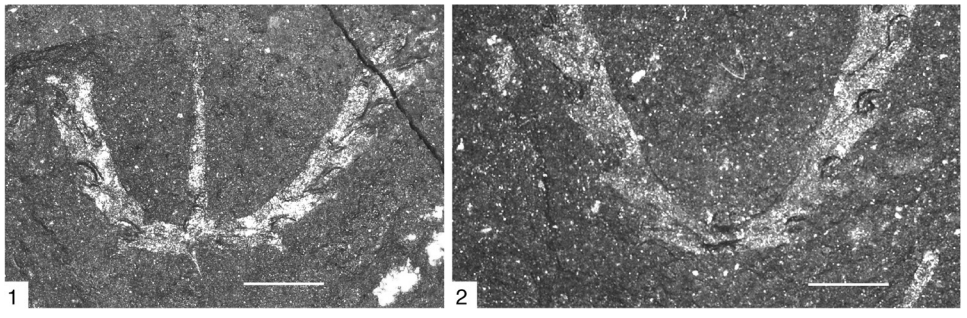


FIG. 58. Resorption in *Dicellograptus jonstrupi* HADDING, 1915a, Risebaeck, Bornholm, Denmark. *1,* LO 2689t, juvenile; *2,* LO 2690t, mature specimen, scale bars, 1 mm (new).

of a partly biserial monograptid that was described by URBANEK (1997a) from isolated material (Fig. 59.1).

A special case of regeneration is the development of pseudocladia (URBANEK, 1963) seen in some species of *Diversograptus* and *Linograptus*. Broken stipe fragments of many monograptids are able to regenerate a complete second stipe as a pseudocladium, producing a bipolar colony without a sicula. RICKARDS (1973a) illustrated a number of Silurian monograptid taxa from shale material, with bipolar colonies that lacked the presence of a sicula, but isolated specimens with evidence of regeneration are extemely rare and usually fragmentary.

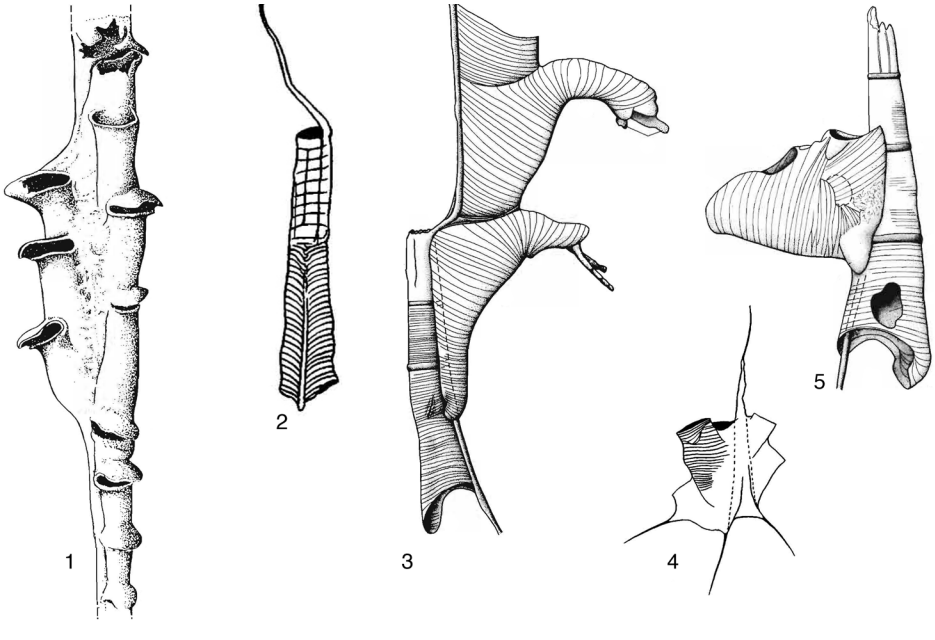


FIG. 59. Malformation and regeneration. *1, Slovinograptus balticus* (TELLER, 1966), abnormal development from uniserial to biserial, upper Silurian, Poland (Urbanek, 1997a, fig. 10); *2, Rectograptus gracilis* (ROEMER, 1861), most proximal portion of prosicula missing (Bulman, 1970, fig. 47); *3, Uncinatograptus spineus* (TSEGELNIUK, 1976), damage to proximal part of sicula and subsequent offset regeneration, upper Silurian, Poland (Urbanek, 1997a, fig. 12); *4, Rectograptus gracilis* (ROEMER, 1861), regeneration of th2[1] (Bulman, 1970, fig. 47; based on Kraft, 1926, pl. 20); *5, Neocolonograptus lochkovensis* (PŘIBYL, 1940a), regeneration of th1 (Urbanek, 1997a, fig. 11).

HEMICHORDATE TAPHONOMY

Jörg Maletz

The investigation of taphonomy has long been neglected in the study of fossil Hemichordata, and the results of taphonomic processes are frequently underestimated. Therefore, misidentifications of pterobranch or graptolite specimens are common, as taphonomic features are repeatedly regarded as genuine taxonomic characters. The extremely poor fossil record of the Enteropneusta (see Maletz, 2014a) indicates that preservation is even more difficult in soft-bodied organisms. The taphonomical changes of a specimen start with the death of the organism and the beginning of the decay of its body. Nanglu, Caron, and Cameron (2015) investigated the decay of extant enteropneusts to understand the morphology and early evolution of this group and found some consistent patterns. Cameron (2016) used this information to interpret the early evolution of enteropneusts and to identify characters previously not recognized in fossil taxa (also see Cameron, 2018). Preservational aspects of the few fossil enteropneusts are largely unknown and details have not been investigated. The Burgess Shale species *Spartobranchus tenuis* (Walcott, 1911), as described by Caron, Conway Morris, and Cameron (2013) which represents the oldest known enteropneust taxon, is based on flattened carbonaceous compressions. It represents an extraordinary preservation, with a number of anatomical details not recognized in other fossil enteropneusts, in which only vague outlines were visible. The taphonomy of the closely related but commonly much smaller pterobranchs has been barely investigated, and little is known on the modifications introduced to the fossils during fossilization and weathering processes. Many features found in fossil graptolites can be shown to represent postmortem effects and the interaction of sedimentary, diagenetic, and metamorphic processes affecting the organic material. In the end, it may be impossible to identify a certain fossil as a pterobranch, as all characteristic features may have been lost.

Benthic graptolites may have been preserved *in situ* in the sediments of the environment in which they grew, but planktic graptolites lived in the water column. Thus, they invariably need to be interpreted as transported and deposited in environments other than the ones in which they lived and therefore represent death assemblages. This fact has considerable implication for the interpretation of graptolite taphonomy, as the formative first changes happened to the colonies even before burial in the sediment.

PRESERVATION POTENTIAL

The differences in the preservation potential of the various tissues of the graptolites leads to considerable influence on the decay processes and the degree of preserved anatomical details. Pterobranchs consist of three different parts: 1) the tubaria, the housing constructions secreted by the zooids from organic material; 2) the zooids made from soft organic tissues; and 3) the stolon system of the graptolites (except for the Cephalodiscida), a highly durable strand of organic material connecting the zooids. Within a few days, the graptolite zooids decay into unrecognizable remains (Briggs & others, 1995), and their fossil record is negligible. The presence of fossil zooids was claimed by Durman and Sennikov (1993) and Sennikov (2016) for the Middle Cambrian *Sphenoecium obuti* (Durman & Sennikov, 1993), preserving evidence of anatomical details, such as the soft and hard stolon and the body with the arms associated with the preserved tubarium, showing fuselli (Fig. 60.8–60.9). Surprisingly, the stolon system is largely lacking in this material, even though it should have been more durable (Beli, Piraino, & Cameron, 2017). Specimens of *Psigraptus* Jackson, 1967

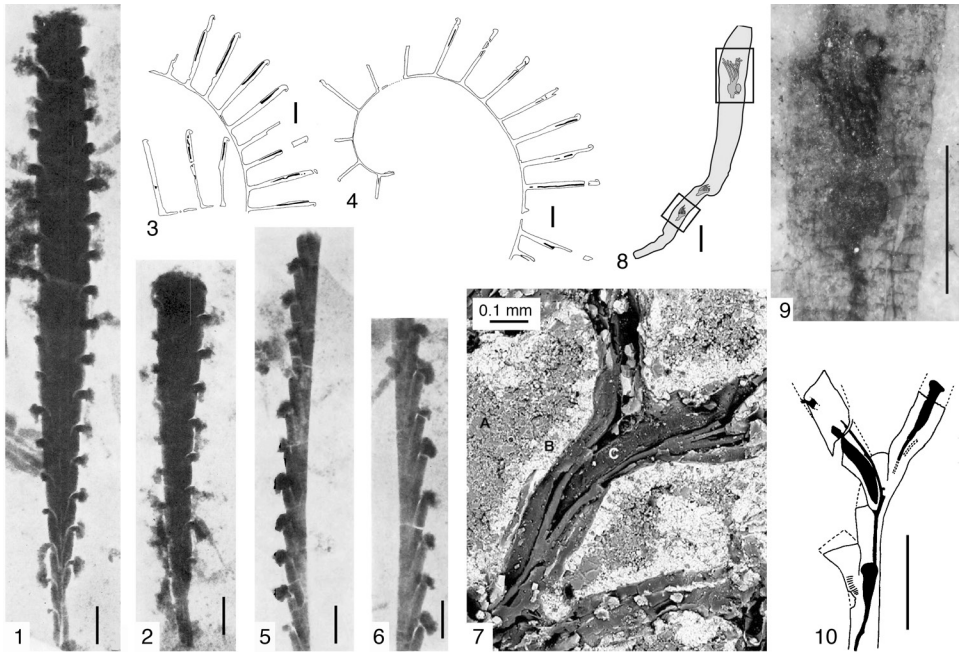


FIG. 60. Remains of fossil zooids and stolons. *1–2, Rhaphidograptus toernquisti* (ELLES & WOOD, 1906) showing pyritic clouds protruding from the thecal apertures (Bjerreskov, 1978, pl. 21); *3–4, Rastrites geinitzii* TÖRNQUIST, 1907, possible remains of the contractile stalk of the zooids in black (Loydell, Orr, & Kearns, 2004, fig. 3); *5–6, Pernerograptus revolutus* (KURCK, 1882), pyritic casts with pyritic clouds at the apertures (Bjerreskov, 1978, pl. 20); 7, *Desmograptus micronematodes* SPENCER, 1884, relief specimen showing stolon system (Saunders & others, 2009, fig. 3); *8–9, Sphenoecium obuti* (DURMAN & SENNIKOV, 1993); *8,* drawing of thecal tube with possible remains of three zooids (Sennikov, 2016, fig. 3); *9,* possible zooidal remains (Sennikov, 2016, pl. 2); *10, Psigraptus jacksoni* RICKARDS & STAIT, 1984, fragment showing remains of zooids (Rickards & Stait, 1984, fig. 4i). Scale bars, 1 mm unless stated otherwise.

(RICKARDS & STAIT, 1984; RICKARDS, PARTRIDGE, & BANKS, 1991) (Fig. 60.10) and some Silurian monograptids (BJERRESKOV, 1978, 1994) may provide evidence of decayed zooids through the presence of mineral accumulations inside the tubaria and as cloudy patches in front of the thecal apertures (Fig. 60.1–60.2, Fig. 60.5–60.6). Anatomical details are not present in this material. Otherwise, pterobranch zooids are known exclusively from extant species, and their anatomy is well known (see *Introduction to the Class Pterobranchia,* p. 19–28).

The only parts of the original zooids that have a higher resistance to decay are the stolons of the graptolites, as decay experiments of *Rhabdopleura* ALLMAN in NORMAN, 1869a specimens indicate (BRIGGS & others, 1995; BELI, PIRAINO, & CAMERON, 2017). The preservation of the resistant stolon system is known to be common in benthic graptolites, and details are available for the Dendrograptoidea, as shown in *Desmograptus micronematodes* SPENCER, 1884 (SAUNDERS & others, 2009) (Fig. 60.7) and the Mastigograptidae (BATES & URBANEK, 2002). Isolated material of the stolon system of benthic taxa has been described as hydroid remains (see MIERZEJEWSKI, 1986; MALETZ, 2014b), and their identification still remains difficult. Stolons in planktic taxa have not been described in detail, but JACKSON (1967) and RICKARDS and STAIT (1984) illustrated pyritized stolonal remains in *Psigraptus* (Fig. 60.10), and HUTT (1974a) indicated the presence of a stolon system in *Adelograptus tenellus* (LINNARSSON, 1871). ZALASIEWICZ and others (2013) discussed a

stolon-like system in the planktic graptoloid *Dicranograptus* Hall, 1865 as an abnormal recalcitrant pectocaulus, but the material appears to represent remains of pressure shadow minerals in a poorly preserved and strongly tectonized graptolite. The described structures do not have any organic material and, thus, may not represent a stolon system. Loydell, Orr, and Kearns (2004) discussed the possible preservation of the contractile stalks (zooidal stalk of Maletz & Cameron, see Fig. 9, p. 18) in *Rastrites geinitzii* Törnquist, 1907 (Fig. 60.3–60.4) and *Neolagarograptus*? Štorch, 1998a from Latvia. The stolon system, however, is not preserved nor are the zooids. The remains are preserved as a two-dimensional film of organic carbon residues surrounded by an early diagenetic pyrite fill of the thecal tubes.The fusellum of the graptolite tubaria is comprised of an organic compound, probably collagen (Towe & Urbanek, 1972; Crowther & Rickards, 1977; Runnegar, 1986), but details on the biochemical composition are not available (Foucart & others, 1965; Florkin, 1969; Sewera, 2011). The tubaria of extant pterobranchs are light brown to completely translucent. In some cephalodiscid taxa, foreign material may be incorporated in the tubarium formation (Harmer, 1905; Harmer & Ridewood, 1913). Fossil graptolites are usually dark brown to black (Fig. 61.1–61.5), indicating some compositional modification through the fossilization processes. Sometimes, specimens are lighter brown and partly translucent, indicating their fusellar composition in shale material (Fig. 61.5), but this preservation may, in part, be due to subsequent weathering.

DECAY

The tubes of extant *Rhabdopleura* begin to show signs of decay after four days in oxic environments, as actuo-paleontological data demonstrate (Beli, Piraino, & Cameron, 2017), but the tubaria remained largely unchanged within the sediments for hundreds of millions of years, as observed in chemically isolatable specimens. These were originally regarded as representing the animals themselves, but are now understood to be the housing constructions (Mitchell & others, 2013; Maletz, 2014b) formed from individual fuselli (e.g., Crowther, 1981; Andres, 1961, 1977, 1980). It is clear that the preservation of graptolite tubaria under oxic conditions is quite limited, and most fossil graptolites are preserved in dysoxic or anoxic sediments or have been entombed in the sediments and protected from the damaging effects of oxigenated organic decay.

Graptolites may be part of the marine snow and the clingfilm preservation (Jones, Zalasiewicz, & Rickards, 2002) described for *Spirograptus turriculatus* (Barrande, 1850) and may be more widely distributed, even though difficult to demonstrate. Even though organic material may be eaten by predators, this has rarely been confirmed for graptolites (Underwood, 1993; Loydell, Zalasiewicz & Cave, 1998). The sinking of planktic graptolite colonies may have been retarded through the decay of the zooids, leading to uplift from decay gases. Eventually, however, they started settling through the water column, and the tiny zooids would have likely disappeared by the time their tubaria reached the seafloor. Once there, the tubaria would have been exposed to microbial attacks and damage by burrowers and grazers. Fine hash consisting of graptolite fragments is common worldwide, indicating considerable destruction and fragmentation of the tubaria prior to final burial. This process may be interpreted as bioturbation and/or scavenging within unlithified sediments containing abundant graptolite specimens. Present day microbial destruction may even occur in organically preserved, chemically isolated material in fossil collections (see example in Fig. 62.3). Radzevičius, Schopf, and Kudryavtsev (2013) described possible fossil bacteria on the tubarium surface of Silurian monograptids, forming spherical and spirally coiled structures.

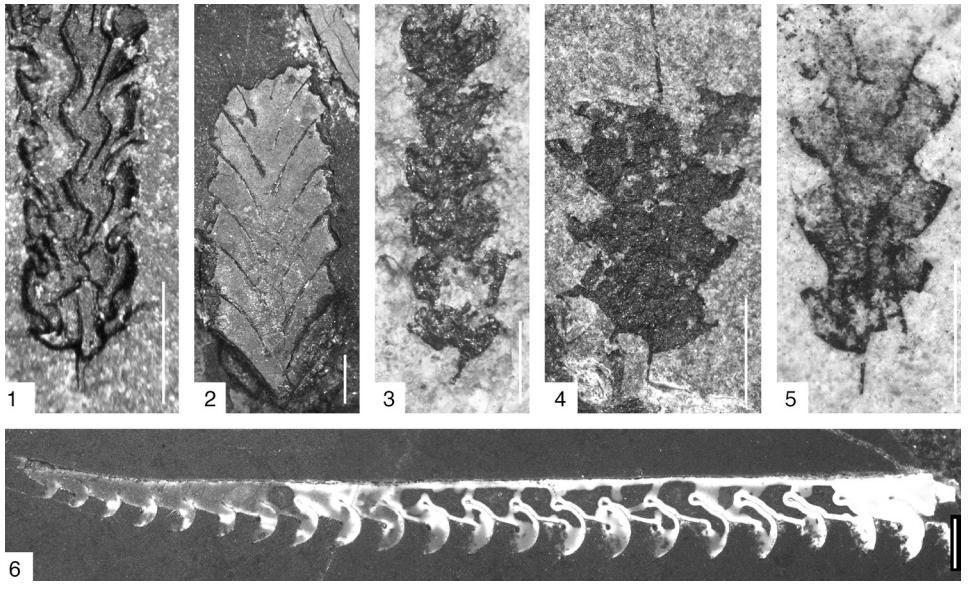


Fig. 61. Graptolite preservation. *1, Archiclimacograptus* Mitchell, 1987 sp., full relief, Darriwilian, western Newfoundland, Canada (new); *2, Petalolithus palmeus* (Barrande, 1850), LO 1116t, full relief, pyrite fill, polished section, Tomarp, Sweden (new); *3, Levisograptus sinicus* (Mu & Lee, 1958), SMF XXIV 424, partial relief, Karga Village, southern Urals, Russia (new); *4, Orthograptus quadrimucronatus* (Hall, 1865), GSC 139251, flattened, L'Egaré Motel, Quebec, Canada (new); *5, Rectograptus gracilis* (Roemer, 1861), SMF 75826, flattened, showing fuselli, Maquokea Group, Graf, Iowa, USA (new); *6, Monograptus priodon* (Bronn, 1835), SMF XXIV 401, silica coating in chert, Schnebes, Frankonian Forest, northern Bavaria, Germany (new). All scale bars, 1 mm. Color images available, *Treatise Online* 110.

There are several ways in which the decay of a graptolite tubarium can be stopped or at least slowed down. Retardation of decay may occur through early lithification of the host rock. Paleozoic limestones commonly bear well-preserved graptolites, which are supposedly entombed in the rock through early lithification of the lime mud, sheltered from a destructive oxic environment. Preservation in a dysoxic to anoxic environment is another way of delaying the decay of organic material. This is how most graptolites were preserved, and the often-used term, graptolite black shale, reflects this preservation. However, the common occurrence of graptolites in black shales does not indicate an environment in which graptolites flourished (Cooper & others, 2017).

DEPOSITION AND BURIAL

A number of processes that modify graptolites before they are entombed in the sediments indicate that their behavior should be regarded as similar to that of sediment particles. Post-mortem transport is commonly demonstrated in graptolite tubaria. Depending on the water current pattern, tubaria of planktic graptolites may either sink vertically down onto the sediment surface or experience a variable lateral displacement. Transport from shallow water regions into deep-water basinal regions appears to be common, exhibited exemplarily by the toe-of–slope environment in which the Lower to Middle Ordovician graptolites of the Cow Head Group in Newfoundland were preserved (Williams & Stevens, 1988, 1991) and in which fragmented specimens of benthic graptolites are also common.

Graptolites can be randomly distributed in a sediment pile or current aligned (Hundt, 1935b; Moors, 1970; Cooper & others, 2017), showing postmortem transport. It is not clear whether premortem

transport in the water column can also lead to alignment on the sediment surface, but it is unlikely in the case of planktic taxa. Current transport may, however, be a reason for the death of the colonies, in which case the alignment is only the final result of transport into unsuitable environments and subsequent death and settlement of the dead colonies. Graptolites are found in turbidites and tempestites (Hills & Thomas, 1953; Schleiger, 1968; Moors, 1969, 1970) and even in bentonite beds (Mitchell, Brussa, & Astini, 1998), indicating a possible transport as living organisms caught in water turbulences and, on occasion, trapped in volcanic ash.

Time averaging (Kidwell & Bosence, 1991) may be common in areas of low sediment accumulation rates, causing high concentrations of taxa that were not living in the same environment or at the same time in suitable environments (Cooper & others, 2017). Time-averaged faunas may also indicate a quite variable preservation, because specimens deposited earlier on the sediment surface may already have partly decayed before the latest specimens arrived on the seafloor and before the specimens were covered by a new layer of sediment. Time averaging is most prominent in regions with very low sediment input, commonly in pelagic and hemipelagic sediments, but may also be present in shelf regions with low sediment input.

Benthic graptolites may be covered by layers of sediment and preserved *in situ* (e.g., Bouček, 1957; Erdtman, 1976), but in most cases their fossil remains represent fragments transported from shallow shelf regions into deeper water environments (Maletz, 2006), where they may be found in association with numerous planktic taxa (e.g., Hall, 1865). However, quite a number of well-known planktic graptolite faunas are not associated with benthic taxa. There are barely any benthic graptolites associated with the famous Ordovician graptolite faunas of the Tøyen Shale and Elnes formations of Scandinavia (Monsen, 1937; Maletz, 1997a; Maletz & Egenhoff, 2005) or the Silurian faunas of Thuringia, Germany (Schauer, 1971).

Reworking is expected to have been rare or even impossible in graptolites, as the tubaria may easily break into pieces when exhumed from a sediment. Transport, thus, was restricted to recently deceased colonies and likely records a secondary depositional site. However, transport of graptolites in clasts of resistant rock types is more common. The best examples are from the glacial erratic boulders of Scandinavian origin in northern Germany and Poland (Roemer, 1861; Heidenhain, 1869; Kraft, 1926; Eisenack, 1951; Urbanek, 1958; Maletz, 2008, 2010a; Radzevičius & others, 2010; Maletz & Schöning, 2017). Here, Ordovician and Silurian graptolites occur in sediments deposited during the Pleistocene glaciations. A Paleozoic example of transport of graptolites in clasts appears in the Daniel's Harbour conglomerate of western Newfoundland (Whittington & Rickards, 1969; Stenzel, Knight, & James, 1990). Reworked clasts of the Table Cove Formation occur in this conglomerate bed, bearing a graptolite fauna that is out of place and older than the conglomerate and the surrounding sediments of the American Tickle Formation. A good example of larger scale transport is the olistostromes of the allochthonous Dauphin Formation of the Hamburg succession of Pennsylvania, USA, which have been tectonically moved twice. Boulder to kilometer-sized masses containing an Early Ordovician graptolite fauna of slope origin were first transported to a Middle Ordovician trench and encased within a clastic matrix containing a Darriwilian fauna. Tectonic slices of the trench sequence were then structurally transported to the Martinsburg foreland basin during the Taconic orogeny in the Sandbian (Ganis, Williams, & Repetski, 2001; Ganis, 2005).

During transport, the graptolite tubaria may have experienced bending and breakage, especially in long and robust taxa, but slender forms remained more flexible. Eisel (1908) and Hundt (1910, 1951b)

already described the influence of tectonic deformation in kinked monograptid taxa, thus, indicating the possibility of bending of tubaria without breakage. Bent specimens were, however, rarely illustrated or mentioned (for an exception, see Haberfelner, 1931, pl. 1,*19b*). Fragmentation may be more common, but astonishingly large, thought to be complete specimens have been described, such as *Paratemnograptus magnificus* (Pritchard, 1892) with an estimated diameter reaching nearly one meter and an incompletely preserved specimen of the straight monograptid *Stimulograptus halli* (Barrande, 1850), with a length of 1.45 m (Loydell & Loveridge, 2001).

POST-BURIAL MODIFICATIONS

Graptolite tubaria need to be covered within the sediment before stabilization and protection from decay can be established, because they are quite vulnerable to organic decay and destruction when exposed on the sediment surface. After they are covered by a layer of sediment, other factors begin to play a role in the preservation of these seemingly very delicate fossil remains.

Graptolites can be preserved in sediment in full relief (Fig. 61.1) or partly flattened (Fig. 61.3) through infilling with sediment or diagenetic mineral growth before the compaction, leaving the three-dimensional construction still recognizable. Specimens fully preserved in relief may have little outward detail, but slight compaction can reveal the median septum and thecal septae in axonophorans (Fig. 61.1). Early formation of carbonate concretions prevented the compaction of graptolite colonies in many places. Most notably are the beautifully preserved Llandovery, Silurian graptolites in the Kallholn Shale of Dalarna, Sweden (Hutt, Rickards, & Skevington, 1970; Loydell, 1991b; Loydell & Maletz, 2004, 2009); Arctic Canada (e.g., Lenz & Kozłowska, 2006; Lenz & Melchin, 1987; Melchin, 1998); and the glacial erratic boulders of Scandinavian origin mentioned earlier, all of which represent carbonate concretions.

The first post-burial diagenetic effects on the graptolite tubaria are related to the compaction and dewatering of the surrounding sediment, leading to flattening of the specimens. Because the graptolite tubaria are made from flexible organic material, flattening within the sediment usually does not cause noticeable effects such as breakage and fractures, but certain other effects of deformation, such as shape distortion, may be noticeable (Briggs & Williams, 1981; Williams & others, 1982). Flattened graptolites are preserved as thin films of organic material in which only the outlines of the colonies are apparent (Fig. 61.4). Thus, several layers of organic material of the originally three-dimensional fossil (Fig. 61.1) can be superimposed so that thecal outlines, sicular shape, and other features become compressed into a relatively thin, difficult to untangle, layer. Even with IR photography or through chemical bleaching of the specimens, most details cannot be recovered (Bates, Maletz, & Zalasiewicz, 2015). Flattened specimens chemically isolated from shales may preserve their fusellar structure (Fig. 62.1), but also have considerable crumbling of the fusellum without breakage (Fig. 62.2).

Although evidence of chemical alteration of the organic material of the tubaria is problematic, it is to be expected. The dark color of most fossil material reveals an incipient alteration, at the very least. Gupta, Briggs, and Pancost (2006) indicated the presence of aliphatic polymers and lack of proteins in fossil graptolites. Various authors have supposed that the material was originally collagen (Towe & Urbanek, 1972; Bustin, Link, & Goodarzi, 1989), modified by *in situ* polymerization.

Graptolite tubaria preserved in three dimensions can be filled with various mineral material. Pyrite (Fig. 61.2) is the most common mineral infilling graptolites and can lead to beautiful golden shimmering casts when the covering fusellum is lost. Williams (1990b) described winnowed beds of three-dimensional pyritic graptolites originally formed as internal casts from the Young-

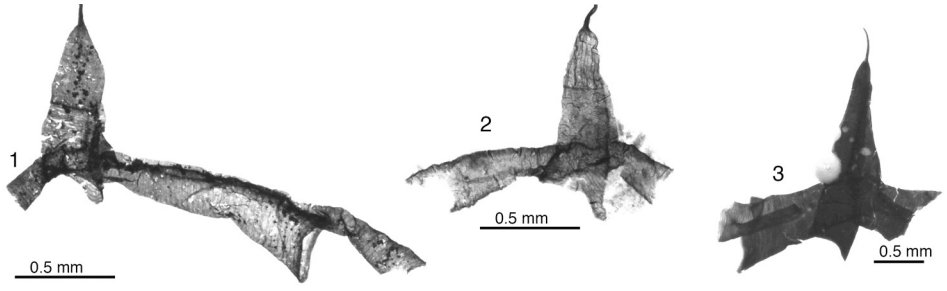


FIG. 62. Flattened graptolites from shales. *1,* Sigmagraptine indet., GSC 140110, showing fusellar construction and prosicula with longitudinal rods, Table Head Group, western Newfoundland; *2,* Sigmagraptine indet., GSC 140111, showing fusellar construction and considerable crumpling, Western Brook Pond, Cow Head Group, western Newfoundland, Canada; *3, Tetragraptus* SALTER, 1863a sp., SGU 9621, specimen showing contemporary fungus growth, Skattungbyn, Dalarna, Sweden. All specimens flattened, chemically isolated from shales, bleached (new). Color images available in *Treatise Online* 110.

sters Gulch Member of the Powers Steps Formation from Bell Island, Newfoundland, Canada. The presumed origin of the pyrite was early diagenetic, sulphide-rich conditions in a prodelta environment that also replaced associated oolites; BJERRESKOV (1991) recognized incomplete infilling with geopetal orientation and pyritic stalagmites and stalactites in Silurian monograptids. The pyrite fill may be weathered to oxides of various colors and the spectacular pink to white examples of *Cymatograptus bidextro* TORO & MALETZ, 2008 are a good example. Phosphatic casts are rare, but have been described for *Climacograptus putillus* (HALL, 1865) from the Elgin Member of the Maquoketa Formation at Graf, Iowa (WERNER & ECHOLS, 1958; GOLDMAN & BERGSTRÖM, 1997). MALETZ and STEINER (2015) discussed the preservation of the Middle Cambrian *Sphenoecium wheelerensis* MALETZ & STEINER, 2015 and noted a lack of organic material. Thus, they interpreted the remains as a replacement of the fusellum with clay minerals, which could be a secondary development due to weathering processes and not a replacement within the sediment.

A replacement of the graptolite tubaria has repeatedly been noted, but appears to be a misinterpretation in most cases. A closer look at the material usually shows a mineral infill or coating of the tubarial walls. A number of papers described silicified graptolites from Silurian chert pebbles of Germany found in various secondary deposits of glacial or glacio-fluvial origin (HUNDT, 1934, 1946, 1957b; RICHTER, 1948, 1951; MÜNCH, 1951; HORSTIG, 1952). These graptolites actually have internal and external coatings of silica (Fig. 61.6) forming a thin crust around the tubarium (GREILING, 1958). MALETZ (2009) described another instance of silica-coated graptolites from the Middle Ordovician of Quebec, Canada. The specimens possess an irregular mass of silica around the tubaria, keeping the colonies intact when the graptolites were chemically isolated from the limestones. They were, apparently, already somewhat distorted tectonically, before the silica was formed around them. It is not known whether the specimens are also filled with silica. Silica also replaced the biomineralized shells of ostracods in the samples.

The thermal alteration of the graptolite fusellum is known in some detail as a result of the investigation of coalification of organic material to understand the potential for oil and gas generation of graptolite-bearing rocks. This alteration can be regarded as essentially similar in its geological behavior to cuticles of arthropods or to plant tissues. The effect of the thermal alteration is, therefore, similar to the coalification of plant material and can even be compared and correlated with the Color Alteration Index for conodonts (EPSTEIN, EPSTEIN, & HARRIS, 1977; HARTKOPF-FRÖDER & others, 2015).

The material changes considerably in its optical properties (Teichmüller, 1978; Goodarzi, 1990; Hoffknecht, 1991; Inan & others, 2016; Schmidt Mumm, & Inan, 2016). Unaltered fossil graptolite material has a dark brown to black color (Fig. 61.1, Fig. 61.3–61.5) that changes with increasing maturation to an intense silvery shine (Fig. 63.1) that may have been mistaken as a pyritization in the past. This is typical of many graptolite faunas of Scandinavia that were affected by regional or local contact metamorphism. The organic material of the graptolite tubaria disappears completely at a moderate to high metamorphic rank but casts may still be recognizable, such as in schists. In these cases, flattened graptolites would have been destroyed without a trace. Graptolite remains may be able to survive considerable alteration; Dieni and others (2005) described identifiable graptolites from boudins in a greenschist unit in the eastern Alps of northern Italy. The material does not have any discernible tectonic deformation. Greenschist-grade metamorphism can also occur in the sediments yielding early Darriwilian graptolites at Bratland in the Gausdal region of Norway (Lapworth, 1906; Williams, 1984).

DEFORMATION AND RETRODEFORMATION

The morphology of most fossil groups is susceptible to shape distortion from structural deformation in the rock body in which they are found. This, of course, can affect graptolites, sometimes dramatically, and was recognized early. Ironically, the distortion of fossils can assist the structural geologist in kinematic analysis if the undeformed shape of the fossil is known for comparison. Graptolites have been frequently used in this endeavor. Conversely, kinematic analysis can assist the paleontologist in retrodeformation of deformed fossils. Techniques for these procedures have advanced from relatively simple to highly technical. Eisel (1908, p. 219) discussed the deformation of graptolites and the influence on the taxonomic identification of the material. He used a black rubber layer on which he drew the specimens and then imitated the distortion by pulling the material in various directions. Various methods have subsequently been used to understand graptolite deformation (Hills & Thomas, 1944; Jenkins, 1987; Cooper, 1970, 1990; Williams, 1990a).

A closer look at graptolite deformation shows that the effects are more severe and do not just concern the taxonomic identification of the material. The graptolite specimens are distorted with the tectonic deformation of the encasing sediments. This deformation may be dramatic as demonstrated by the changes in dimensions described by Maletz and others (1998) from Albania and is known from the classic locality of the Wenlock graptolites at Goni, Sardinia, Italy (Gortani, 1922). The direction of deformation can have considerable influence on the appearance of the graptolite specimens as the example of *Spirograptus turriculatus* indicates (Fig. 64.2). Specimens with a wide and low cone are associated with ones having narrow and high cones. On closer examination, the graptolite fusellum shows parallel lines of fractures (Fig. 64.1,Fig. 64.5), indicating the tectonic deformation if the organic material is still preserved and recognizable (Mitchell, Brussa, & Maletz, 2008). Characteristic and easily recognizable tectonically deformed graptolites are preserved as pale mineral films on black shale (Fig. 64.4). In these cases, the graptolites are clearly outlined and provide strong contrast to the surrounding dark sediment. These mineral films can be identified as phyllosilicate minerals growing as pressure shadow minerals around the organic remains of the graptolites (Underwood, 1992). Typically, the organic material of the graptolites is preserved in unweathered specimens. The mineral films can be of various colors, from whitish to yellow and orange, and light green to blue, depending of the composition of the minerals and the amount of weathering. The minerals are often loosely termed chlorite-group minerals and were

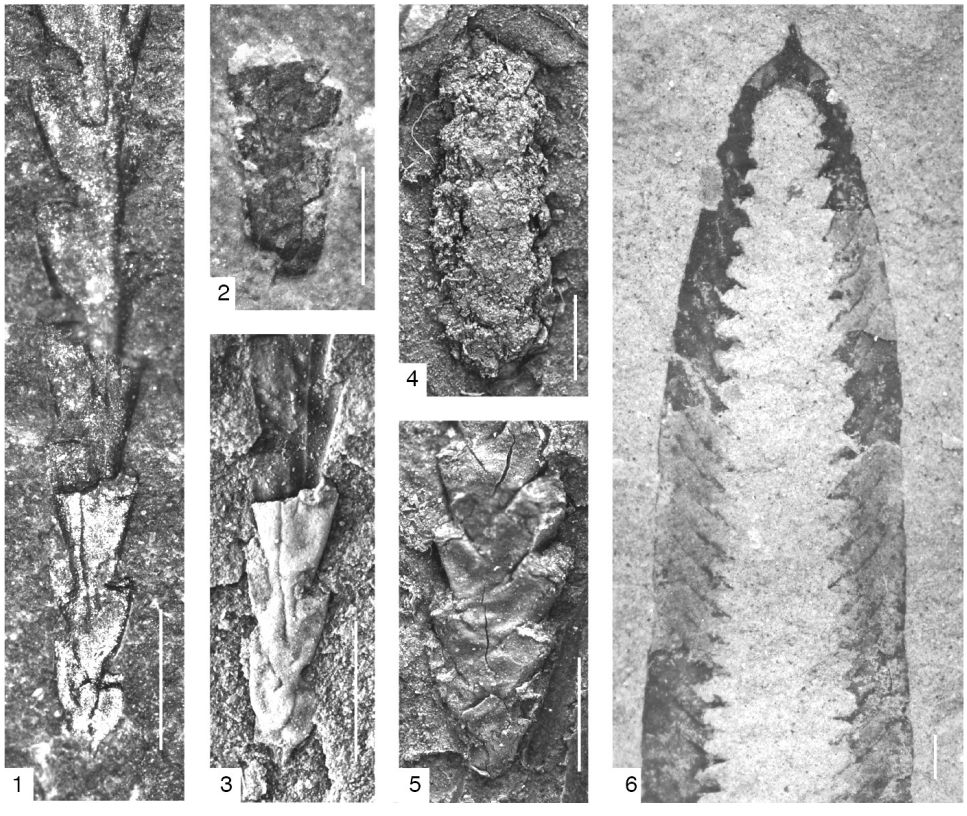


Fig. 63. Weathering. *1, 3, Pronormalograptus antiquus* (Ge in Ge, Zheng, & Li, 1990), PMO 234.061, preserved in relief, Elnes Formation, Slemmestad, Norway; *1,* showing highly coalified, silvery shining fusellum; *3,* same specimen coated with ammonium chloride to highlight structure; *2, Normalograptus mohawkensis* (Ruedemann, 1912), GSC 139252, low relief, weathered pyritic cast with preserved dark fusellum, L'Egaré Motel, Quebec, Canada; *4–5, Pseudorthograptus cyperoides* (Törnquist, 1897), Tomarp, Scania, Sweden; *4,* LO 1294T, strongly weathered pyritic cast; *5,* LO 1296t, weathered pyritic cast, surrounding fractured fusellum; *6, Didymograptus murchisoni* (Beck in Murchison, 1839), SMF 75827, flattened, weathered, Darriwilian, Jordan, exact locality unknown; all scale bars, 1 mm (new).

regarded as replacement of the graptolites in earlier literature. Richter (1853) originally described them as fibrous, silvery white to greenish minerals from the Silurian of Thuringia, but Geinitz (1852) had already termed the material talcum. Gümbel (1868) described the mineral as a pyrophyllite and compared it with the minerals surrounding many Carboniferous plant fossils. Kobell (1870) described the mineral as gümbelite, but this name has rarely been used in the scientific literature.

The scanning electron microscope backscatter method (BSEM) can easily differentiate the films of pressure shadow minerals from the organic material of the graptolite fusellum (Fig. 64.5), which is difficult to see with the unaided eye (Fig. 64.6). Even in deeply weathered material, the tectonic lineation or foliation may provide clear evidence of deformation of a graptolite (Fig. 64.3). In this specimen, the fusellum is not preserved and the reddish material represents iron-stained pressure shadow minerals.

WEATHERING

Weathering effects (Fig. 63, Fig. 64) have rarely attracted attention in graptolite

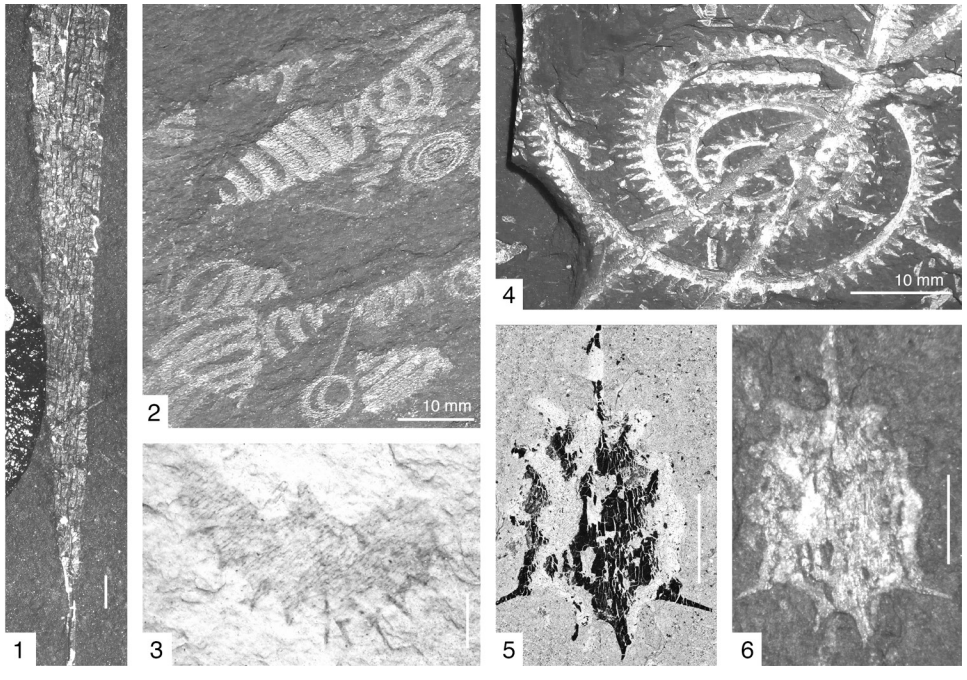


FIG. 64. Deformation and weathering. *1, Normalograptus rectangularis* (M'COY, 1850), SMF XXIV 350, flattened, strongly tectonically distorted, showing parallel fractures in fusellum, Ölsnitz, Voigtland, Germany; *2, Spirograptus turriculatus* (BARRANDE, 1850), SMF XXIV 328 (acquired through exchange from Hemmann), flattened, tectonically distorted, zone 15, locality unknown, Hemmann collection; *3, Arienigraptus angulatus* (MU, GEH & YIN, in MU & others, 1962), SMF 75825, flattened, tectonically distorted and weathered, Wellsford Riffle Range, east of Bendigo, Victoria, Australia; *4, Oktavites spiralis* (GEINITZ, 1842), SMF PK 767, flattened, showing high amount of pressure shadow minerals (white), Grobsdorf, Thuringia, Germany; *5–6, Nanograptus phylloides* (ELLES & WOOD, 1908), paratype, GSE 5495; *5,* BSEM photo showing preserved fusellum in black; *6,* normal light photo, showing light color of fusellum and pressure shadow minerals in contrast to dark sediment; all scale bars, 1 mm, unless stated otherwise (new). Color images (*1, 3*) available in *Treatise Online* 110.

research, even though it is obvious in many graptolite specimens. Black shale may weather to a light grey, yellow, or even whitish color, and the organic material of the graptolites in these cases show a strong contrast, whereas in fresh material they are barely visible. Red iron staining may also be common in specimens and on pressure shadow minerals (Fig. 63.6). Surface weathering of strata or the mineral infilling of the tubaria can degrade or destroy graptolite specimens. Pyrite weathering (Fig. 63.2) may destroy beautiful relief specimens in short time and even affect material in collections as pyrite disease (BIRKER & KAYLOR, 1986; NEWMAN, 1998) (Fig. 63.4–63.5). Weathering of pyritic casts may lead to the formation of reddish to yellow iron minerals or staining of the sediment surface (Fig. 63.2). Weathering is independent of tectonic deformation and both factors may be difficult to separate in seemingly well-preserved material.

PALEOECOLOGY OF THE PTEROBRANCHIA (CEPHALODISCIDA AND GRAPTOLITHINA)

ROGER A. COOPER, SUE RIGBY, DENIS E. B. BATES, and JÖRG MALETZ

INTRODUCTION

The Pterobranchia is a widely distributed group of marine colonial organisms with its acme during the early Paleozoic and a few surviving, extant members. The modern taxa are all benthic and live in waters ranging from shallow-coast to deep-marine environments. Consequently, they are of limited use for interpreting the ecology of the extinct planktic Graptoloidea. Nevertheless, the living pterobranchs provide us with important information on the soft-body anatomy of the Pterobranchia that is not available from fossil taxa. The comparison with the modern pterobranchs enables us to reconstruct graptolites as living entities and better understand their biology, including their feeding and tubarium secretion.

Most of the work on graptolite ecology has been directed toward the planktic faunas, and little is known about benthic graptolite ecology. This imbalance sources from a primary focus on the planktic taxa because of their exceptional biostratigraphic utility and the fact that benthic faunas are rarely preserved in their original environments. The following account is based largely on COOPER and others (2012).

LIFE MODE

The Pterobranchia can easily be differentiated into benthic (sessile) and planktic taxa, and interpretation of their lifestyles is based on this knowledge. Benthic taxa have an elongated dome as the initial part of the colony, as in *Rhabdopleura* ALLMAN in NORMAN, 1869a or *Epigraptus* EISENACK, 1941a (Fig. 65.1–65.2) or a tubular sicula with a flat base for attachment, as in *Dendrograptus* HALL, 1858 and related taxa (Fig. 65.3, Fig. 65.5). In encrusting taxa, the ventral parts of the tubarium adhere to the substrate, whereas the erect, bushy, or tree-like colonies have a specialized structure—a holdfast of varied shape. However, the attachment mode is known from relatively few taxa. In erect-growing Graptolithina, the attachment structure may be rootlike or disk-shaped, but it is invariably a surface attachment feature (Fig. 65.4) and does not extend into the sediment as a root system. All nematophorous graptoloids can be interpreted as planktic (BULMAN, 1970; FORTEY & COOPER, 1986). They possess a free nema and do not show any indication of attachment (Fig.65.6).

Since benthic graptolites are rarely found *in situ* with their attachment intact, the attachment mechanism is little understood. The erect *Mastigograptus* aff. *tenuiramosus* (WALCOTT, 1883) is known to have overgrown calcitic shells, as indicated by the features of an attachment disk (BATES & URBANEK, 2002), which indicates the need for a solid surface for attachment. Also, the benthic *Rhabdotubus johanssoni* BENGTSON & URBANEK, 1986, may be attached to shell, adhering to the phosphatic shells of the small brachiopods *Acrothele* LINNARSSON, 1876 and *Dictyonina* COOPER, 1942, and, more rarely, to trilobite fragments. Rarely, benthic encrusting taxa have been found *in situ* (e.g., MITCHELL, WILSON, & ST. JOHN, 1993). Most examples of encrusting material have been obtained from chemically isolated material (e.g., KOZŁOWSKI, 1949). ERDTMANN (1976) described dendroid faunas supposedly preserved *in situ* in the Mississinewa Shale of Huntington, Indiana, USA, as occurring under low-oxygen, low-energy conditions within the photic zone (less than 60 m deep). Some of the specimens appear to be in growth position, but others clearly indicate at least minor transport because of their lateral orientation on the shale surfaces.

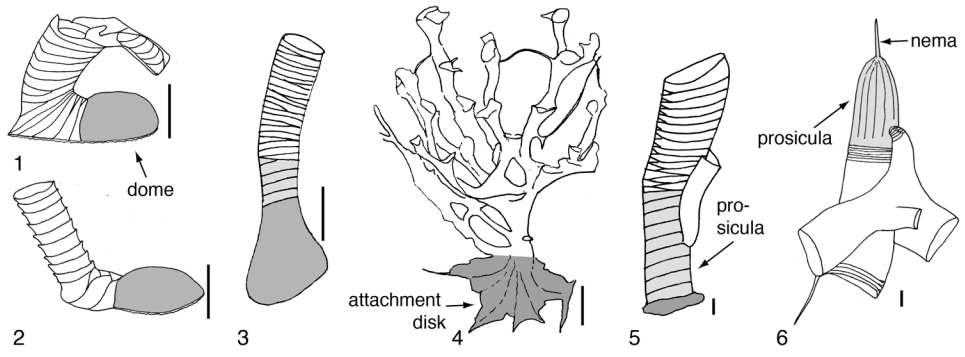


FIG. 65. Sicular development and attachment. *1, Epigraptus* sp. (adapted from Kozłowski, 1971, fig. 1); *2, Rhabdopleura compacta* HINCKS, 1880b (adapted from Stebbing, 1970a, fig. 3); *3, Kozlowskitubus erraticus* (KOZŁOWSKI, 1963) (adapted from Kozłowski, 1971, fig. 5); *4, Dictyonema cavernosum* WIMAN, 1896a with attachment disk (adapted from Wiman, 1896a, pl. 1, fig. 1); *5, Dendrograptus communis* KOZŁOWSKI, 1949, tubular prosicula (adapted from Kozłowski, 1949, fig. 1); *6, Xiphograptus* sp., showing prosicula with free nema (new). Scale bars, 0.1 mm in *1–3, 5–6;* 1 mm in *4*.

The Graptoloidea, as a planktic group of the Graptolithina, have long been recognized as an important component of the Paleozoic plankton (e.g., LAPWORTH in WALTHER, 1897; BULMAN, 1964, 1970; and many others). However, interpretation of the graptoloid habitat within the Paleozoic oceans has proved difficult, and a variety of habitat models have been proposed (see COOPER & others, 2012). Fundamental to all models is the observed distribution of graptoloids in a range of bio- and lithofacies representing all depositional depth zones, from shallow shelf (inshore) to open ocean. Evidence from morphology, inferred feeding mode, and facies preference suggests that graptoloids were able to control the depth at which they lived in the water column, either actively or passively by buoyancy adjustment (RIGBY & RICKARDS, 1989). In other respects, however, graptoloids were largely passive occupants of the water mass in which they lived, and drifted with the ocean currents, both seasonally and as part of the ocean circulatory system. Thus, new species were able to disperse widely and rapidly around the world and establish themselves in new regions.

LOCOMOTION

Benthic graptolites obviously were not actively moving, but their dispersal by means of planktic larvae in extant taxa (e.g., *Rhabdopleura*, *Cephalodiscus* M'INTOSH, 1882) provides a mechanism for their wider geographical distribution. In graptoloids, tubarium structures such as spines, vesicles, or nematularia, and a disk-shaped or netlike colony form have been interpreted as hydrodynamic drag structures and evidence for a passive mode of life (RICKARDS, 1975; FINNEY, 1985b; FINNEY & JACOBSON, 1985). However, ecological models for the planktic graptoloids now generally assume that they were able to move relative to the water mass in which they lived, particularly for feeding efficiency. Among the movement mechanisms suggested are turbulence, buoyancy control, and active swimming. Wind turbulence was no doubt significant for graptoloids living in the surface waters of the ocean (RICKARDS, 1975), but it is unlikely that all species lived in this zone. Models of movement by buoyancy control through gas buildup require extrathecal soft tissue (BULMAN, 1964; RICKARDS, 1975; FINNEY, 1979), which is incompatible with the pterobranch zooid model (CROWTHER & RICKARDS, 1977). Automobility of the tubarium by ciliary propulsion was suggested by KIRK (1969, 1972a, 1972b) and BATES and KIRK (1986). BATES (1987b) also suggested that the negative buoyancy of the tubarium could have been at least partly offset by low density fats within the fibrous fusellar tissue.

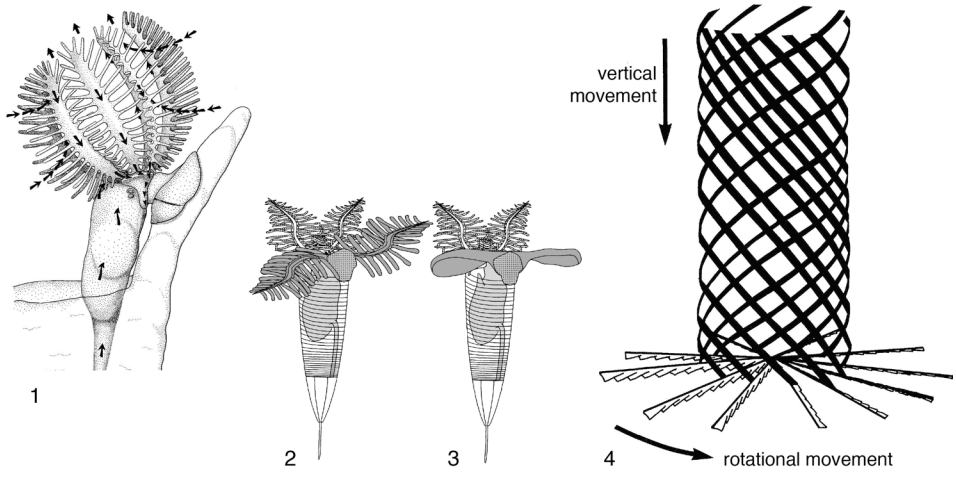


FIG. 66. Feeding and locomotion of graptolites. *1, Cephalodiscus* sp., *arrows* indicate movement of food particles along the arms of a cephalodiscid zooid (Lester, 1985, fig. 3); *2–3,* zooidal reconstruction of MELCHIN and DEMONT, showing enlarged arms (*2*) and possible wing-like muscular extensions of the cephalic shield (*3*) for locomotion (Melchin & Demont, 1995, p. 117, fig. 1); *4,* diagram showing rotational movement of multiramous colony (adapted from Rigby & Rickards, 1989, fig. 4).

MELCHIN and DEMONT (1995) suggested a new model of automobility of the colonies using putative winglike extensions of the cephalic shield for rowing (Fig. 66.2–66.3), as they considered passive buoyancy control unlikely due to the size, architecture, and phylogenetic history of the graptolites. RIGBY and RICKARDS (1989) and RIGBY (1991, 1992) modeled graptoloids in relation to rotation and feeding efficiency during passive sinking.

All considered, however, there are significant problems with all locomotory mechanisms proposed for the graptoloids (COOPER & others, 2012). The topic remains one of the major questions in graptoloid ecology.

FEEDING

The example of the living pterobranchs can be used to infer the feeding mechanisms of fossil benthic graptolites. The extant *Cephalodiscus* and *Rhabdopleura* use their ciliated arms to extract food from the water column. The cilia on the tentacles move water into the center of the basket formed by the arms of the zooid (Fig. 66.1). Food particles are separated and collected in the median canal of each arm. The food is then transported into the mouth (LESTER, 1985).

It is generally agreed that the zooids of fossil benthic graptolites fed by sampling water that passed through the colonies (as seen in extant taxa), but just how the feeding mechanism might have worked is mostly conjecture. KIRK (1969, 1990, 1991) suggested that in conical forms, afferent flows entered through the central opening, and efferent flows passed out through the mesh. This is in conflict with the observations of similarly organized organisms such as modern sponges and bryozoans. Modeling by MELCHIN and DOUCET (1996) showed that afferent flows through the sides and efferent flows through the top of the colonies were more likely. Different colonial morphologies may also be related to the paleoenvironmental conditions under which the graptolites lived (RICKARDS, BAILLIE, & JAGO, 1990; MELCHIN & DOUCET, 1996).

Modeling of planktic graptoloid colonies and water tank experiments (RIGBY & RICKARDS, 1989; RIGBY, 1991, 1992) suggested that flat, horizontal colonies as well as conical to umbrella-shaped colonies may have maintained a stable horizontal orientation in the water and were able to rotate during ascent and descent to improve water sampling and feeding efficiency (Fig. 66.4). Straight

axonophorans are sometimes found on bedding planes with their long axes aligned; this is interpreted to indicate the direction of bottom currents (Moors, 1970; Rantell & Rigby, 2002). Modern analogs may help to infer details of the feeding strategies. Some filter-feeding euphausiids in the Humboldt Current of the eastern Pacific migrate from the surface to the oxygen-minimum zone at 300–400 m deep in the daytime to harvest microplankton and avoid predators (Antezana, 2009).

The fluid-dynamic models of Rigby and Tabor (2006) suggested that water flowed toward the thecal apertures in taxa with simple thecae; however, the complex development of the thecal apertures in many taxa and the development of the external lacinia and ancora sleeve in axonophorans suggest that this model has limited applicability.

PARASITES, EPIBIONTS, AND PREDATORS

Examples of parasites in modern pterobranchs are extremely rare despite the fact that records go back more than a hundred years. However, a few parasites have been found in the following extant species. Calman (1908) described the parasitic copepod *Zanclopus cephalodisci* Calman, 1908 (Fig. 67.1–67.5) from the stomach of *Cephalodiscus gilchristi* Ridewood, 1906. Calman (1908) referred *Z. cephalodisci* to the family Ascidicolidae (now Enterognathidae; Boxshall & Halsey, 2004; Ohtsuka, Kitazawa, & Boxshall, 2010, p. 689). Calman recognized *Enterognathus comatulae* Giesbrecht, 1900, a species infesting the echinoderm *Antedon* de Fremin-ville, 1811, as possibly the closest relative of *Zanclopus* Calman, 1908. A second species of the genus *Zanclopus*, *Z. antarcticus* Gravier, 1912b, was found in the stomach of *Cephalodiscus anderssoni* Gravier, 1912a. Also, Ridewood and Fantham (1907) described the protozoan *Neurosporidium cephalidisci* Ridewood & Fantham, 1907 from the nervous system of *Cephalodiscus nigrescens* Lankester, 1905 as a parasite.

Parasitism has been recognized in well-preserved, chemically isolated material of the fossil record of various benthic graptolite groups and in the graptoloids but is limited to instances in which it resulted in a response by the zooids to the parasite. The parasites themselves have not been preserved. For example, anomalous outgrowths formed from fusellar and cortical tissue are thought to indicate response to infestations by parasites (Kozłowski, 1970a; Maletz, 1997a). The best examples of these infestations include the tubothecae described by Kozłowski (1970a) (Fig. 67.8), tubular growths from cortical material attached to the tubaria in a number of benthic graptolites (e.g., Wiman, 1901; Skevington, 1963a; Urbanek & Mierzejwski, 1982). These tubes do not indicate any internal communication with the tubaria to which they are attached. Kozłowksi (1970a) and Conway Morris (1981) concluded that tubothecae resulted from graptozooids secreting cortical tissue over the parasites (perhaps annelids) living on the graptolite colonies.

In describing possible parasitism in Graptoloidea, Bates and Loydell (2000) differentiated between open-ended tubes and closed blisters of various shapes (Fig. 68). The structures include mostly round or oval blisterlike protuberances (Jackson, 1971; Bates, 1994) on the obverse and reverse side of the colonies (Fig. 68.3–68.4, Fig. 68.7). The most spectacular features are eight tubular outgrowths on a proximal end of *Geniculograptus typicalis* (Bates & Loydell, 2000) that might have considerably changed the hydrodynamic behavior of the colony, but were apparently non-lethal (Fig. 68.1–68.2). Abnormalities in Silurian monograptids were extremely rare. Urbanek and Teller (1974) and Teller (1998, 1999) described a few unusual features in monograptids, but none of these were similar to the blisters and tubes found in Ordovician taxa.

Although called parasites, these outgrowths could alternatively be interpreted as indications of epibionts, organisms growing on

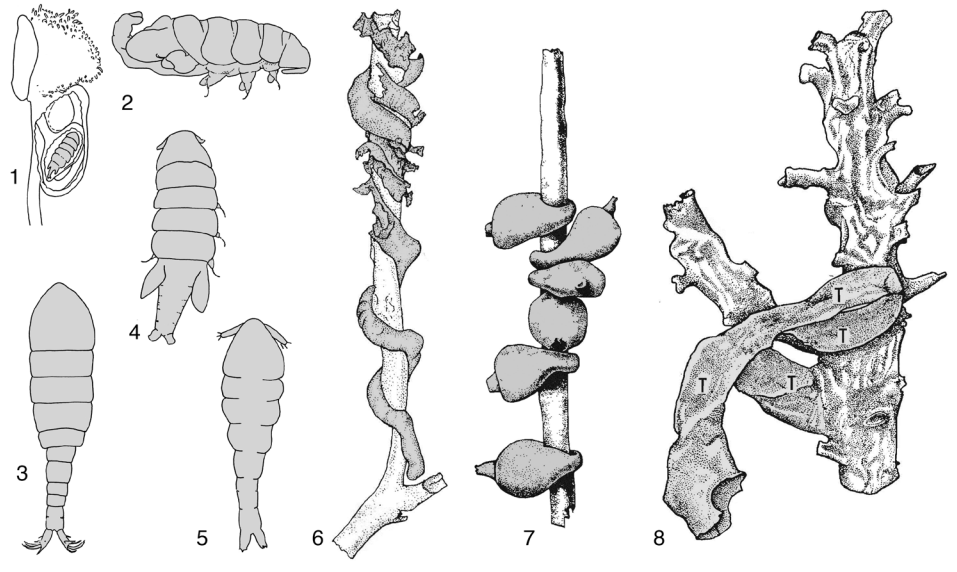


FIG. 67. Pterobranch epibionts and parasites: *1–5,* extant, *6–8,* Middle Ordovician, upper Darriwilian. *1, Cephalodiscus gilchristi* RIDEWOOD, 1906, showing the position of the parasite *Zanclopus gilchristi* CALMAN, 1908 in its stomach; *2–5, Z. gilchristi, 2, 4,* female in two views; *3,* male in 5th copepodid stage, appendages omitted; *5,* earliest known larval stage (*1–5* adapted from Calman, 1908, pl. 18–19); *6, Helicotubulus dextrogyra* (KOZŁOWSKI, 1967), holotype on fragment of *Mastigograptus* sp. (adapted from Kozłowski, 1967, fig. 7); *7, Clistrocystis graptolithophilius* KOZŁOWSKI, 1959b (adapted from Kozłowski, 1965, fig. 1); *8,* tubotheca (*T*) on *Acanthograptus* sp. (adapted from Kozłowski, 1970a, fig. 5).

the graptolite tubaria without harming the colony. Other possible epibionts include *Clistrocystis graptolithophilius* KOZŁOWSKI, 1959b, an organic-walled microfossil, invariably attached to the stipes of *Mastigograptus* RUEDEMANN, 1908 (Fig. 67.7). KOZŁOWSKI (1965) interpreted this fossil as possible eggs of cephalopods. Another enigmatic fossil is *Helicotubulus dextrogyra* (KOZŁOWSKI, 1967) (see MIERZEJEWSKI & KULICKI, 2003b), originally referred to the Phoronida (Fig. 67.6). MARKHAM (1971, fig. 5) illustrated a number of possible folliculinid ciliates on an empty tube of the extant *Cephalodiscus* (*Orthoecus*) *densus* ANDERSON, 1907. Small phosphatic brachiopods are known as epibionts (WANG & others, 2012) on the possible pterobranch *Malongitubus quangshanensis* HU, 2005, an erect, multibranched fossil identified as an alga in the past.

Graptoloids may represent primary consumers (UNDERWOOD, 1998) and have been placed close to the base of the Paleozoic food web. It is possible that they also formed an important food source for other marine organisms, but there is very little evidence of predation on graptolites (UNDERWOOD, 1993; LOYDELL, ZALASIEWICZ & CAVE, 1998). However, UNDERWOOD (1993)described possible fecal packages of Silurian monograptids and interpreted accumulations of biserial colonies as fecal accumulations, which could support predation. On the other hand, BATES and KIRK (1986) have suggested that the fusellum of the graptolites might have been too tough for ingestion and that the soft tissues might have been poisonous.

LIFE HISTORY STRATEGIES

Graptolite colonies grew by the distal addition of new thecae. Controls on colony size in benthic graptolites are not clear, because most taxa are found only as fragmented remains and their original growth pattern and size cannot be reliably determined. Diverse benthic graptolite faunas indicate that colonies were able to reach dimensions of more than 50 cm in diameter

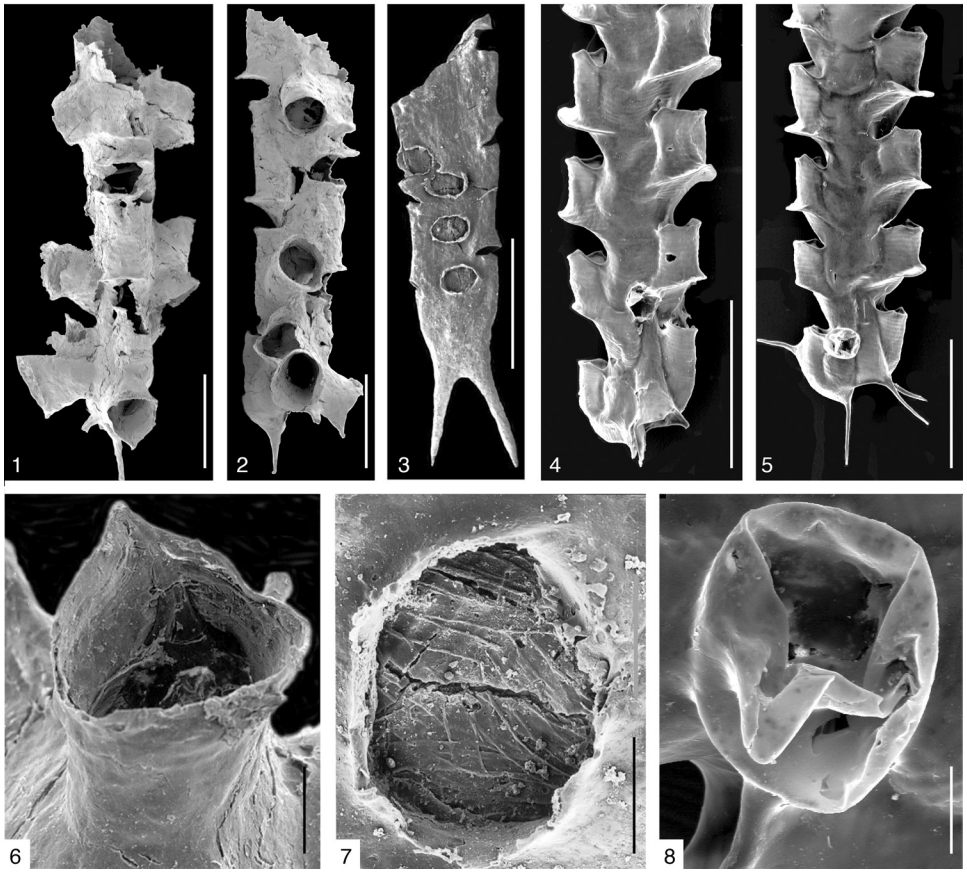


FIG. 68. Possible parasitic developments on Graptoloidea. *1–2, Geniculograptus typicalis* (HALL, 1865) specimen in different views (new; photos provided by David Loydell); *3, Diplacanthograptus spiniferus* (RUEDEMANN, 1912) (Bates, 1994, pl. 1); *4–5, Anticostia lata* (ELLES & WOOD, 1906), from type block of *Climacograptus inuiti* COX, 1933, SMF 75822, 75817 (new); *6,* detail of *1; 7,* detail of *3; 8,* detail of *5*; scale bars, 1 mm in *1–5,* 0.1 mm in *6–8*.

containing thousands of zooids (BOUČEK, 1957; BULL, 1987). Modern *Rhabdopleura* colonies, on the other hand, are relatively small but still may contain dozens of zooids (see LANKESTER, 1884, pl. 37). Growth and final size appears to be restricted mainly by their ecology.

In multiramous planktic graptolites, colonies grew by the distal addition of thecae simultaneously on all stipes in the colony. Their maximum size appears to be unconstrained by their colony design, with some colonies reaching as large as a meter in diameter (see PRITCHARD, 1892). Some Silurian monograptids were also of considerable length (LOYDELL & LOVERIDGE, 2001). In a few axonophoran species, maximum length appears to have been constrained by the development of an appendix (as in the Retiolitidae) or by the presence of distal vanes (nematularia) at the extremity of the nema, which usually were not overgrown by the developing stipes (e.g., *Archiclimacograptus decoratus* [HARRIS & THOMAS, 1935]). In many graptolites, there were no obvious constraints on stipe development, yet colonies never exceeded a few centimeters in length or, in extreme cases (e.g., *Brevigraptus* MITCHELL, 1988; *Corynoides* NICHOLSON, 1867a; *Peiragraptus* STRACHAN, 1954), a few thecae in total.

RIGBY and DILLY (1993) estimated the life span of individual graptolite colonies.

They used the rate of fusellar ring accretion in *Rhabdopleura* to calculate that a graptoloid zooid takes an average of 6.6 days to secrete a theca. According to these estimations, the life span of a 3 cm long biserial graptoloid was 1.6–2.4 years, and a 75 cm long *Monograptus flemmingii* (Salter, 1852) approximately 13 years. Damage and repair and possible re-colonization of tubes by successive generations of zooids (Rigby, 1994b) may even increase this estimate.

Population structure and dynamics of graptoloids in bedding-plane assemblages have been investigated by Rigby (1993), and in chemically isolated material from limestone nodules by Underwood (1998). The survivorship analyses by Rigby indicated increasing mortality rates with age, but analyses by Underwood indicated constant to decreasing mortality rates with age. Clearly, further such studies are needed before reliable conclusions can be drawn about their ecological implications.

Synrhabdosomes are monospecific assemblages of radially arrayed tubaria attached by the distal extremities of their nemata and occur in various groups of graptolites, from the Dichograptina to biserial and uniserial axonophorans. They have been interpreted as: 1) reproductive adaptations (e.g., Ruedemann, 1895; Kozłowski, 1949; Zalasiewicz, 1984; Underwood, 1993; Ge & Chen, 1995); 2) as chance entanglements (Rigby, 1993; Goldman & Mitchell, 1994); and 3) as adaptations for a variety of other purposes (Kirk, 1969; Gutiérrez-Marco & Lenz, 1998). Synrhabdosomes are rare and known only in a few species; they were clearly not obligate associations that formed part of the life history and ecology of most graptoloids (Maletz, 2015).

SPECIES ASSOCIATIONS AND LOCAL POPULATIONS

Within most graptolitic black shale formations, occasional bedding planes are crowded with colonies, sometimes dominantly of one species. Sometimes all tubaria are at about the same stage of astogenetic growth, suggesting mass mortality (Fig. 69). On the other hand, recurring species associations are common. On some layers, juveniles are associated with mature specimens of the same species, whereas on others either only juveniles or only mature specimens are present (Moors, 1968; Pannell, Clarkson, & Zalasiewicz, 2006). Recurring species associations and monospecific assemblages suggest some segregation of species within water masses.

Multiple species on single bedding planes are common. Highly diverse bedding plane assemblages are less common but not rare in black shale settings (Fig. 70). Although time averaging probably enhanced this diversity, a range of species is likely to have lived in the overlying waters. A diverse Middle Ordovician fauna preserved within a volcanic ash fall was interpreted by Mitchell, Brussa, and Astini (1998) as an instantaneous "catastrophic kill" of the entire suite of depth-stratified populations that lived in the overlying water column. Current evidence, therefore, suggests that many graptolite species lived in swarms, spatially differentiated from neighboring swarms (Cooper & others, 2012). These same species and others, however, are also found in low abundance at widely scattered localities, so swarming was not obligatory. However, quantitative evidence is sparse, and the effects of current sorting and transport need to be considered, particularly in turbidites (Moors, 1970).

PATTERNS OF FACIES OCCURRENCE

Graptolite tubaria are made of an organic scleroproteic material that can be destroyed under oxic conditions. Thus, they are best preserved in organic-rich sediments in the typical graptolitic black shales (see Ruedemann, 1911), where the decay of organic material is hindered by the anoxic conditions under which the sediments were formed.

Graptolites occur in a wide range of marine sediments, from shales of various colors to silt- and sandstones, carbonates,

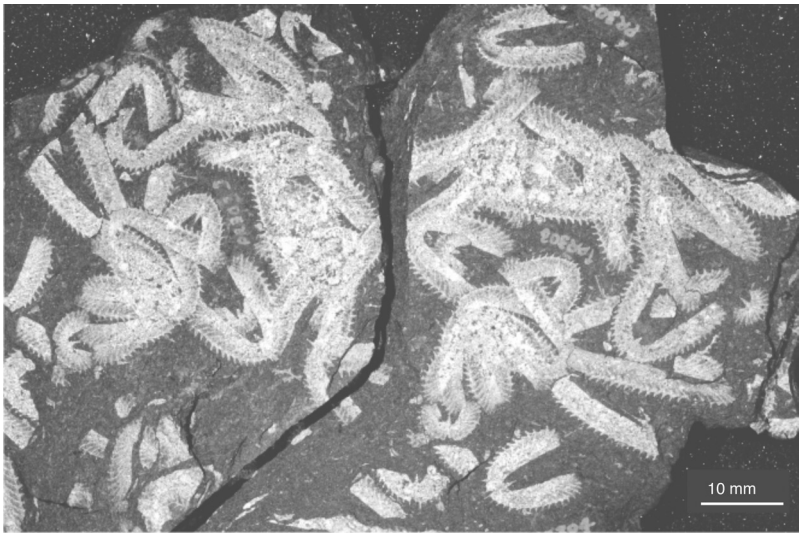


Fig. 69. A monospecific death assemblage of *Isograptus victoriae maximus* (counterparts) from the Dapingian (Castlemainian), Middle Ordovician, Aorangi Mine, New Zealand (Cooper & others, 2012, fig. 7). Color version available in *Treatise Online* 86.



Fig. 70. A diverse bedding plane assemblage from the Dapingian (Yapeenian), Middle Ordovician, Aorangi Mine, New Zealand (Cooper & others, 2012, fig. 9). Color version available in *Treatise Online* 86.

and cherts (Fig. 71). They are most common, however, in fine-grained clastics in black or dark shales, where the flattened remains are present on numerous bedding surfaces. This sedimentary facies is characteristic of the outer shelf to deep-water regions or basinal regions of the oceans, but graptolites can be found in most sediments representing inner cratonic to deep, marine-basin settings. They are associated with various fossil groups, but in shale sequences they are commonly the only fossil group present. Rarely, groups such

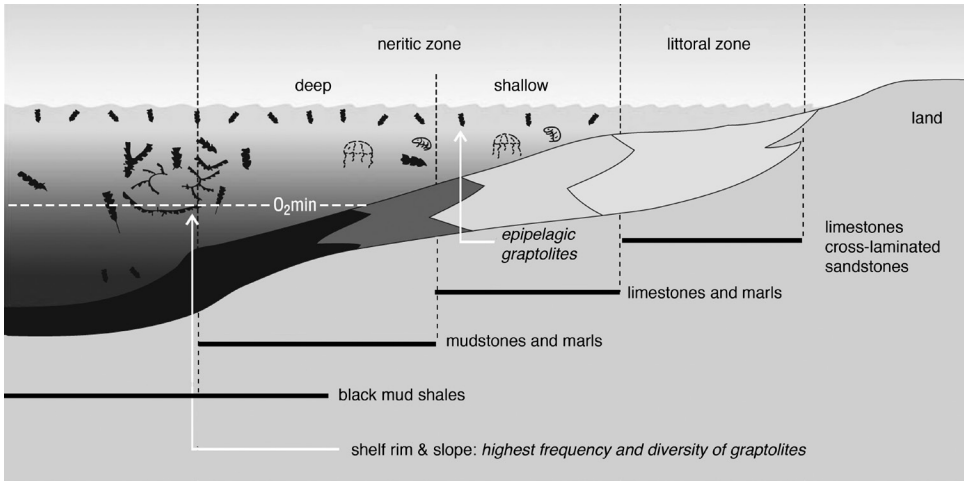


FIG. 71. Schematic distribution of the lithofacies and graptolite biofacies (adapted from Podhalańska, 2013, fig. 3).

as conodonts, scolecodonts, and phosphatic brachiopods are also present on the same bedding planes. However, organic-walled microfossils (acritarchs, chitinozoans) may be common in these sediments.

In turbidite successions, graptolites are mainly preserved in the fine-grained E horizon of the Bouma sequence or in intercalated, pelagic black shales (HILLS & THOMAS, 1953; MOORS, 1969, 1970; COOPER, 1979). More rarely, they are preserved in the A or C horizon as transported fragments (FINNEY & BERRY, 1997; COOPER & others, 2012). Alignment of tubaria on the bedding plane is common and indicates bottom currents and possible transportation (e.g., RUEDEMANN, 1897; MOORS, 1968).

GRAPTOLOID BIOFACIES AND BIOTOPES

The abundance and diversity of graptoloids in sedimentary rocks bordering the Ordovician continents (FORTEY & COCKS, 1986; CHEN, ZHANG, & MITCHELL, 2001; FINNEY & BERRY, 2003) suggest that a favorable life zone existed in the region of the outer shelf and slope. FINNEY and BERRY (1997) interpreted the favorable habitat to be associated with upwelling zones providing nutrients and enhancing bioproductivity.

Although graptoloids are preserved in sedimentary rocks representing depositional environments ranging from inner shelf and craton to the open ocean, many workers have recognized the preferred association of some species with a particular depth facies or offshore facies belt. Both lateral partitioning and depth partitioning of the graptoloid biotope have been proposed and many models have been advanced (Fig. 73). Many researchers have recognized a depth zonation of graptoloids in the water column (ROSS, 1961; BERRY, 1962a, 1974; BERRY & BOUCOT, 1972; ERDTMANN, 1976, 1984; KALJO, 1978; KIRK, 1978; MU & others, 1979, 1986; CISNE & CHANDLEE, 1982; BATES & KIRK, 1984; LENZ & CHEN, 1985; CHEN, 1990; COOPER, FORTEY, & LINDHOLM, 1991; LENZ & others, 1993; GOLDMAN, BERGSTRÖM, & MITCHELL, 1995; GOLDMAN, MITCHELL, & JOY, 1999; CHEN, ZHANG, & MITCHELL, 2001; COOPER & SADLER, 2010), and most models incorporate a depth component. Some models proposed lateral partitioning as the dominant differentiating mechanism of species groups.

Although quantitative data are sparse and the biofacies preference of most species is unknown, a consensus model employing both lateral and vertical partitioning was formed (CHEN, 1990; CHEN, MELCHIN, &

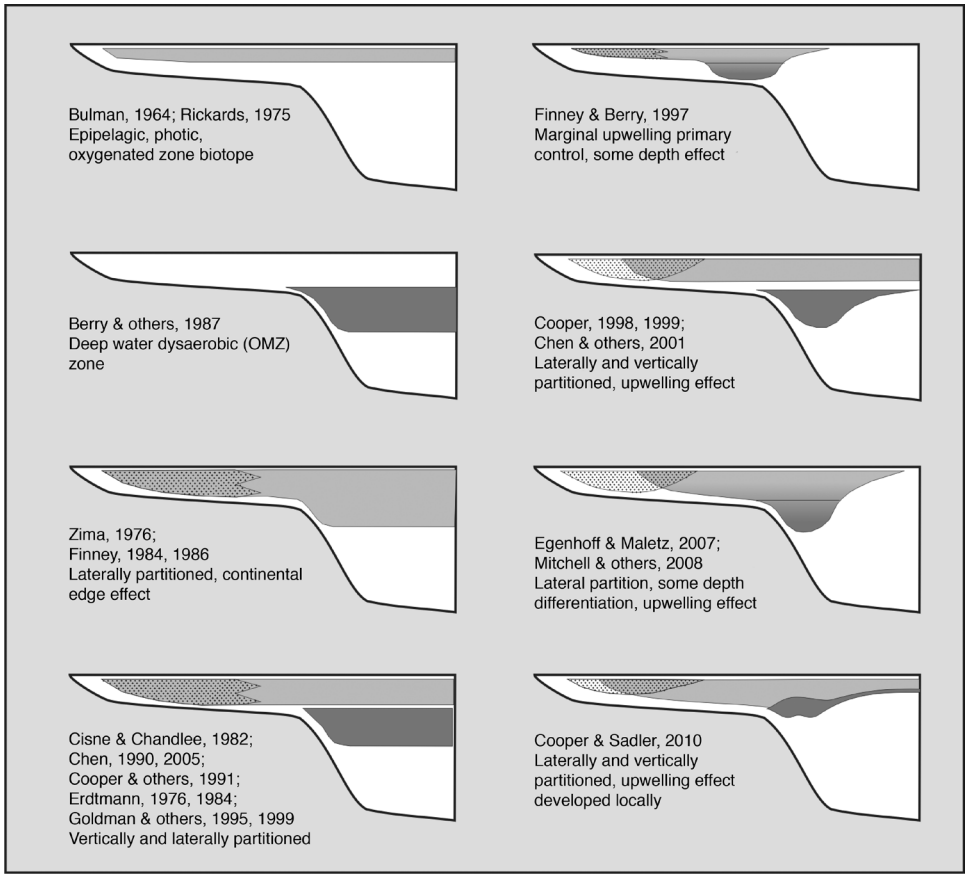


FIG. 72. Some previous models of the graptoloid habitat (adapted from Cooper & others, 2012, fig. 18).

others, 2005; COOPER, FORTEY, & LINDHOLM, 1991; COOPER & others, 2012). This model was based mainly on species of the Early to Middle Ordovician age, the time period in which most ecological analysis has been done. Three species groups were recognized: 1) taxa restricted to the deep-water facies; 2) taxa present in both the neritic and deep-water facies; and 3) taxa found only in the neritic facies. Group 1 species were inferred to have lived in a deep water biotope and group 2 species in a shallow, epipelagic biotope (Fig. 72, Fig. 73); these two groups were thus separated primarily by depth zonation, which, in modern oceans, is caused by such factors as vertical gradients in water temperature, chemistry, aeration, light intensity, and nutrient supply. The distinctness of the two groups is confirmed by their species extinction probabilities; extinction risk is significantly higher for group 1 species than for group 2 species (COOPER & SADLER, 2010; see also BOYLE & others, 2014). Group 3 species, which are restricted to inner- and mid-shelf waters (neritic biotope), were constrained by lateral partitioning of the water mass, perhaps comparable with the modern continental edge effect. Groups 1 and 2 contained many pandemic species, whereas group 3 species were largely endemic in their distribution. The model was applied to Late Ordovician graptoloid species (GOLDMAN & others, 2013) and, more loosely, to Silurian species (BERRY & BOUCOT, 1972; MU & others, 1986; LENZ & others, 1993; BOUCOT & CHEN, 2009).

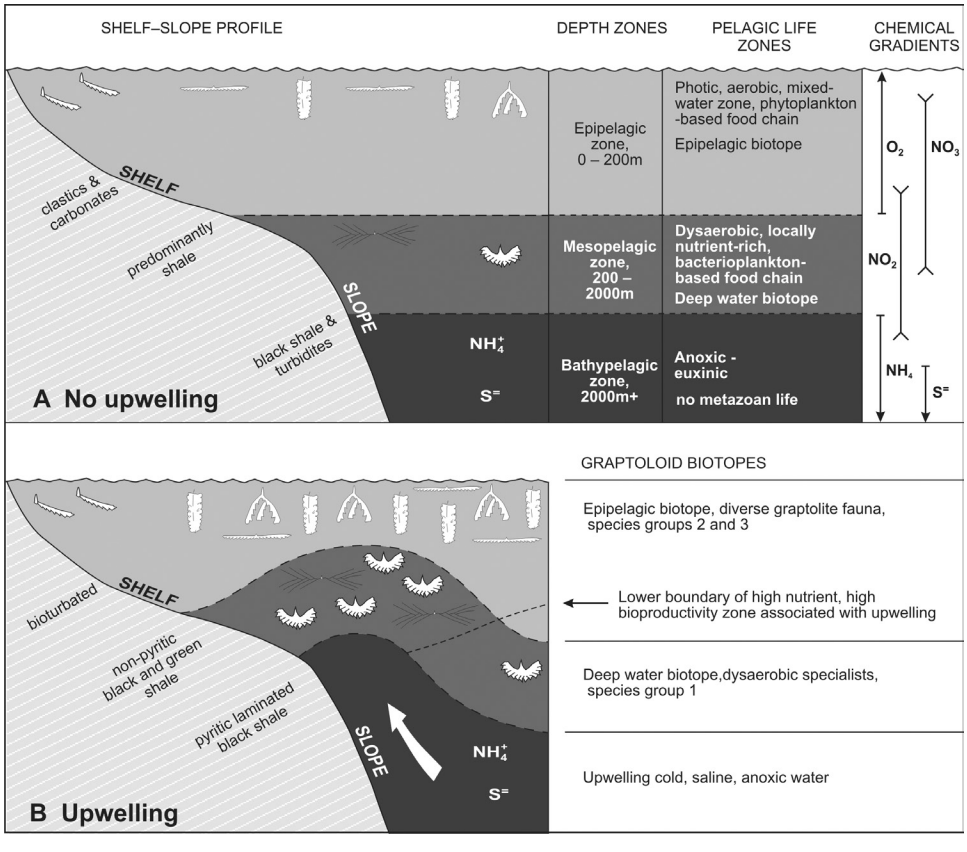


FIG. 73. *A,* Inferred graptoloid life zones in a density-stratified ocean with no upwelling. Epipelagic and deep water graptoloid biotopes are indicated, neritic (inshore) biotope not shown; *B,* in marginal upwelling zone, tongues of dense, oxygen-depleted but nutrient-rich water are brought up into the epipelagic zone (the nutrient pump) generating a nutrient-rich, high-bioproductivity environment (adapted from Cooper & others, 2012, fig. 19 and references cited therein).

In an alternative approach, lateral partitioning is assumed to be the dominant discriminating mechanism (ZIMA, 1976; FINNEY, 1984, 1986). The model proposed by EGENHOFF and MALETZ (2007) and MALETZ and others (2011) does not recognize a discrete habitat for group 2 species or the distinction between species groups 1 and 2.

In modern oceans, the epipelagic life zone extends from the water surface to a depth of ~200 m, where the light level is only at ~1% of that at the surface. Nearly 90% of all marine life exists in this zone, and it is where nearly all primary productivity takes place, mainly by the phytoplankton. This is the obvious biotope of group 2 and group 3 species and was most likely the zone in which most planktic (and benthic) graptolites thrived. In the mesopelagic zone, below 200 m depth to ~2000 m, the ocean waters are depleted of oxygen and there is no light. Bacterioplankton are the basis of the food web, and bioproductivity is generally lower than in the epipelagic zone, although locally, highly productive subzones are present (BRINTON, 1979; LONGHURST & HARRISON, 1989).

In marginal upwelling areas, nutrient-rich waters enrich the epipelagic zone and greatly increase bioproductivity. This in turn enhances the development of a high-nutrient dysaerobic zone at depths where

specialized mesopelagic-zone species thrive (Longhurst, 1967; Judkins, 1980; Longhurst & Harrison, 1989; Brasier, 1995). This deep-water biotope is thought to be the analog of the group 1 species habitat (Berry, Wilde, & Quinby-Hunt, 1987, 1989; Cooper & others, 2012) and ancient upwelling zones to be the sites of abundant and diverse graptolite assemblages (Finney & Berry, 1997).

BIOSTRATIGRAPHY

Jörg Maletz

THE FOSSIL RECORD OF THE HEMICHORDATA

It is now accepted that the Hemichordata are likely to have originated during the late Precambrian to early Cambrian (Fig. 74), given that the fossil record indicates a presence of pterobranchs as early as the Fortunian (basal Cambrian), with the possible rhabdopleurid *Sokoloviina costata* (Kirjanov, 1968) discovered in the Ukraine (Maletz, 2019a). However, early Cambrian records of Pterobranchia are rare, and it isn't until the upper Cambrian (Series 2, Stage 4) and the Miaolingian (Wuliuan) (Fig. 74) that a better fossil record became available, following the discovery of the first Enteropneusta fossils in the Burgess Shale in Canada (Caron, Conway Morris, & Cameron, 2013).

The fossil record of the Enteropneusta is limited to very few specimens and few localities in the Palaeozoic to Mesozoic. The described fossil taxa have been incorporated into the taxonomic scheme and, in part, are referred to extant groups (Cameron, 2018). The early genera *Oesia* Walcott, 1911 and *Spartobranchus* Caron, Conway Morris, & Cameron, 2013 are included in a stem group.

The Cambrian record of the Pterobranchia is of interest largely for taxonomy and evolutionary studies, but the planktic Graptolithina represent one of the most important fossil groups of the Paleozoic for biostratigraphical dating of rock sequences. Their origin close to the base of the Ordovician System (Cooper, Nowlan, & Williams, 2001; X.-F. Wang & others, 2019) can be regarded as one of the major evolutionary events in the history of life on planet Earth and marks the onset of the evolution of planktic macro-organisms. The extinction of the planktic graptoloids during the Early Devonian was a slow process. The reason for this remains unexplored but may be related to the emergence of plankton feeders in the world's oceans (Maletz, 2017a). This chapter focuses on the interval of biostratigraphical use of the Graptolithina and does not discuss the sparse younger fossil record of the Hemichordata.

GRAPTOLITE BIOSTRATIGRAPHY

As early as 1850, Hall estimated that graptolites, although at that time poorly known, were valuable for identifying certain geological periods. Thus, Hall's 1850 study might be regarded as the starting point of graptolite biostratigraphy, even though at the time few graptolite species had been described. Furthermore, a precise biostratigraphical use was not yet possible. In the same year, Barrande (1850) indicated the practical biostratigraphic use of the Silurian graptolite faunas in the Barrandean region. Nicholson (1868b) provided the first chart showing the distribution in time (biostratigraphic distribution, in modern terms) of graptolite faunas in Britain. It was, however, the impact of Lapworth's (1878) influential study on the Moffat Series that established graptolites as a prime fossil group for biostratigraphy and relative dating of rock sequences of the Paleozoic (Fortey, 1993).

Inevitably, mistakes are made in science, and it has occurred in the interpretation of graptolite biostratigraphy. One of the most glaring examples may be the record of supposed Ordovician graptolites on a small island in the South Orkney Island complex of Antarctica (Dalziel, 1979). Fossil material from the island, now called Graptolite Island, was initially identified as Ordovician graptolites by Gertrude Elles and published by Pirie (1905), leading to considerable problems for the interpretation of the geology of the region. The fossils were

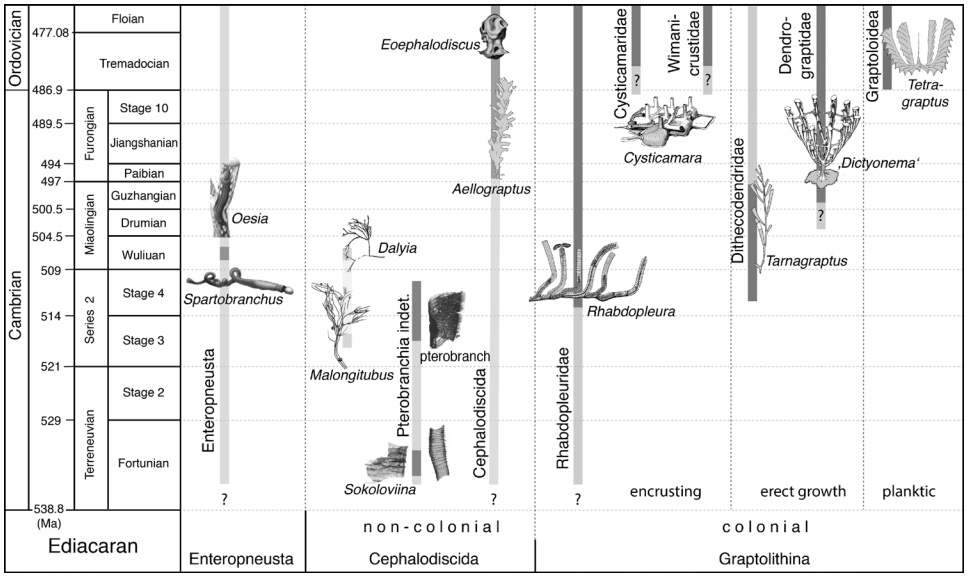


FIG. 74. The Cambrian fossil record of the Enteropneusta and Pterobranchia (Hemichordata) (adapted from Maletz, 2019a, fig. 3).

later identified as possible Carboniferous plant material (STRACHAN in ADIE, 1957, p. 22) but the misleading name of the island still exists and is present today on Google Earth. The geological map of the South Orkney Islands shows a Carboniferous to Triassic age for the Greywacke Shale Formation, but paleontological data are poor. The dating is based on Triassic radiolarians from the Weddell Islands to the northwest (FLOWERDEW, RILEY, & HASELWIMMER, 2011). This example demonstrates how important precise identification of fossil material is.

Currently used graptolite biozones are quite different from those first developed during the late nineteenth and early twentieth centuries. Scientists most commonly use the concept of the First Appearance Datum (FAD) to define the base of a fossil biozone, which in general is a local level and may not represent the worldwide first appearance of a taxon. This is especially noticable in the definitions of chronostratigraphic units based on graptolites. There are now 13 out of 16 stage boundary levels from the base of the Ordovician System to the base of the Devonian System that are defined by the level of the FAD of a particular graptolite species in a certain section (OGG, OGG, & GRADSTEIN, 2016). Absolute dates for the following charts (Fig. 75–80) are generally taken from GRADSTEIN and others, 2020, which represent the latest available information. Dates have changed considerably over the years as a result of new information. Details are available from the website of the International Commission on Stratigraphy (stratigraphy.org). The website also includes uncertainty intervals of radiometric dates.

Numerous biostratigraphic range charts have been published over the years, many of them providing local biozones, but general overviews are rare. ELLES and WOOD (1914) tabulated the biostratigraphic ranges of all graptolites known at the time from Britain into 36 graptolite zones, preceded only by the succession of LAPWORTH (1880f), which counted 20 zones. This initially local (British) ELLES and WOOD biozonation became a worldwide standard and was used unchanged for more than 60 years until RICKARDS (1976) and later ZALASIEWICZ and others (2009) revised the British standard biozonation and counted 60 biozones and

subzones leading up to the middle Ludlow. Younger graptolite zones were not recognized in Britain. Bulman (1955, fig. 5) provided a chart in *Treatise,* Part V showing the stratigraphic distribution of the main groups of graptolites and later added graptolite biozonal schemes for Britain and Australia as a guideline to the graptolite biostratigraphy in the second edition of *Treatise,* Part V (Bulman, 1970). Unified international biostratigraphies are difficult to construct due to the biogeographic differentiation of many faunas (e.g., Goldman & others, 2013), but a generalized graptolite zonal sequence for the Silurian was proposed by Jaeger (1991) and Koren' and others (1995, 1996). A standard graptolite biozonation may also be used for the Lower Devonian, as the faunas of this time interval are fairly monotonous (Jaeger, 1978b, 1988; Lenz, 2013).

A number system was introduced in Germany by Eisel (1899), based on the succession of Lapworth (1880f, table 11–12), but slightly different index species were employed (Eisel, 1903). This scheme was still used by Münch (1952) in his overview on Silurian graptolites of Germany, but Jaeger (1991) used and adjusted the succession of Elles and Wood (1914) for the German Silurian and indicated a number of intervals not covered in their scheme. Maletz (2001a) suggested abandoning the number system in Germany, following Rickards (1995a, p. 133) and advocated using only index species for the biozonation.

The graptolite biozonation presented here is largely based on the excellent compilation of Loydell (2012), including additional references in his figure captions. New information needing to be incorporated is reflected herein.

ORDOVICIAN

According to Goldman, Sadler, and Leslie (2020), the Ordovician System (Lapworth, 1879a) is approximately 43.78 Ma in duration (486.85–443.07 Ma), including three series, the Lower Ordovician (15.59 Ma), the Middle Ordovician (13.08 Ma), and the Upper Ordovician (15.11 Ma), of which the middle one is somewhat shorter. The three series include seven stages, highly uneven in length. The Darriwilian Stage (458.18–469.42 Ma) is the longest stage at approximately 11.24 Ma, and the Hirnantian (443.07–445.21 Ma) is the shortest at only about 2.14 Ma, including two graptolite zones (note, the precise radiometric ages may differ considerably based on the source used). Gradstein and others (2012, 2020) is used for all units discussed herein, but numbers may change in the future (compare with Cooper & Sadler; 2012; Ogg, Ogg, & Gradstein, 2016).

The (informal) Ordovician stage slices of Bergström and others (2009) are not correlated herein. They were introduced as defined chronostratigraphical units, based on biostratigraphical data and explained to have "potential for precise correlations in both carbonate and shale facies" (Bergström & others, 2009, p. 97). They were used to correlate the $\delta^{13}C_{org}$ curve to the chronostratigraphy. These stage slices should not be confused with the time slices in Webby and others (2004), a term created to provide a precise key to correlate biostratigraphic intervals based on various fossil groups. The individual intervals were estimated to be between 1.6 and 2.5 Ma in duration.

THE LOWER ORDOVICIAN

The Lower Ordovician includes the Tremadocian and Floian stages (Fig. 75). The base of the Ordovician System and the Tremadocian Stage is defined at the level of the FAD of the conodont *Iapetognathus fluctivagus* Nicoll & others, 1999 (Cooper, Nowlan, & Williams, 2001; Terfelt, Bagnoli, & Stouge, 2012; X.-F. Wang & others, 2019, 2021). The occurrence of *Rhabdinopora* Eichwald, 1855 is typically more easily recognized in dark shale in basal Ordovician strata (Henningsmoen, 1973; Bassett & Dean, 1982; Norford, 1982, 1988), although the FAD of *Rhabdinopora* occurs at a level slightly higher than the Global

Stratotype Section and Point (GSSP) level. The biozones in the Australasian succession are named by index species, but only their widely known and commonly used zonal notations are shown herein (Fig. 75–77). See VandenBerg and Cooper (1992) and Percival, Quinn, and Glen (2011) for details and full biozonal names.

The base of the Floian Stage is defined at the level of the FAD of *Paratetragraptus approximatus* (Nicholson, 1873) in the Diabasbrottet section, Västergötland, Sweden (Bergström, Löfgren, & Maletz, 2004; Bergström & others, 2006). This level is equivalent to the level of the FAD of the common Scandinavian graptolite *Tetragraptus phyllograptoides* Strandmark, 1902. The name *Tetragraptus phyllograptoides* Biozone is usually used to identify the interval in Scandinavia (Baltica) and South America (Egenhoff, Maletz, & Erdtmann, 2004; Toro & others, 2015).

Maletz, Egenhoff, and Alonso (2010) and Maletz and Ahlberg (2018) published the latest biozonation for the Tremadocian to early Darriwilian of Baltica, representing one of the most complete successions known (Fig. 75). Maletz, Egenhoff, and Alonso (2010), following Maletz and Egenhoff (2001), identified a local *Kiaerograptus stoermeri* Biozone beneath the *Kiaerograptus supremus* Biozone of Lindholm (1991), which is not indicated in the chart (Fig. 75), because it has been identified in only a single section. Zalasiewicz and others (2009) discussed the graptolite biostratigraphy of Britain and listed the known faunas of the Lower Ordovician. Maletz and Ahlberg (2011a, fig. 8) provided a correlation of the British succession to the Scandinavian succession, showing that the British graptolite succession is fairly incomplete, and some intervals are not documented by fossil faunas (Fig. 75). Zhang and others (2019) provided the latest overview on the Ordovician graptolite biostratigraphy of China as a combination of the North China platform and the Yangtze Region. The North China succession starts with the *Rhabdinopora proparabola* interval (Fig. 75) but is not known with certainty from other regions of China (Maletz, Wang, & Wang, 2022).

The basal Ordovician (early Tremadocian) and the Floian intervals of the North American succession are best known from western Newfoundland (Williams & Stevens, 1988; Cooper, Nowlan, & Williams, 2001), but the late Tremadocian to early Floian succession of Yukon Territory, Canada (Jackson & Lenz, 2003, 2006) is a more detailed succession of *Paradelograptus* Erdtmann, Maletz, & Gutiérrez Marco, 1987 species used to subdivide the latest Tremadocian strata. Williams and Stevens (1991) recognized only the *Aorograptus victoriae* Biozone in the late Tremadocian of western Newfoundland, which is probably correlatable with the *Kiaerograptus kiaeri* interval of Baltica (Maletz, 1999b).

Lower Ordovician successions are widely distributed in South America and have been described in some detail from Bolivia and Argentina (Maletz & Egenhoff, 2003; Egenhoff, Maletz, & Erdtmann, 2004; Toro & others, 2015). They have been correlated with the Scandinavian successions by Maletz and Ahlberg (2011a). Albanesi and Ortega (2016) discussed the Ordovician successions of Argentina and provided the latest information on the graptolite biostratigraphy (Fig. 75–77), which revealed distinct differences between the Argentinian Precordillera and the Gondwanan part of South America. In the eastern Cordillera of Argentina, a differentiation of the *Paratetragraptus akzharensis* Biozone into two subzones, *Cymatograptus protobalticus* and *Baltograptus vacillans* biozones, may even be possible (Vento & Toro, 2011; Vento, Toro, & Maletz, 2012).

The Australasian succession appears to be quite incomplete, at least in the Lower Ordovician (Fig. 75). VandenBerg and Cooper (1992) provided index species for the biostratigraphic intervals, and Percival, Quinn, and Glen (2011) updated the succession in New South Wales. Maletz and Ahlberg (2011a) discussed the correlation of the Australasian

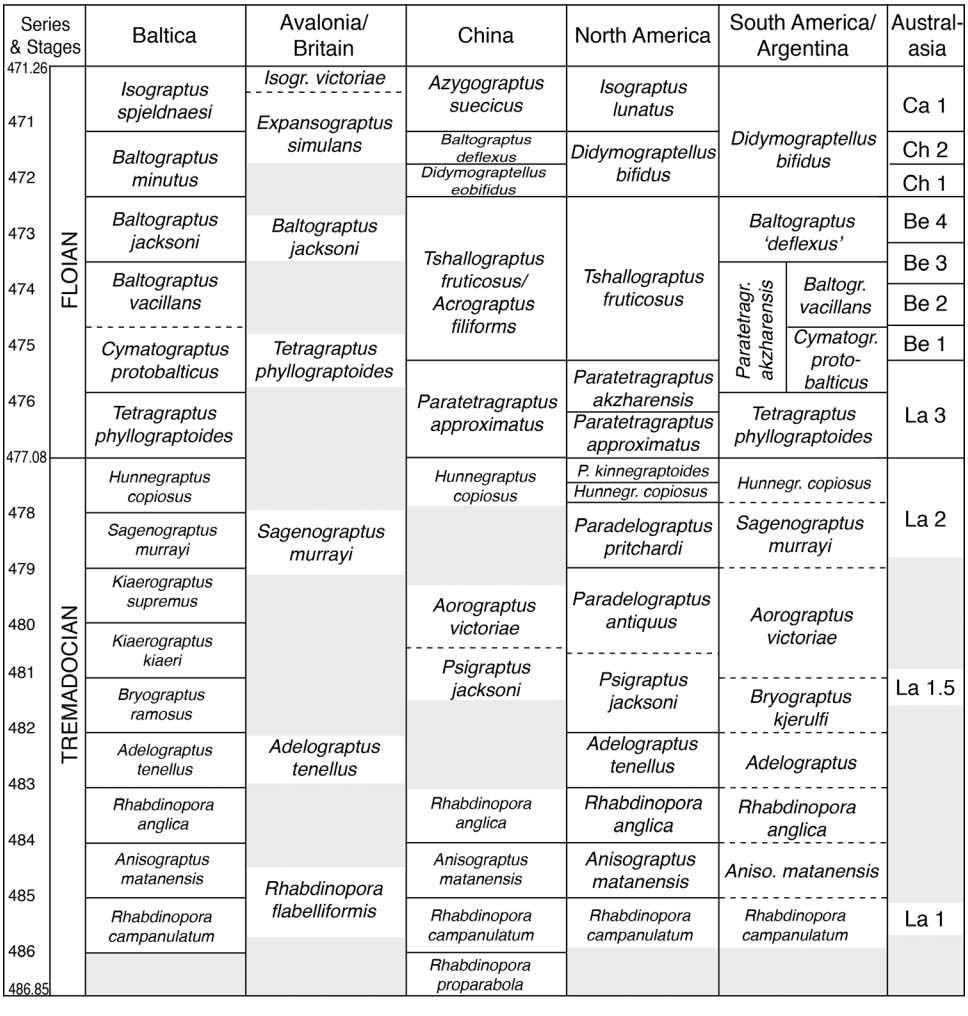


FIG. 75. Correlation of Lower Ordovician graptolite biozones. Shaded intervals indicate possible gaps (not recognized faunal intervals) in the successions.

succession and noted this incompleteness of the Tremadocian, in which only a few graptolitic horizons were recognized, leading to a number of biostratigraphic gaps (Fig. 75). VANDENBERG (2017) revised the early Floian succession, but new data on the Middle and Upper Ordovician are not available.

THE MIDDLE ORDOVICIAN

The Middle Ordovician includes the Dapingian and Darriwilian stages (Fig. 76). The base of the Dapingian is set at the stratigraphic level of the FAD of the conodont *Baltoniodus triangularis* (LINDSTRÖM, 1955) in the Huanghuachang section of China (WANG & others, 2009). This level is within the local *Azygograptus suecicus* graptolite Biozone, but the graptolite record is poor in the type section. WANG and others (2013) described the graptolite fauna of the GSSP section and provided a detailed international correlation of the graptolite faunas. The base of the Dapingian is approximately correlatable with the base of the *Isograptus victoriae* Biozone in other regions (MALETZ, 2011a). The Dapingian is characterized by

a succession of isograptid species (*Isograptus* Moberg, 1892, *Oncograptus* T. S. Hall, 1914, *Cardiograptus* Harris & Keble in Harris, 1916) as important index taxa (Cooper, 1973; VandenBerg & Cooper, 1992; Maletz, 2011a). Recently, Herrera-Sánchez, Toro, & LoValvo (2019) and Toro and others (2020) discussed the correlation of the Floian and Dapingian succession of Argentina and correlated the regional *Azygograptus lapworthi* Biozone with the early Dapingian (Fig. 76), followed by the *Isograptus victoriae* Biozone of the Central Andean Basin of Argentina and Bolivia.

The base of the Darriwilian is defined at the level of the FAD of *Levisograptus austrodentatus* (Harris & Keble, 1932) in the Huangnitang section, Zhejiang Province, China, and two subzones are differentiated (Mitchell & others, 1997). Maletz and Ahlberg (2020) and Maletz, Ahlberg, and Lundberg (2020) discussed the international correlation of the Darriwilian in some detail. The authors also included the complex succession of Bohemo-Iberia (Gutiérrez-Marco & others, 2017), in which the chronostratigraphical differentiation includes the regional Arenigian, Oretanian, and Dobrotivian Stages (not shown in Fig. 76). In the past, the correlation of the Darriwilian had been difficult due to the presence of latitudinally restricted taxa, especially the pendent didymograptids (see Goldman & other, 2013), but Maletz (1997a) and Maletz and others (2011) used pandemic faunal elements to introduce a biostratigraphical succession of the late Darriwilian (the Llanvirn of the British regional chronostratigraphy) as an international standard. Maletz (1997b) revised the Darriwilian succession of Quebec, Canada, and differentiated the *Levisograptus austrodentatus* and *Levisograptus dentatus* biozones into two subzones each (Fig. 76). Maletz, Ahlberg, and Lundberg (2020) discussed the Darriwilian interval of South America, showing a fairly complete succession from the *Levisograptus austrodentatus* Biozone to the *Pterograptus elegans* Biozone. This succession was pieced together from numerous localities. The *Pseudamplexograptus distichus* Biozone from the Puna region of Argentina (Brussa, Toro, & Vaccari, 2008) was not used in their compilation. Kaufmann (2019) described the Darriwilian to basal Katian succession of the Sierra de Villicum in the Argentinian Precordillera.

THE UPPER ORDOVICIAN

The Upper Ordovician is differentiated into three stages, the Sandbian, Katian, and Hirnatian (Fig. 77), each stage being defined at the level of the FAD of a graptolite species.

The base of the Sandbian Stage is taken at the level of the FAD of the distinctive *Nemagraptus gracilis* (Hall, 1847) in the Fågelsång section, Scania, Sweden (Bergström & others, 2000), a species that is known to have a worldwide distribution (Brussa & others, 2007). The precise level of the FAD of this species in southern Scandinavia has recently been questioned (Maletz & Ahlberg, 2020). Chitinozoan records may also indicate problems with the GSSP section at Fågelsång (Vandenbroucke, 2004; Hennissen & others, 2010). A detailed correlation of the Sandbian graptolite succession, including the *Nemagraptus gracilis* Biozone and the overlying *Climacograptus bicornis* Biozone, is difficult to make (Williams & others, 2004).

The base of the Katian is defined at the level of the FAD of *Diplacanthograptus caudatus* (Lapworth, 1876a) in the Black Knob Ridge section, Oklahoma, USA (Goldman & others, 2007) and is followed by a rapid succession of first appearances of other graptolite species useful for a wider correlation of the level. Katian graptolite faunas are widely distributed, but the correlation is invariably difficult due to the presence of endemic faunal elements. A separate biozonation was established in the Appalachian Basin of eastern North America (Ruedemann, 1912, 1925a; Riva, 1974b; Goldman, Mitchell, & Joy, 1999; Achab & others, 2011) and is shown here (Fig. 77). It includes a number of endemic faunal

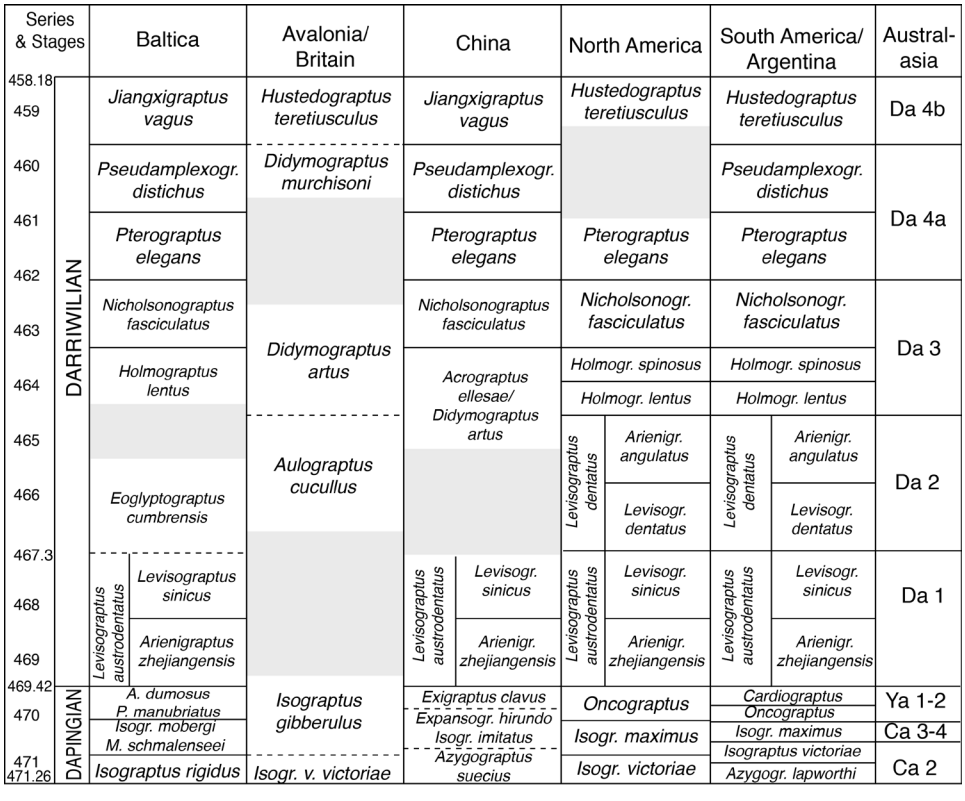


FIG. 76. Correlation of Middle Ordovician graptolite biozones. Shaded intervals indicate possible gaps.

elements of the genera *Geniculograptus* MITCHELL, 1987 and *Paraorthograptus* MU & others, 1974 that occur only in this basin (GOLDMAN & others, 2013). They represent the best example of a restriction of Upper Ordovician graptolite faunas to a certain biogeographic area.

The Katian includes a *Geniculograptus pygmaeus* Biozone in China (CHEN & others, 1995; ZHANG & others, 2019), but the taxon is not discussed or illustrated in MU and others (2002). Thus, because *Geniculograptus* is considered to be an endemic taxon of eastern North America, its presence in China may be questioned (GOLDMAN & others, 2013). *Alulagraptus uncinatus* (KEBLE & HARRIS, 1934) is used in Australia to determine the Australasian Bolindian 1 (Bo 1), the *Alulagraptus uncinatus* Biozone, in the middle Katian. The species was recently found in the *Anticostia macgregorae* beds in East Qilianshan, northwestern China (CHEN & others, 2019), a region in which a highly local biostratigraphy was described for the Katian interval (not shown in Fig. 77). It is also common in the Bolindian 1 of Idaho, USA (CARTER, 1972; MITCHELL & others, 2003). A *Diceratograptus mirus* Subzone of the *Paraorthograptus pacificus* Biozone may be differentiated locally on the Yangtze Platform of China and in Nevada, USA (CHEN & others, 2006a; ŠTORCH & others, 2011).

The base of the Hirnantian is defined in the Wangjiawan North section, near Wangjiawan Village, Hubei Province, China, at the level of the FAD of *Metabolograptus extraordinarius* (SOBOLEVSKAYA, 1974) (CHEN, FAN, & others, 2005, Chen & others, 2006a). The whole Hirnantian is less than 80 cm thick in the type section. It includes the *Metabolograptus extraordinarius* Biozone, overlain by the *Metabolograptus persculptus*

Series & Stages		Baltica	Avalonia/ Britain	China	North America		South America Argentina	Australasia
443.07								
444	HIRNANT.	*Metabolograptus persculptus*	*Metabolograptus persculptus*	*Metabolograptus persculptus*	*Metabolograptus persculptus*		*Metabolograptus persculptus*	Bo 5
445.21		graptolite faunas unknown	*Metabolograptus extraordinarius*	*Metabolograptus extraordinarius*	*Metabolograptus extraordinarius*		*Metabolograptus extraordinarius*	Bo 4
446	KATIAN		*Dicellograptus anceps*	*Diceratograptus mirus* / *Paraorthograptus pacificus*	*Paraorthograptus pacificus*		possible gap	Bo 3
447				*Dicellograptus complexus*	*Dicellogr. ornatus*	*Paraorthogr. prominens*	*Dicellograptus ornatus*	Bo 2
448		*Dicellograptus complanatus*	*Dicellograptus complanatus*	*Dicellograptus complanatus*	*Dicello-graptus complanatus*	*Dicello-graptus complanatus*	*Dicellograptus complanatus*	Bo 1
449								
450		*Pleurograptus linearis*	*Pleurograptus linearis*	*Dicellogr. elegans* / *O. quadrimucronat.*	*Styraco-graptus tubuliferus*	*Paraorthogr. mani-toulinensis*	*Styracograptus tubuliferus*	Ea 4
451				*Geniculograptus pygmaeus ?*		*Geniculogr. pygmaeus*		Ea 3
452		*Dicranograptus clingani*	*Dicranogr. clingani* / *Dicellogr. morrisi*	*Diplacanthogr. spiniferus*	*Diplacanthogr. spiniferus*	*Diplacanthogr. spiniferus*	*Diplacantho-graptus caudatus*	Ea 2
452.75			*Diplacanthogr. caudatus*	*Diplacanthograptus caudatus*	*Diplacanthogr. caudatus*	*O. ruedemanni* / *C. americanus*		Ea 1
453	SANDBIAN	*Mesograptus foliaceus*	*Mesograptus foliaceus*	*Climacograptus bicornis*	*Climaco-graptus bicornis*	*Diplogr. foliaceus*	*Climacograptus bicornis*	Gi 2
456		*Nemagraptus gracilis*	*Nemagraptus gracilis*	*Nemagraptus gracilis*	*Nemagraptus gracilis*		*Nemagraptus gracilis*	Gi 1
458.18								

FIG. 77. Correlation of Upper Ordovician graptolite biozones. Local biozonation of Appalachian Basin (*gray*).

Biozone. A thin limestone with the Hirnantian brachiopod fauna (the Kuanyinchiao bed) separates the graptolite biozones. CHEN and others (2006b) discussed the worldwide correlation of the Hirnantian Stage in some detail.

The British Upper Ordovician succession of ZALASIEWICZ and others (2009) combined elements of the biozonations used in Baltica and Scotland. A detailed biostratigraphic zonation for the Upper Ordovician of South America does not presently exist because few faunas have been described from this interval. ALBANESI and ORTEGA (2016) indicated a possible gap between the *Dicellograptus ornatus* Biozone (Katian) and the *Metabolograptus extraordinarius* Biozone (Hirnantian).

SILURIAN

After the introduction of the Silurian System by MURCHISON (1839), numerous changes were made before the modern concept emerged and series and stages were established. DAVIES and others (2011) provided the latest overview on its development in Britain, along with information to understand the individual chronostratigraphic intervals. According to MELCHIN, SADLER, and CRAMER (2020), the Silurian System is approximately 24.07 Ma long (443.07–419.0 Ma) and is quite unevenly differentiated into four series, the Llandovery (10.14 Ma), Wenlock (6.19 Ma), Ludlow (4.01 Ma), and Pridoli (3.73 Ma). Interestingly, the GSSPs were initially

defined biostratigraphically with reference to standard graptolite zones, although the index taxa for these zones are not present in some of the GSSP localities (Melchin, Sadler, & Cramer, 2012, p. 526). Some of the stages are currently under revision and details may change accordingly (see Melchin, Sadler, & Cramer, 2020). The main information on the Silurian graptolite biostratigraphy (Fig. 78–80) is based on Loydell (2012) with revisions as indicated herein.

THE LLANDOVERY SERIES

The Llandovery Series (Fig. 78) is differentiated into three stages: the Rhuddanian, Aeronian, and Telychian (Bassett, 1985; Holland, 1985; Melchin, Cooper, & Sadler, 2004). The base of the Rhuddanian is defined at Dob's Linn, Scotland, UK, at 1.6 m above the base of the Birkhill Shale at the level of the FAD of *Akidograptus ascensus* (Cocks, 1985). Originally, the base of the Rhuddanian was defined at the level of the FAD of *Parakidograptus acuminatus* (Nicholson, 1867a) in the same section, but due to a revison of the graptolite fauna, the definition was revised (Melchin & Williams, 2000; Rong & others, 2008).

The base of the Aeronian has been defined at a level "just below the level of occurrence of *Monograptus austerus sequens,* which indicates the *Demirastrites triangulatus* Zone" (Melchin, Sadler, & Cramer, 2012, p. 526). Štorch (2015) and Štorch and Melchin (2019) discussed the graptolites from the Rhuddanian-Aeronian boundary interval of the Czech Republic. The authors redescribed the zonal index for the base of the Aeronian, *Demirastrites triangulatus* (Harkness, 1851), and the anagenetic changes in the *Demirastrites triangulatus* lineage. The GSSP level has recently been re-investigated at Rheidol Gorge, Wales, UK, since the original location was insufficient for further correlations (see Melchin & others, 2018). The gap in the late Aeronian of the Yangtze Platform of China indicated by Loydell (2012) can be closed, at least in part, by the record of *Stimulograptus sedgwickii* (Portlock, 1843) (Maletz & others, 2021). Maletz, Wang, and Wang (2021) recognized a considerably extended *Lituigraptus convolutus* Biozone in the Yichang region, Hubei Province, China, and subdivided it into the *Metaclimacograptus sculptus* and *Paramonoclimacis sidjachenkoi* subzones based on the common occurrence of the index species.

The base of the Telychian is defined between the LAD of the brachiopod *Eocoelia curtisi* Ziegler, 1966 and the FAD of *Eocoelia intermedia* (Hall, 1860), a level correlated to the base of the *Spirograptus turriculatus* Biozone by Holland (1985). According to a revision of the genus *Spirograptus* Gürich, 1908, this level now equals the base of the *Spirograptus guerichi* Biozone (Loydell, Štorch, & Melchin, 1993; Melchin, Sadler, & Cramer, 2012). The detailed biostratigraphy of the *Spirograptus guerichi* and *Spirograptus turriculatus* biozones (seven subzones) in Wales, UK (Loydell, 1992) has not been used outside this region and is not discussed herein. Melchin, Lenz, and Kozłowska (2017) revised the Llandovery succession of Arctic Canada and subdivided the *Campograptus curtus* Biozone into two subzones, a lower *Demirastrites triangulatus/Demirastrites pectinatus* Subzone and a *Rastrites orbitus* Subzone.

THE WENLOCK SERIES

The base of the Wenlock Series and the Sheinwoodian Stage (Fig. 79) is defined in the Hughley Brook section, Shropshire, UK, at the base of bed G of the Buildwas Formation (Bassett & others, 1975; Holland, 1980; Martinsson, Bassett, & Holland, 1981). This level was supposed to correlate with the base of the *Cyrtograptus centrifugus* Biozone, but no graptolites were found in the section. The inference was, in fact, based on other localities. Mullins and Aldridge (2004) indicated that the GSSP level correlates with a level in the upper *Cyrtograptus centrifugus* Biozone or the lower *Cyrtograptus murchisoni* Biozone. Melchin, Sadler, and Cramer (2012) considered the GSSP level to be in the lower part of the *Cyrtograptus murchisoni* Biozone. The

Series & Stages		Britain Avalonia/Baltica	Peri-Gondwana	China	Laurentia Arctic Canada	Gondwana North Africa
432.93	TELYCHIAN	*Cyrtograptus murchisoni*	*Cyrtograptus murchisoni*	not recognized	*Cyrtogr. murchisoni*	not recognized
		Cyrtograptus centrifugus	*Cyrtograptus centrifugus*		*Cyrtograptus centrifugus*	
		Cyrtograptus insectus	*Cyrtograptus insectus*		*Cyrtograptus insectus*	
434		*Cyrtograptus lapworthi*	*Cyrtograptus lapworthi*	*C. sakmaricus* / *C. lapworthi*	*Cyrtograptus sakmaricus*	
		Oktavites spiralis	*Oktavites spiralis*	*Monoclimacis geinitzi* / *Oktavites spiralis*	*Oktavites spiralis*	
435		*Monoclimacis crenulata*	*Torquigraptus tullbergi*	*Torquigraptus tullbergi*	*Monoclimacis crenulata/ Monoclimacis griestoniensis*	*Metaclimacograptus flamandi + Parapetalolithus meridionalis*
		Monoclimacis griestoniensis	*Monoclimacis griestoniensis*	*'Monoclimacis griestoniensis'*		
436		*Streptograptus sartorius*	*Streptograptus crispus*			
437		*Streptograptus crispus*		*Streptograptus crispus*	*Streptograptus crispus*	
		Spirograptus turriculatus	*Spirograptus turriculatus*	*Spirograptus turriculatus*	*Spirograptus turriculatus*	*Spirograptus turriculatus + Spirograptus guerichi*
438		*Spirograptus guerichi*	*Spirograptus guerichi*	*Spirograptus guerichi*	*Spirograptus guerichi*	
438.59	AERONIAN	*Stimulograptus halli*	*Stimulograptus sedgwickii*	*Stimulograptus sedgwickii*	*Stimulograptus sedgwickii*	*Stimulograptus sedgwickii*
439		*Stimulograptus sedgwickii*				
		Lituigraptus convolutus	*Lituigraptus convolutus*	*Lituigr. convol.* / *P. sidjachenkoi* / *M. sculptus*	*Lituigraptus convolutus*	*Lituigraptus convolutus*
		Pribylograptus leptotheca	*Pribylograptus leptotheca*	*Pribylograptus leptotheca*	*Campograptus curtus* / *Rastrites orbitus*	*Pribylograptus leptotheca*
440		*Neodiplograptus magnus*	*Demirastrites simulans*	*Coronograptus gregarius*		*Coronograptus gregarius/ Paraclimacograptus lybicus*
		Demirastrites triangulatus	*Demir. pectinatus* / *D. triangulatus*		*D. pectinatus* / *D. triangulatus*	
440.49	RHUDDANIAN	*Coronograptus cyphus*	*Coronograptus cyphus*	*Coronograptus cyphus*	*Coronograptus cyphus*	*Neodiplograptus fezzanensis*
		Lagarograptus acinaces	*Cystograptus vesiculosus*	*Cystograptus vesiculosus*	*Lagarograptus acinaces*	*Neodiplograptus africanus*
442		*Atavograptus atavus*			*Atavograptus atavus*	
		P. acuminatus / *A. ascensus*	*P. acuminatus*	*P. acuminatus*	*P. acuminatus*	*Neodiplograptus imperfectus* / *Neodiplograptus incommodus* / *Parclimacograptus kiliani* / *Normalograptus tilokensis*
443.07			*A. ascensus*	*A. ascensus*	*A. ascensus*	

Fig. 78. Correlation of Llandovery (Rhuddanian to Telychian) graptolite biozones.

Sheinwoodian is largely zoned by species of the genus *Cyrtograptus* Carruthers in Murchison, 1867a, which are the most conspicuous faunal elements. Loydell and Large (2019) revised the British biozonation of the Sheinwoodian slightly and eliminated the *Cyrtograptus perneri*/*Cyrtograptus ramosus* Biozone (see Loydell, 2012, fig. 5) in the uppermost Sheinwoodian. Lenz and others (2012) revised the succession of Arctic Canada. Zalasiewicz and others (2009) listed *Cyrtograptus perneri* Bouček, 1933 from the British *Cyrtograptus lundgreni* Biozone of basal Homerian age and questionably from the *Cyrtograptus rigidus* Biozone of the latest Sheinwoodian age.

The base of the Homerian is defined at the level of the FAD of *Cyrtograptus lundgreni*

Tullberg, 1883 at Sheinton Brook, Homer, UK (Holland, 1980; Martinsson, Bassett, & Holland, 1981). The Homerian time interval includes one of the largest extinction events in graptoloid history, the *Lundgreni* Extinction Event (Koren', 1987; Jaeger, 1991), during which most graptoloid taxa disappeared at the top of the *Cyrtograptus lundgreni* Biozone (e.g., Jaeger, 1991). Porębska, Kozłowska-Dawidziuk, and Masiak (2004) discussed three separate events from the local biostratigraphic scheme of the Bartoszyce section of Poland (Fig. 79), partly supported by an investigation by Manda and others (2019) from the Czech Republic. Both suggested additional graptolite biozone intervals above the *Cyrtograptus lundgreni* Biozone and below the *Pristiograptus parvus* interval. However, these biozone intervals are not recognized worldwide.

Barca and Jaeger (1990) refined the Wenlock graptolite biostratigraphy supported by the detailed work of Koren' (1992, 1994) from Central Asia. The Wenlock is poorly represented in China, and very few graptolites have been described from this region. Chen (1984) provided information on the Silurian graptolite biozonation, including the Wenlock succession of southern Shaanxi, China as the most complete succession of this interval, listing a number of biozones defined by *Cyrtograptus* species. Lenz, Chen, and Ni (1996) discussed Wenlock to Pridoli graptolites from Guangxi, China and recognized a few levels with late Homerian (late Wenlock) and Gorstian to early Ludfordian (Ludlow) graptolites. They also reported a single taxon from the Pridoli, *Monograptus* cf. *rectiformis* Přibyl, 1981. Ni (1997) described a fauna of late Homerian graptolites from western Yunnan, China, indicating the presence of the *Colonograptus praedeubeli/Colonograptus deubeli* Biozone.

THE LUDLOW SERIES

The Ludlow Series and Gorstian Stage (Fig. 79) have their stratotype at Pitch Coppice, Shropshire, England, UK, at the base of the Lower Elton Formation, based on the level of the FAD of *Neodiversograptus nilssoni* (Barrande, 1850) (Holland, 1980; Holland & Bassett, 1989). However, the fossil record of the GSSP section is extremely poor and unreliable; only two poorly preserved specimens identified as *Neodiversograptus nilssoni* and *Saetograptus varians* (Wood, 1900) have been discovered (White, 1981). Štorch and others (2016) discussed the graptolite fauna of the Wenlock-Ludlow boundary interval of the Czech Republic. These authors stated that *Saetograptus varians* first appeared in the biostratigraphically higher *Lobograptus progenitor* Biozone. Biostratigraphically important successions are present in Arctic Canada (Lenz & Kozłowska-Dawidziuk, 2004), Kyrgyzstan (Koren' & Sujarkova, 2004) and the East European Platform (Urbanek & Teller, 1997).)

Many of the late Wenlock (*Cyrtograptus lundgreni* Biozone) to Ludlow (*Saetograptus leintwardinensis* Biozone) graptolites are known from chemically isolated specimens collected from glacial boulders of northern Germany and Poland (e.g., Urbanek, 1958; Radzevičius & others, 2010; Maletz & Schöning, 2017). This material has its origin in the Silurian foreland basin succession of the Colonus Trough of Scania, southern Sweden (Beier, Maletz, & Böhnke, 2000; Eriksson, 2012), which is poorly exposed. These graptolites have been investigated mainly in drill core material from Poland (e.g., Urbanek, 1963, 1966, 1970).

THE PRIDOLI SERIES

Kříž and others (1986) discussed and defined the Přídolí (now Pridoli) Series (Fig. 80) in great detail, based on the GSSP section in the Prague Basin. The level of the FAD of *Skalograptus parultimus* (Jaeger, 1975) defines the base of the Pridoli. Their work also provided a detailed graptolite biostratigraphy of the whole interval. Teller (1997a, 1997b) and Urbanek (1997a) provided the latest overview on the Pridoli graptolite biostratigraphy and taxonomy of the East European Platform. Ni, Lenz, and Chen (1998) discussed the record of Pridoli graptolites in China and recognized only a single biozone, based on collections

Series & Stages			Baltica/ E. European Platform	Peri-Gondwana (Europe)	Britain	Laurentia Arctic Canada
422.73						
423	LUDLOW	LUDFORDIAN	*Uncinatograptus spineus*	*Formosograptus formosus*	No later zones recorded in Britain	*Formosograptus formosus*
			Uncinatogr. protospineus			
			Uncinatograptus acer			
			Ps. latilobus/S. balticus	*Ps. latilobus/S. balticus*		*Bohemograptus tenuis + Bohemograptus praecornutus*
			Neocucullogr. kozlowskii	*Neocucull. kozlowskii*		
424			*Neocucull. inexpectatus*	*Neocucull. inexpectatus*	*Bohemograptus*	
			Neolobogr. auriculatus	*Bohemograptus tenuis*		
			Bohemograptus cornutus			
			Bohemogr. praecornutus		*Saetograptus leintwardinensis*	
425.01			*C. aversus/S. leintwardinensis*	*Saetogr. linearis*		*'M.' ceratus-S. linearis*
		GORSTIAN	*Cucullogr. hemiaversus*	*Lobograptus scanicus/ Saetograptus chimaera*	*Saetograptus incipiens*	*Lobograptus scanicus*
			Lobograptus invertus			
426			*Lobogr. parascanicus*		*Lobograptus scanicus*	
			Lobograptus progenitor	*Lobograptus progenitor*	*Neodiversograptus nilssoni*	*Lobograptus progenitor*
426.74			*Neodiversogr. nilssoni*	*Neodiversogr. nilssoni*		
427	WENLOCK	HOMERIAN	*Colonograptus ludensis*	*Colonograptus ludensis*	*Colonograptus ludensis*	*Colonograptus ludensis*
428			*Colonograptus deubeli + Colonogr. praedeubeli*	*Colonograptus deubeli+ Colonogr. praedeubeli*	*Gothograptus nassa*	*Colonograptus deubeli+ Colonograptus praedeubeli*
429			*Gothograptus nassa*	*Gothograptus nassa*		*Pristiograptus dubius+ Gothograptus nassa*
			Pristiograptus dubius (Poland)	*Pristiograptus parvus*		
			M. flemingii/P. dubius (Poland)			
430			*Testograptus testis* (Poland)			
			Cyrtograptus lundgreni	*Cyrtograptus lundgreni*	*Cyrtograptus lundgreni*	*Cyrtograptus lundgreni*
430.62		SHEINWOODIAN	*Cyrtograptus perneri*	*Cyrtograptus perneri/ Cyrtograptus ramosus*	*Cyrtograptus rigidus*	*Cyrtograptus perneri*
431			*Cyrtograptus rigidus*	*Cyrtograptus rigidus+ Monogr. belophorus*		*Monograptus opimus*
			Pristiograptus dubius	*Pristiograptus dubius*	*Pristiograptus dubius*	*Monoclimacis flumendosae*
432			*Monogr. riccartonensis*	*Monograptus riccartonensis*	*Monograptus riccartonensis*	*Monograptus instrenuus Cyrtograptus colobus*
			Monograptus firmus	*Cyrtograptus murchisoni*	*Monograptus firmus*	*Cyrtograptus murchisoni*
433			*Cyrtograptus murchisoni*		*Cyrtograptus murchisoni*	
432.93						

Fig. 79. Correlation of Wenlock-Ludlow (Silurian) graptolite biozones.

from northern Xinjiang, northwest China. The fauna is similar to that described by Koren' (1983, 1989) from Kazakhstan and Koren' and Sujarkova (1997) from southern Tian Shan, Kyrgyzstan. Lenz and Kozłowska-Dawidziuk (2004) introduced the *Uncinatograptus birchensis* Biozone in the Arctic Islands, Canada, and suggested

it to be largely of basal Devonian age. They suggested a possible latest Silurian age for the base of the interval, but Lenz (2013) included it entirely in the Pridoli.

DEVONIAN

It is well established that planktic graptolites range biostratigraphically into the Lower Devonian (Fig. 80), but the exact level of their disappearance is still in discussion. The base of the Devonian System is defined at the level of the FAD of *Uncinatograptus uniformis* (Přibyl, 1940a) in the Klonk section, Czech Republic (Chlupáč & Kukal, 1977; Chlupáč & Vasek, 2003). The absolute ages of the Devonian graptolite zone FADs are based on Becker, Gradstein, and Hammer (2012) and indicate a much longer duration of Early Devonian graptolite biozones in comparison with the Silurian time intervals (Fig. 80). The base of the Pragian Stage (Lower Devonian) is based on the level of the FAD of the conodont *Eognathodus sulcatus sulcatus* Philip, 1965 in the Velká Chuchle Quarry, Czech Republic. This level is considered to be above the *Uncinatograptus hercynicus* graptolite zone (Chlupáč & Oliver, 1989). The base of the Emsian is defined at the level of the FAD of the conodont *Polygnathus kitabicus* Yolkin & others, 1994 in Uzbekistan (Yolkin & others, 1997), but a discussion for revision has begun (Carls, Slavík, & Valenzuela-Ríos, 2008). Jaeger (1978b) suggested an early Emsian age for the youngest monograptids and later supported this view in his discussion of the correlation with the conodont record (Jaeger, 1988). Jaeger (1970, 1978b, 1988) described the Devonian graptolite biostratigraphy in some detail using all data available to him at the time. Jaeger (1970) suggested *Uncinatograptus pacificus* Jaeger in Churkin, Jaeger, and Eberlein, 1970 as the youngest Devonian monograptid and established the *Uncinatograptus pacificus* Biozone as the latest graptolite zone, but it is now known that the interval can be correlated with the *Uncinatograptus yukonensis* Biozone (Lenz, 2013).

Koren' (1974, 1975, 1978) discussed the Early Devonian graptolite faunas of central Asia. Lenz (2013) provided the most recent overview on the Early Devonian graptolite faunas of the Arctic Islands, Canada, which has a fairly high number of these faunas interpreted as cosmopolitan. Porěbska (1984) described the Early Devonian graptolites from the Bardo Mountains and established a very detailed biostratigraphy for the region. The author discussed a 30 cm thick linograptid interregnum (Porěbska, 1984) at the top of the Pridoli *Skalograptus transgrediens* Biozone that Lenz (2013) correlated with the *Uncinatograptus birchensis* Biozone of Arctic Canada.

Lenz (1988) recognized *Uncinatograptus yukonensis* (Jackson & Lenz, 1963) as the youngest Devonian monograptid in the Yukon region of Canada. Lenz (2013) rejected the *Uncinatograptus pacificus* Biozone of Jaeger (1970) due to new records in Arctic Canada and considered the *Uncinatograptus yukonensis* Biozone as the youngest Devonian graptolite biozone (Fig. 80). Chen and others (2015) revised the Devonian graptolite faunas of China (Fig. 80) and differentiated four biozones, stating that the succession has only moderate diversity and that certain intervals are not recognizable by their index species. However, this general succession compares well with the worldwide standard.

THE DURATION OF GRAPTOLITE BIOZONES

The duration of graptolite biozones has always been considered quite variable, and the duration of Silurian intervals was regarded as shorter than the Ordovician or Devonian intervals (Rickards, 1976; Hughes, 1995; Zalasiewicz & others, 2009). The advent of radiometric dating finally provided better information on the precise duration of biostratigraphic intervals, but there are few reliable radiometric dates from the early Paleozoic. Loydell (2012) used the timescale of Ogg, Ogg, and Gradstein (2008) to estimate the duration of graptolite

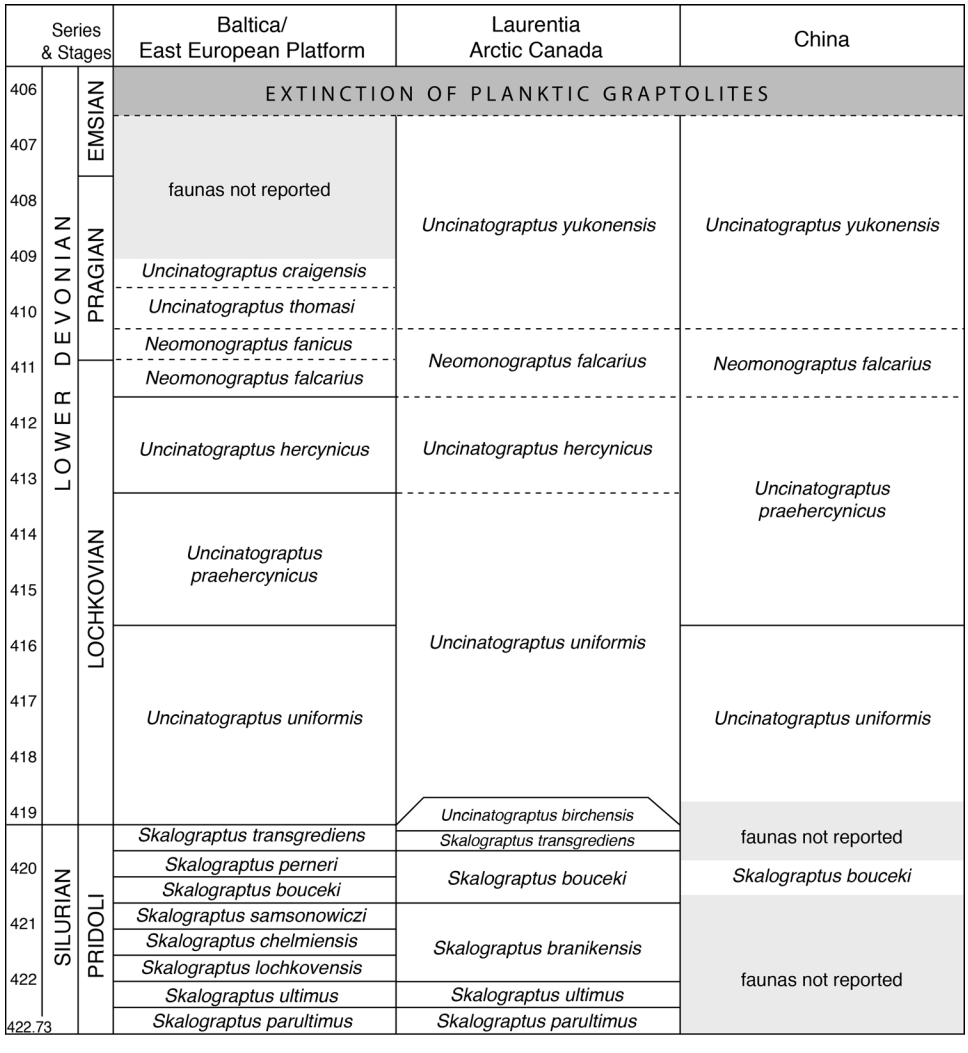


FIG. 80. Correlation of Pridoli (Silurian) and early Devonian graptolite biozones.

zones. General estimates for the Early and Middle Ordovician based on GRADSTEIN and others (2020) indicate a duration of ~1 Ma for a graptolite biozone and a duration of ~1.5 Ma for a graptolite biozone in the Late Ordovician. The estimates are between 400,000 and 600,000 years for the Silurian and ~2 Ma for the Lochkovian. The estimation for the Pragian, the youngest interval for a graptolite biozone, is ~1.5 Ma. Only a few intervals may be zoned more precisely, as the differentiation of the *Spirograptus guerichi* and *Spirograptus turriculatus* biozones demonstrates. LOYDELL (1992, fig. 7) indicated a combined seven subzones for this interval, which lasted ~1 Ma.

Because graptolites are most common in dark and black shales, in which other fossils are rare or lacking, a precise correlation of the graptolite biostratigraphy with the succession of other fossil groups may be difficult. More information on other groups exists in biostratigraphic literature and especially in the discussion of chronostratig-

raphy (see GRADSTEIN & others, 2012; OGG, OGG, & GRADSTEIN, 2016). Biostratigraphic relevant acritarchs and chitinozoans are most commonly associated with graptolites; but because they are microfossils, different methods have to be used for their extraction from the sediments. Graptolites are associated in limestones with numerous other fossils, including conodonts, radiolarians, ostracods, and other small organisms; and these cases can be used for direct biostratigraphic integration (e.g., BERGSTRÖM, 1986; NOBLE & MALETZ, 2000).

Graphic correlation and quantitative biostratigraphy is very useful—and in some cases, absolutely key—to determining biostratigraphic successions and gaining insight into the correlation of various fossil groups as well as to integrating sedimentological data and event horizons with paleontological data (SADLER, 2004, 2012; SADLER, COOPER, & MELCHIN, 2009, 2011; SADLER, COOPER & CRAMPTON, 2014; GOLDMAN, NÕLVAK, & MALETZ 2015). Efforts to produce a more precise chronostratigraphic time scale for the Paleozoic have been undertaken by integration of various means (CRAMER & others, 2010).

Automated stratigraphic correlation (see SADLER, 2004, 2012) integrates biostratigraphic and chemostratigraphic data with radiometric dates, producing a single composite of stratigraphic data. This method has increasingly been used to develop the Ordovician and Silurian time scales. It has also enabled analysis of the changing global graptolite biodiversity and its relationship with environmental change.

PALEOGEOGRAPHY OF THE HEMICHORDATA

Jörg Maletz

INTRODUCTION

Nearly all organisms exhibit at least some biogeographic restriction in their distribution, and this aspect has commonly been used to interpret paleogeographic issues in geology, e.g., plate tectonic configuration, oceanic development, latitudinal differentiation. Plate tectonics is one of the major aspects, initially relying largely on paleontological data and dating back to Wegener (1915), even though the concepts of continental drift and modern plate tectonics appear to describe somewhat different things. Still, they are based on various geological and paleontological investigations, and modern plate tectonics and paleobiogeography are closely connected (see Harper & Servais, 2013; Torsvik & Cocks, 2013).

The Graptolithina, one of the major fossil groups of all marine environments in the early Paleozoic, are not an exception when we, as paleontologists, think of Paleozoic paleobiogeography. However, little is known on the biogeographic distribution of their sister group, the Enteropneusta. Extinct taxa are known only from a few specimens, and extant taxa have not been in the focus of biologists either. Thus, their biogeographical distribution is very incompletely documented. Even the precise biogeographic distribution of the extant Pterobranchia is largely unknown, as the recent description of the first *Rhabdopleura* Allman in Norman, 1869a species in the Mediterranean demonstrates (Beli & others, 2018). Equally, not a single species of the non-colonial Cephalodiscida has been discovered in the Mediterranean to date, but a new *Cephalodiscus* M'Intosh, 1882 species from Sagami Bay, Japan, was recently introduced by Miyamoto, Nishikawa, and Namikawa (2020). Therefore, the remark, that "rhabdopleurids can only be found close to marine research stations" (Maletz, 2017a, p. 12), is not just an oversimplification, but clearly shows that scientific interest often limits our knowledge and that more new records of Pterobranchia may be expected in the future.

EXTANT HEMICHORDATA

The two extant groups of the Hemichordata have not attracted much scientific interest by biologists in a long time, and even knowledge of their living taxa is relatively poor, while the fossil Graptolithina, as an exception, has gained considerable interest by paleontologists and geologists in the past due to their application in biostratigraphic interpretations and the dating of marine sedimentary sequences.

Extant enteropneusts are widely distributed and occur in marine environments from shallow water shelf regions to the deep waters of the abyssal regions of the oceans and can also be found attached to rocks close to hydrothermal vents at the mid-ocean ridges (Woodwick & Sensenbaugh, 1985). Four families can be differentiated, all exclusively in marine regions, usually burrowing into the sediment and rarely living as epibenthos (Cameron, 2018). The epibenthic torquaratorids have been discovered only quite recently. Thus, their record is still extremely spotty; and, due to their dwelling in deeper oceanic regions, it is difficult to ascertain their possibility for a worldwide biogeographic distribution (Jabr, 2017; Jabr, Archambault, & Cameron, 2018). Valuable zoogeographical conclusions are also unavailable for the other enteropneust families, because most species have been reported from a single locality only or are known from relatively small geographical regions (Cameron, Deland, & Bullock, 2010). Only a few species have been described from larger regions or are

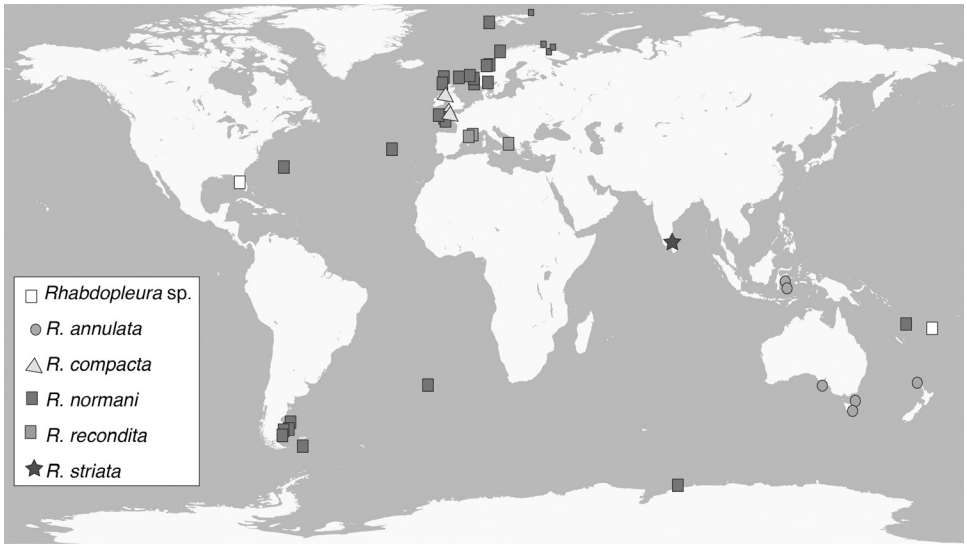


FIG. 81. Global distribution of *Rhabdopleura* ALLMAN in NORMAN, 1869a species (adapted from Beli & others, 2018, fig. 4).

reported to have a wider but often patchy and discontinuous distribution. The documented distribution of extant enteropneusts may be interpreted in different ways as relict populations, either of once more widely distributed taxa or as the result of too little systematic search. CAMERON, DELAND, and BULLOCK (2010) suggested that the enteropneusts represent an ancient and declining group, which may be supported by their spotty fossil record and their possibly early Cambrian origin (MALETZ, 2019a).

BELI and others (2018) discussed the biogeographical distribution of extant rhabdopleurids and differentiated five species of which *Rhabdopleura normani* ALLMAN in NORMAN, 1869a appears to be the taxon with the widest geographical distribution. It is present in the northern and southern Atlantic Ocean but has also been collected in the Antarctic Ocean (Fig. 81). Rhabdopleurids occur from the deeper waters of the polar regions to the shallow tropical regions close to the equator and, thus, do not have extensive ecological restrictions.

The relatively uneven geographical distribution of the few known taxa (Fig. 81) may be based on lack of scientific interest and the difficulty of collecting these small and inconspicuous organisms.

FOSSIL HEMICHORDATA

Fossil hemichordates are largely known from the tubaria of the Graptolithina, whereas the fossil Enteropneusta are too rare to provide sufficient information for a paleobiogeographic interpretation. CAMERON (2018) discussed the fossil material of the Enteropneusta, of which the most specimen-rich material comes from the Burgess Shale of British Columbia, Canada and includes specimens of *Spartobranchus tenuis* (WALCOTT, 1911) and *Oesia disjuncta* WALCOTT, 1911, also representing the oldest known enteropneusts. None of the fossil taxa are known from more than one locality and most taxa are described from single specimens, except for the Carboniferous *Mazoglossus ramsdelli* BARDACK, 1997 from the Mazon Creek fauna of Illinois, USA, which is a moderately common species (MALETZ, 2014a; CAMERON, 2016).

Large data sets on fossil graptolite faunas have been collected in the past and provide a good insight into the ecology and paleobiogeography of the Graptolithina (see

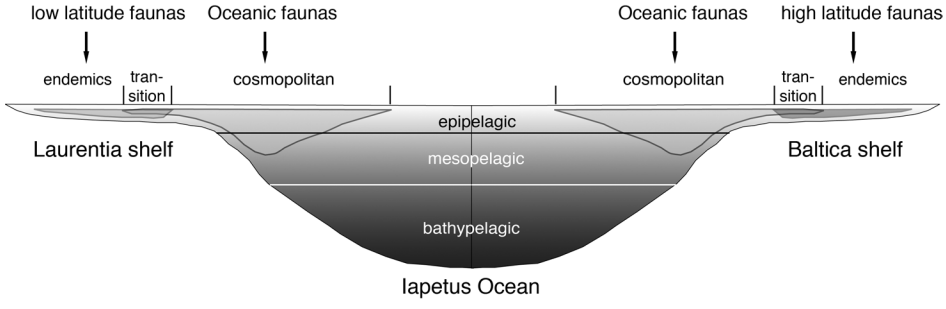


Fig. 82. Biogeographical and paleoecological distribution of the Graptolithina across the Lower Paleozoic Iapetus Ocean, showing endemic and cosmopolitan oceanic graptolite faunas, as well as shallow to deeper water distributions (adapted from Maletz & others, 2011, fig. 9).

Cooper & others, 2004, 2017; Goldman & others, 2013). The problems of precise biostratigraphic correlation between continents during the Lower to Middle Ordovician initiated the research into the paleobiogeography of graptolite faunas. A number of factors were suggested to be responsible for faunal differentiations (e.g., Berry, 1960, 1962a, 1979; Bouček, 1972; Ross, 1961; Berry & Boucot, 1972; Cisne & Chandlee, 1982; Bulman, 1964, 1971a), leading to two main competing models to explain the ecological controls on graptolite species distribution. Skevington (1973, 1974) discussed the cool-temperate Atlantic Province and the paleo-tropical Pacific Province and considered latitudinal variation in surface water temperature as the main control for graptolite provincialism. Cisne and Chandlee (1982) suggested a depth stratification model to explain graptolite distribution patterns during the Late Ordovician Utica Shale of the Taconic foreland basin of the northeastern Appalachians (USA); Finney (1986) explained the same pattern by lateral differentiation of water mass specificity and not depth stratification. Cooper, Fortey, and Lindholm, 1991 and Cooper and others (2012, 2017) recognized a shallow epipelagic biotope with cosmopolitan species, combining two models: 1) a deeper mesopelagic biotope, the isograptid biofacies; and 2) an inshore biotope that included largely endemic species, the didymograptid biofacies. Maletz and others (2011) discussed the faunal differentiation on a transect across the Iapetus Ocean from the moderate to higher latitudes of Baltica to the low latitudes of Laurentia (Fig. 82) during the Darriwilian (Middle Ordovician) and recognized endemic and pandemic faunal elements due to their presence and absence. Goldman and others (2013) stated that both depth and surface temperature played an important role in the biogeographic differentiation of graptolite faunas. The authors also suggested discussing graptolite distributions in terms of low, medium, and high latitudes and abandoning the Atlantic and Pacific Provinces of Skevington (1973, 1974), which are based on modern geographical concepts and not applicable to plate tectonic configurations in the Paleozoic. The main differentiation of Paleozoic planktic graptolite faunas is clearly based on paleo-latitude, but certain graptolite taxa may be restricted to a certain paleocontinent or restricted depositional basin (Goldman & other, 2013). Thus, a latitudinal gradation from low latitude to high latitude faunas is combined with true endemicity based on other factors in the Paleozoic oceans.

BIOGEOGRAPHY

Goldman and others (2013) provided a current overview on the knowledge of biogeographical differentiation of planktic graptolite faunas through time and is useful to consult for details. Paleogeographic interpretations are based on plate tectonic

reconstructions of which the Scotese maps (McKerrow & Scotese, 1990; www.Scotese.com) are the best known. Early Paleozoic paleogeography has generated considerable interest in recent years (Harper & Servais, 2013) and sedimentological and paleontological data still form a considerable part of the interpretations (Torsvik & Cocks, 2013) to which data on the distribution of individual graptolite taxa may be added (Fig. 83). Biogeographic differentiation of graptolite faunas is best known from the Ordovician, a time period that numerous papers have identified as having a high endemicity of graptolite faunas (Goldman & others, 2013).

Unfortunately, there is no information available for the paleogeographical distribution of the dendroid (benthic) graptolites. They are usually described from small fragments of their colonies, and complete, undistorted specimens are comparatively rare. It is likely that their distribution is restricted by temperature barriers, as is the distribution of some planktic taxa. Otherwise, a restriction of individual species or even genera to certain paleocontinental plates may be supposed but cannot be verified.

THE ORDOVICIAN

The base of the Tremadocian experienced a rapid dispersal of early planktic graptolites and any biogeographic differentiation is lacking, as can be surmised from the worldwide correlation of graptolite zones (see Cooper & others, 1998; Cooper, 1999; Loydell, 2012). The middle Tremadocian genus *Bryograptus* Lapworth, 1880a demonstrates the start of some faunal differentiation, as it appears to be restricted to the cooler water regions of higher latitudes (Maletz, Egenhoff, & Alonso, 2010), possibly indicating the start of a general biogeographic faunal differentiation. In the upper Tremadocian, *Kiaerograptus supremus* Lindholm, 1991 represents another taxon restricted to high latitude regions (Lindholm, 1991; Maletz & Egenhoff, 2001). The best-known and investigated interval to document Ordovician graptolite biogeography appears to be the Floian to Darriwilian time interval (Cooper, Fortey, & Lindholm, 1991; Goldman & others, 2013). During this time interval, the planktic graptolite faunas attained a diversity and faunal differentiation not known in this extreme in younger time intervals.

The problems of the differentiation of pendent didymograptids (Berry, 1960, 1967; Skevington, 1963b; Cooper & Fortey, 1982; Maletz, Goldman, & Cone, 2005), commonly used for biostratigraphic purposes, led to the detailed investigation of their proximal end construction and a revision of taxonomy and biostratigraphy of the Floian to Darriwilian graptolite faunas (Cooper & Fortey, 1982; Gutiérrez Marco, 1986; Maletz, 1994b, 2010a; VandenBerg, 2018a). Thus, a number of graptoloid genera occurring in high latitudes (*Aulograptus* Skevington, 1965; *Azygograptus* Nicholson & Lapworth in Nicholson, 1875; *Baltograptus* Maletz, 1994b; *Didymograptus* M'Coy in Sedgwick & M'Coy, 1851–1854; *Jenkinsograptus* Gutiérrez-Marco, 1986) and low latitudes (*Didymograptellus* Cooper & Fortey, 1982; *Paraglossograptus* Mu in Mu & others, 1962; *Yutagraptus* Riva, 1994) were differentiated and are useful as biostratigraphical markers in the individual regions (Beckly & Maletz, 1991; Maletz, 1994b; Toro 1996; Toro & Maletz, 2007). Due to the co-occurrence with other pandemic faunal elements in mixed assemblages, these endemics can generally be correlated indirectly with coeval shallow-water endemic faunas from other continental regions. During the Dapingian, the isograptids formed the main stock of pandemic faunal elements and were used extensively for long distance biostratigraphic correlations (Harris, 1933; Cooper, 1973; Williams & Stevens, 1988; Maletz, 2011a). They were very useful to correlate many largely endemic faunas of this time interval. Fortey and Cocks (1986) even successfully used the presence of isograptids, the isograptid biofacies, to infer the presence

of oceanic basins and the rims of ancient continents.

The base of the Darriwilian had a major rearrangement of graptolite faunas with the evolution of the Axonophora, and faunal differentiation became more difficult due to the apparent similarities of flattened biserial graptolites in shales. However, axonophorans can also be demonstrated to have a considerable provincialism in the Middle and Late Ordovician, and a number of endemic taxa have been described (Maletz & others, 2007; Goldman & others, 2013). In eastern and southeastern North America, the endemic genus *Geniculograptus* Mitchell, 1987 evolved during the Late Ordovician but is absent even in western Laurentia, leading to considerable problems in the intra-continental correlation of Laurentia as well as correlation to other continents (Riva, 1969, 1974b; Berry 1977; Bergström 1978; Goldman, Bergstöm, & Mitchell, 1995). Some of the apparent faunal endemism of the South China platform faunas has been revised by the discovery of species previously considered to be endemic in other regions (e.g., *Tangyagraptus* Mu, 1963a; Chen, Melchin, & others, 2005; Goldman & others, 2007).

Provinciality increased throughout the later Ordovician (Katian) due to the onset of climate change leading to the Hirnantian glaciation. Faunal differences made it increasingly difficult to correlate between low latitude and high latitude faunal localities during this time interval (e.g., Williams & others, 2003; Zalasiewicz, Rushton, & Owen, 1995).

A major reorganization of graptolite faunas occurred due to the Hirnantian glaciation in the latest Ordovician. The Dicranograptidae-Diplograptidae-Orthograptidae (or DDO) faunas of Melchin and Mitchell (1991) were rapidly replaced by species of *Normalograptus* Legrand, 1987 (their Monograptidae fauna; now the Neograptina) that invaded from the southern high latitudes (Goldman & others, 2011). During the *Metabolograptus extraordinarius* to *Metabolograptus persculptus* biozones, neograptine



Fig. 83. Floian, Lower Ordovician paleobiogeography showing the distribution of *Baltograptus* species in *dark gray* (high latitude faunas). Low latitude faunal regions in *light gray*. Cross-section line shows approximate position of section in Fig. 82 (adapted from Egenhoff & Maletz, 2007, fig. 2).

elements dominated the graptolite faunas and the diplograptines were forced into extinction. The neograptines originated during the early Darriwilian and experienced a dramatic radiation that formed the base from which all clades of the Silurian and Early Devonian graptoloids (e.g., Štorch & others, 2011; Maletz, 2019b) originated.

THE SILURIAN

Graptolite provincialism during the Silurian has only more recently been explored and commonly has been considered as of lesser degree than graptolite provincialism in the Ordovician, especially as a standard biozonation was easily applied in the Silurian (e.g., Rickards, 1976; Koren' & others, 1995, 1996; Loydell, 2012). Štorch (1998b) and Legrand (2009) discussed the endemic graptolite faunas of the northwest African part of Gondwana, interpreted as a distinct cool water paleobiogeographic region during the Llandovery and Wenlock, with the strongest endemicity present during the late Hirnantian to Rhuddanian. Melchin (1989) demonstrated that a number of taxonomic groups were

restricted to the paleotropical regions of Laurentia, Baltica, Siberia, Kazakhstan, and China and considered these as a circum-equatorial faunal province, supported by the interpretation of Rickards, Rigby, and Harris (1990). Štorch (1998b) noted that the lower paleolatitude regions of Avalonia and southern Baltica represent transitional faunas between the cooler-water faunas of the peri-Gondwanan and circum-equatorial regions. Little is known about biogeographic differences in the Ludlow to Pridoli interval (e.g. Koren', 1979; Berry & Wilde, 1990). However, according to Goldman and others (2013), considerable differences in the faunal composition between Kazhakstan, northern Laurentia, and Bohemia (see Koren', 1989; Lenz, 1988, 1990; Přibyl, 1983) may indicate the presence of faunal provinces in the late Silurian.

THE DEVONIAN

The graptolite faunas of the Devonian have low diversity and no apparent biogeographic provinciality. Jaeger (1978b, 1988) discussed a worldwide distribution of Lower Devonian graptolite faunas, but it is clear from new paleogeographic interpretations that these faunas appear to be restricted to equatorial regions (Berry & Wilde, 1990). Lower Devonian graptolites of southwestern Europe were usually restricted to outer shelf regions and are not found in inner shelf areas (Lenz & others, 1996), suggesting that the expanses of the Paleozoic oceans may have been the last refuge of the planktic graptoloids in order to escape from competition with other planktonic organisms. Koren' (1979) suggested that this restriction of Devonian planktic graptolites may have been a significant factor in their final extinction. Lenz (2013) demonstrated the distribution of Early Devonian graptoloids was not limited to tropical, equatorial regions. He indicated a presence also in cold-water sites and suggested a probably universally moderate climate for the Early Devonian but regarded the reasons for the graptoloid extinction as not understood.

HISTORICAL BIOGEOGRAPHY

The paleogeographical origin of certain graptolite taxa or clades, or historical paleobiogeography, has rarely been considered in the interpretation of graptolite faunas. Erdtmann (1982b) and Cooper (1999, p. 9) discussed the possible origin of the first planktic graptolites of the genera *Rhabdinopora* and *Staurograptus* Emmons, 1855 in a deep-water biotope on the continental slope and a subsequent expansion into the shallow-water shelf regions. As benthic graptolites appear to be largely limited to the shallow water regions of the oceans, the idea of a deeper water origin of planktic graptoloids might be difficult to explain and needs further investigation. Zhang and Chen (2007, 2008) suggested a deep-water origin and shallow-water dispersal model in graptolite evolution, based on the distribution of early Darriwilian pseudisograptids and early axonophorans in China. The authors suggested that the Axonophora evolved in the deep-water regions in which their ancestors, the isograptids and pseudisograptids, lived. Thus, they favored a model of evolution of certain planktic graptoloid clades from equally planktic ancestors in oceanic regions, in which the planktic graptoloid taxa were supposedly living, but they did not discuss the origin of planktic graptolites per se.

Goldman and others (2013) discussed historical biogeography in order to explain the patterns of changes of graptolite faunas through time and to recognize regions of evolutionary innovations and origins of faunal dispersal. The authors used published cladistics trees to pinpoint the evolutionary origin of certain clades to particular regions, based on a parsimony-based analysis, mapping geographical states to ancestral nodes. They noted a possible origin of early axonophorans in South China but also recognized a considerable diversification center in high- to mid-latitudinal regions, leading to a number of new clades. These

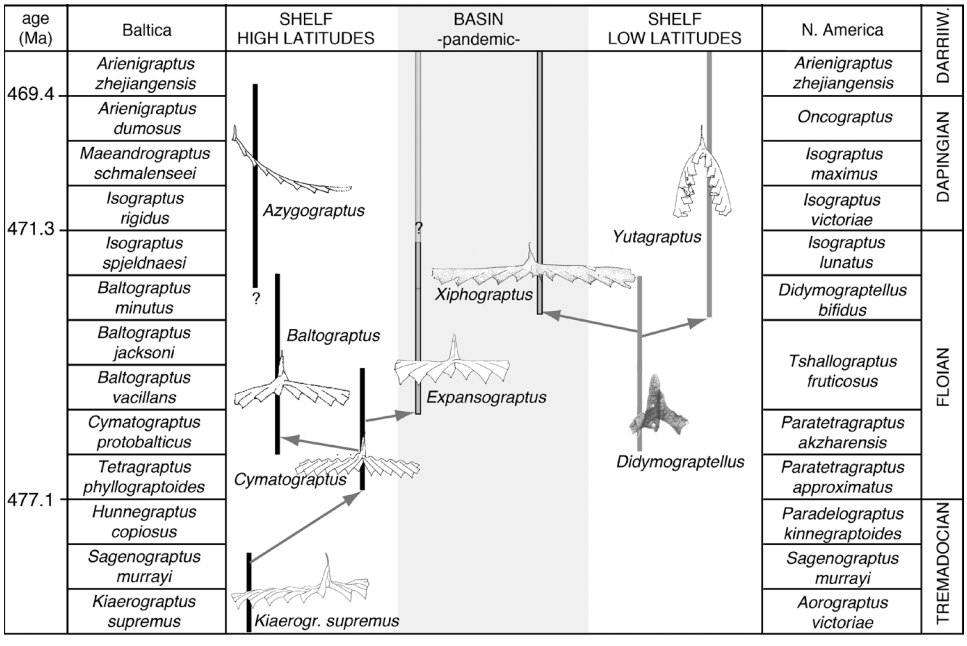


FIG. 84. Historical paleobiogeography of the late Tremadocian to early Darriwilian time interval, showing the introduction of the genera *Expansograptus* BOUČEK & PŘIBYL, 1952a and *Xiphograptus* COOPER & FORTEY, 1982 into the pandemic graptolite faunas of the marine basins from the respective low latitude and high latitude shelf regions (new; radiometric ages (MA) from Cooper & Sadler, 2012) .

interpretations, however, are regarded as preliminary by the authors, as they consider the available data sets as incomplete.

GOLDMAN and others (2013) provided a number of examples to document historical biogeography of graptolite clades. Thus, the origin of the expansograptids (e.g., *Expansograptus* BOUČEK & PŘIBYL, 1952a; *Didymograptus; Baltograptus*) was considered to be in the shallow-water regions of the high latitudes, preceded by the two-stiped *Kiaerograptus supremus* LINDHOLM, 1991 (Fig. 84). The genus *Cymatograptus* JAANUSSON, 1965 suddenly appeared during the middle of the *Tetragraptus phyllograptoides* Biozone, considerably before the origination of the cosmopolitan genus *Expansograptus* (EGENHOFF & MALETZ, 2007). *Cymatograptus* is present in most high latitude regions, but only a single record has been established in lower latitude regions—in the Cow Head Group of western Newfoundland (TORO & MALETZ, 2008, p. 981). The *Expansograptus holmi-Expansograptus suecicus* group in the upper part of the *Cymatograptus protobalticus* Biozone (EGENHOFF & MALETZ, 2007, fig. 3) made the expansograptids successful on a global scale after several million years of evolution as high latitude faunal elements (Fig. 84) with a probable origin in the middle Tremadocian. The evolution of xiphograptids in the low latitude regions demonstrates another example of a biogeographically determined origin of clades in graptoloid evolution. The genus *Didymograptellus* in the *Paratetragraptus akzharensis* Biozone, as discovered in western Newfoundland, represents the oldest xiphograptid in the fossil record as an endemic of the low latitude fauna (MALETZ, 2010a). Global dispersal and invasion of the derived genera *Xiphograptus* COOPER & FORTEY, 1982 and *Pterograptus* HOLM, 1881a into the cosmopolitan oceanic biofacies happened during the Dapingian to Darriwilian, where these taxa enjoyed long-time success until the demise of the

group in the upper Darriwilian. The genus *Didymograptellus,* mainly represented by the short-lived *Didymograptellus bifidus* (Hall, 1865), was only moderately successful in the late Floian in the low latitude fauna. *Yutagraptus* had greater species longevity, originating in the late Floian and lasting until the early Darriwilian, but was also restricted to the low latitudes or perhaps even endemic to Laurentia (Maletz, 2010a).

The radiation of the Neograptina, and especially of the genus *Normalograptus,* represents an excellent example of the biogeographic component of macroevolutionary processes. *Normalograptus* species were uncommon during the Darriwilian to Sandbian and were widely distributed in high latitudes, but during the early Hirnantian, species of *Normalograptus* invaded the paleotropics and rapidly replaced DDO species during the Late Ordovician extinction event (Melchin & Mitchell, 1991; Chen, Melchin, & others, 2005). Eventually, only species of *Normalograptus* survived the extinction and re-populated the early Silurian oceans before a new diversification occurred during the Rhuddanian (early Silurian), initially based on biserial Neograptina but followed by the origin and radiation of the Silurian Monograptidae.

The genus *Cyrtograptus* Carruthers in Murchison, 1867a may in the future provide another useful example to understand the evolutionary history of graptoloids through the late Llandovery and Wenlock (mid-Silurian). The genus *Cyrtograptus* has significant provincial differences in distribution during the late Telychian, and Melchin (1989) used the distribution of *Cyrtograptus sakmaricus* Koren', 1968 and related forms as indicators of the circum-tropical faunal province. *Cyrtograptus* disappeared completely from the southern paleolatitudes in the middle Sheinwoodian but is well documented during this interval in the Canadian Arctic (Lenz & Melchin, 1991). In the late Sheinwoodian *Cyrtograptus rigidus* Biozone, *Cyrtograptus* reappears in Avalonia, Baltica, and Bohemia. The reason for this pattern is unclear, especially as the origin and early evolution of the genus *Cyrtograptus* has not been verified. A number of authors discussed a polyphyletic origin of the genus *Cyrtograptus* (e.g., Rickards, Hutt & Berry, 1977; Fu, 1985; Williams & Zalasiewicz, 2004; Lenz & others, 2012). Because this question is not resolved, a suitable phylogenetic analysis and paleobiogeographic interpretation is impossible to provide.

GEOLOGICAL APPLICATIONS

Jörg Maletz and Alfons H. M. VandenBerg

INTRODUCTION

Graptolites are probably best known for their role in biostratigraphic dating of rock sequences and by paleontologists for the fascinating complexity of their colonies. However, they have much more to offer, and a look back into the history of graptolite research shows their importance for a variety of geological applications. The distribution of Middle Ordovician isograptids, for instance, has been used to infer the presence of oceanic basins and to outline the rims of ancient continents (Fortey & Cocks, 1986). Plus, the paleogeographical information graptolites provide make them valuable for tracing natural resources such as petrochemicals and mineral deposits, thus adding an economic dimension to the study and usefulness of this fossil group.

The early understanding of the distribution of graptolites was not without controversies, as illustrated by the debate between Joachim Barrande and Charles Lapworth. Barrande's concept of graptolite colonies place him as a staunch supporter of Cuvier's theory of catastrophism, which interprets faunas from tectonic blocks as originating through a number of extinctions and creations (Barrande, 1859, 1861, 1862, 1865, 1870, 1881). Barrande's views stood in direct contradiction with Lapworth's understanding of graptolite faunas as successions of species through time. At the end, the interpretation of Lapworth (1878) was proven correct, and his graptolite research provided the nucleus of modern graptolite biostratigraphy and the basis for many modern applications of graptolite research.

DATING OF ROCK SEQUENCES

The study of Earth history was initially concerned with dating sedimentary sequences; and very early on, graptolites were used for just that purpose. As early as 1850, James Hall (1850) realized the importance of graptolites for dating certain geological periods, thus laying the groundwork for the biostratigraphic application of graptolite faunas. Henry Alleyne Nicholson (1868b) provided the first workable chart showing the distribution of graptolite species through time. These scientists made the first steps toward the wider application of graptolites in the geological sciences.

Modern stratigraphy is unthinkable without the use of paleontology, even though this was not always acknowledged after radiometric dating became one of the key methods of chronostratigraphic dating. Our modern understanding of deep time employs numerous additional methods (e.g., Gradstein & others, 2020), including the use of fossils and the recognition of a precise and highly reliable succession of fossil faunas that have developed during the last two centuries. For graptolites, this means that internationally recognized chronostratigraphic units in the early Paleozoic, GSSPs (Global Stratotype Sections and Points) are largely defined by the First Appearance Datum (FAD) of graptolite species (Fig. 85). Thus, graptolites are one of the exemplary groups of fossils for dating rock sequences and correlating them across the planet (Maletz, 2017a). As a group of macrofossils, they are also easily used in the field and do not require extensive work in the laboratory, as is typical for the investigation of microfossils (e.g., acritarchs, chitinozoans, conodonts, spores, foraminifera).

STRUCTURAL GEOLOGY AND BASIN RECONSTRUCTION

Lapworth (1878), in his important paper on the Moffat Series of the UK, established graptolite biostratigraphy as an important geological mapping tool for unraveling

complexly folded and faulted lithological sequences based on the distribution of graptolite faunas. However, he had already indicated earlier (LAPWORTH, 1872) that he used graptolites for biostratigraphic purposes (HAMILTON, 2001). Because it used graptolites for the first time to solve a geological problem, LAPWORTH's (1878) work on the Moffat Series was a milestone in graptolite research. It is noteworthy that LAPWORTH's graptolite biostratigraphy for the region is still valid and useful with little revision after nearly 150 years (FORTEY, 1993).

The Lachlan Orogen of eastern Australia is another prime example of the use of graptolite faunas and dating to understand the geological history of the region. The geological structure of the area is complex, but age control on the turbidite-dominated Ordovician rocks is possible using the presence of rich graptolite faunas (VANDENBERG, 1989; VANDENBERG & COOPER, 1992). The work began with publication of a pioneering study of the Castlemaine goldfield by Thomas Sergeant HALL (1895). HALL developed this work during the next 25 years, and additional work by William John HARRIS and David Evan THOMAS in the 1930s achieved the subdivision of the Early and Middle Ordovician rocks into 21 graptolite zones (HARRIS & THOMAS, 1938a). This work made it possible to subdivide the monotonous turbidite–black shale sequence of the Castlemaine Group, which extends over the westernmost Lachlan Orogen, and unravel its structure, which consisted of tight, closely spaced concertina-like folds interrupted by numerous faults that follow strike. This made it possible to map the Bendigo goldfield, with more than 3,000 graptolite localities, at 1:10,000 scale (WILKINSON, WILLMAN, & GARRATT, 1988; WILLMAN, 1992, 1994).

Problems in solving the structural complexity of the eastern Lachlan Orogen, however, could not be tackled until a workable zonation of the Late Ordovician was achieved in the 1980s (VANDENBERG, 1981, 1989; VANDENBERG & COOPER, 1992). With an extent of more than ten million km^2—much of it in mountainous terrain with granites making up about half of the region—the Ordovician rocks seemingly consisted of turbidites with rare intervals of black shale. Mappable lithological units seemed to be absent and, fossils were few over the widely scattered localities. This picture changed when the region was mapped, initially at a regional scale and subsequently in more detail. This demonstrated the Ordovician sequence could be subdivided into two main units, the Adaminaby Group and the overlying Bendoc Group (VANDENBERG & STEWART, 1992). The Adaminaby Group consists of turbidites with rare cherts containing conodonts and very rare graptolites that represented an age ranging from at least the early Floian (Be1) *Paratetragraptus approximatus* plus *Tshallograptus fruticosus* biozones to the late Darriwilian (Da3) *Archiclimacograptus decoratus* Biozone (VANDENBERG & STEWART, 1992). The overlying black shale-dominated Bendoc Group contains an almost complete Late Ordovician graptolite sequence ranging from the early Sandbian *Nemagraptus gracilis* Biozone to the late Katian *Paraorthograptus pacificus* Biozone. Careful mapping demonstrated that the peculiar ribbon-like outcrop pattern of the Bendoc Group was due to thin-skinned deformation, with the slippery black shale providing a preferred horizon for sliding of multiple stacked thrust sheets (GLEN & VANDENBERG, 1987; GLEN, STEWART, & VANDENBERG, 1990; FERGUSSON & VANDENBERG, 1990; VANDENBERG & others, 1990; VANDENBERG, NOTT, & GLEN,1992).

The importance of graptolites to understanding basin evolution can also be demonstrated through the investigation of the Ordovician graywackes of the southern Baltic Sea. A number of drill cores made during the 1960s demonstrated the presence of a thick succession of early Paleozoic strata in the subsurface of the German island of Rügen (JAEGER, 1967). MALETZ (1997c) discussed the succession of the G-14 drill core north of Rügen and demonstrated a

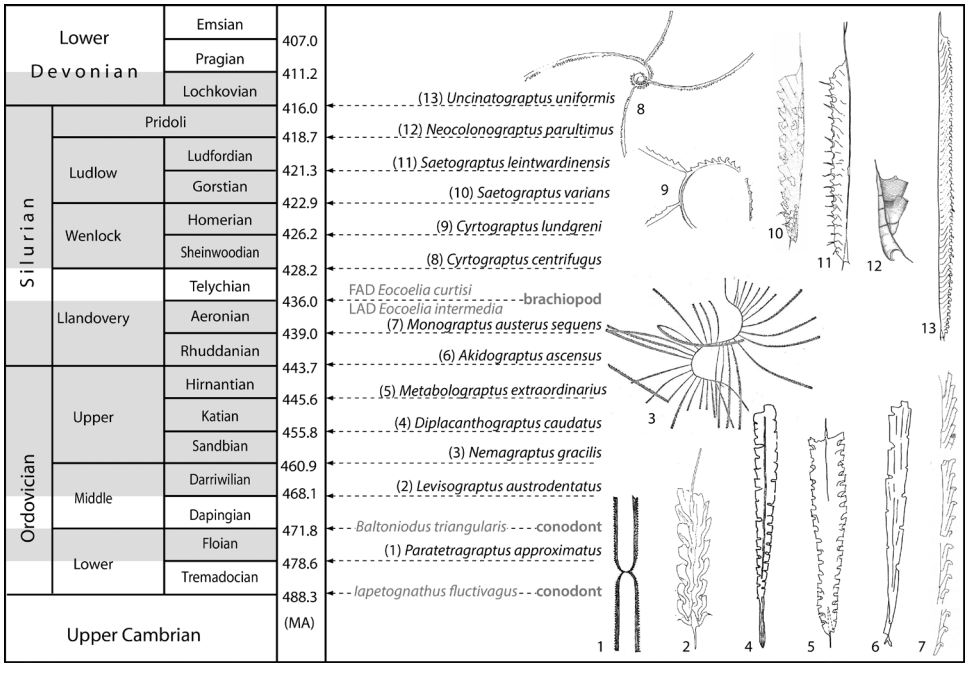


FIG. 85. Index species of graptolites for Global Stratotype Sections and Points (GSSP) in the Paleozoic. Stratigraphic intervals defined by graptolite FADs (First Appearance Datum), highlighted in *gray*. Non-graptolitic fossils defining intervals in *gray* print (adapted from Maletz, 2017c, fig. 8).

close litho- and biostratigraphical connection to the platform succession of Baltica. Whereas the Middle Ordovician Tøyen Shale Formation is strongly condensed, a thick Telychian (Llandovery, Silurian) graptolite succession was documented, similar to that on the Danish island of Bornholm (BJERRESKOV, 1975) and of Scania, southern Sweden (TULLBERG, 1882a). On the island of Rügen, off the southern coast of the Baltic Sea, a number of deep drill cores encountered Middle to Late Ordovician (Darriwilian to Sandbian) graptolite successions with tectonic repetition (MALETZ, 1998a, 2001b). MALETZ and others (1998) and BEIER, MALETZ, and BÖHNKE (2000) interpreted the strata as the remains of a peripheral foreland basin, formed when the microplate East Avalonia collided with Baltica during the Middle Ordovician to late Silurian. The authors interpreted the stacked succession of Ordovician shales, graywackes, and sandstones (Wittow Group; see BEIER & others, 2001) through the effect of thrusting northward onto the shelf region of Baltica. The whole succession was investigated during the unsuccessful exploration for oil and gas in northeastern Germany—a great success, however, for the scientific community because no surface exposures exist of these strata (FRANKE & others, 1994; HOFFMANN & others, 1998).

The Ordovician succession of southern Bolivia provides another example of the use of graptolite faunas for interpreting the basin evolution of an extremely thick monotonous lithological succession (MÜLLER, KLEY, & JACOBSHAGEN, 2002; EGENHOFF, MALETZ, & ERDTMANN, 2004). The Eastern Cordillera of Argentina includes an extremely thick succession of early Paleozoic sediments that only fairly recently have been investigated in more detail. MALETZ and EGENHOFF (2001, 2003) described the diverse Early to Middle Ordovician graptolite faunas of southern Bolivia and recognized a fairly

complete biostratigraphic succession from the Tremadocian to the late Floian that Egenhoff (2000) used to interpret the basin evolution of the region.

Graptolites have also proven useful in other geological applications, based on the style of their occurrence on shale surfaces. Schleiger (1968) and others have demonstrated that graptolite tubaria may be aligned, to a variable degree and depending on their shape, with paleocurrent directions in the turbidites in which they occur, as described by Maletz (see p. 84–85) and Cooper and others (see p. 97) (Fig. 86). From this, paleoslope directions can be determined, and these can be used in basin reconstruction.

In deformed rocks, graptolites with symmetrical tubaria can be used as strain markers (Jenkins, 1987; Maletz, 2020a). Cooper (1990) offered a mathematical method of restoring symmetrical fossils from which strain ellipses could be calculated, thus giving the amount and direction of maximum compression of the host rock. Some 27 years later, VandenBerg (2017, fig. 27–28) demonstrated an easier method that gave similar results using modern image processing software.

ECONOMIC GEOLOGY

The value of graptolites for exploration of economic resources cannot be underestimated. Apart from the modern use of graptolite biostratigraphy in the exploration of oil and gas resources worldwide, a number of further important aspects are worth noting here. These have shaped and even initiated the scientific paleontological research of graptolite faunas in many regions of the world.

URANIUM EXPLORATION

Veski and Palu (2003) discussed the Cambrian–Ordovician Alum Shale Formation, including the early Tremadocian former *Dictyonema* oil shale and the Middle Ordovician kukersite deposits of Estonia that were the focus of intensive exploration (see also Bauert & Kattai, 1997; Dyni, 2005; Soesoo, Vind, & Hade, 2020). In Estonia, kukersite beds can reach an organic content of 40–45 wt% (Bauert, 1994). The exploration for uranium in the *Dictyonema* Shales of Estonia after World War II was of the highest priority (Althausen, 1992). Uranium prospecting also took place in the graptolitic Silurian successions of Thuringia, Germany by SAG/SDAG Wismut, producing ~220,000 tons of uranium ore between 1947 and 1990. The uranium ore was concentrated in lower Paleozoic lithological units, especially in the Unterer Graptolithenschiefer (e.g., Gatzweiler & others, 1997; Wismut, 2010) but also in other units of the succession like the Ockerkalk and the Devonian and Carboniferous intrusions. At the time, the then German Democratic Republic (DDR) in eastern Germany was one of the largest producers of uranium in the world (Kämpf & others, 1995; Czega & others, 2006), and the Ronneburg mining area was the largest uranium mine in Europe, covering an area of 60 km^2 and extending to a depth of 940 m (Paul & others, 2002). Graptolite specialists are familiar with the invaluable monograph on the Silurian graptolite fauna of Thuringia by Schauer (1971), based in part on graptolites collected from sections of the Unterer Graptolithenschiefer (Lower Graptolite Shale) in the Ronneburg area. Most of the paleontological data attained by the uranium industry in central Europe were not officially available for several decades (see Dufka, Kříž, & Štorch, 1995). All information on the uranium production from the Silurian strata by Wismut in eastern Germany (DDR) was under strict confidentiality (Wismut, 2010), indicating the strategic importance of the uranium industry. Thus, very little has been published about the results.

MATURITY STUDIES AND PETROLEUM GEOLOGY

Graptolite shales can be important for the exploration of oil and gas source rocks. Konyukhov and Agapitov (2014) provided a recent overview of the distribution of

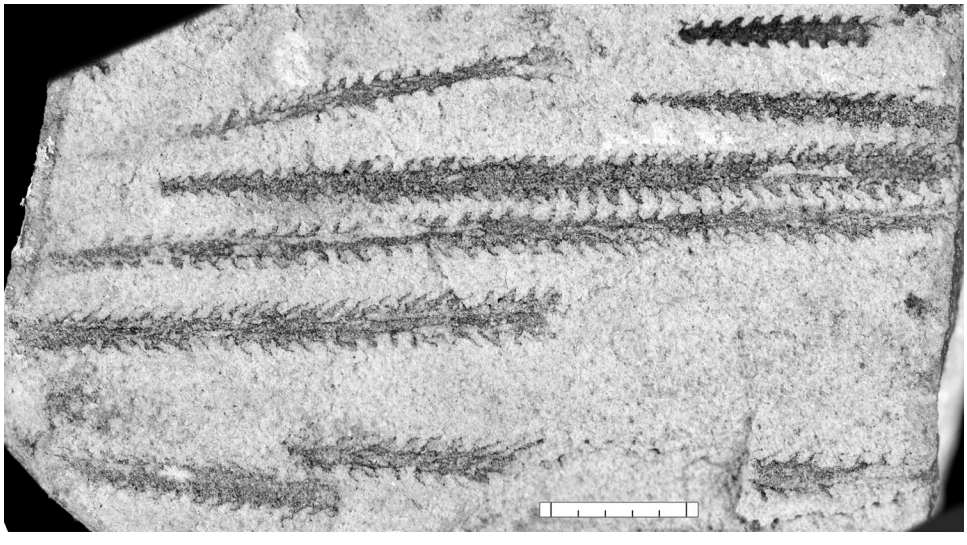


Fig. 86. Current-aligned biserial graptolites from Tb (planar laminated) portion of a turbidite bed from Late Ordovician Sunbury Group, central Victoria, Australia, scale bar, 5 mm (new; A.H.M. VandenBerg). Color version available in *Treatise Online* 155.

Paleozoic graptolite shales around the world and their potential as hydrocarbon resources. They noted that Silurian graptolite shales may have been the source of 80–90% of the hydrocarbons stored in the giant oil fields of North Africa and also may have played the main role in the formation of the gas field of the Persian Gulf, the largest natural gas field in the world. Graptolites are made from organic material and thus provide a useful tool for identifying unconventional hydrocarbon deposits, including shale gas, without the need of complicated and expensive analytical studies. Graptolites are equally important for estimating the TOC (Total Organic Carbon) contents. There are many examples of investigations of hydrocarbon potential in graptolite-bearing Paleozoic successions around the world (e.g., Fello & others, 2006; Grundman & others, 2012; Podhalańska, 2013; Colţoi, Nicolas, & Safa, 2016; Şen, 2017; Luo & others, 2016, 2018, 2020; Borjigin & others, 2017; Ye Wang & others, 2019; Gong & others, 2020).

Numerous authors have used the reflectance of the graptolite fusellum to determine the organic maturity of lower Paleozoic sediments (Fig. 87), because its behavior is similar to that of other organic materials like plants, chitinozoans, and scolecodonts (Teichmüller, 1978; Bertrand & Héroux, 1978; Bertrand, 1990; Goodarzi, 1990; Petersen, Schovsbo, & Nielsen, 2013; Hartkopf-Fröder & others, 2015; Zheng & others, 2021). Graptolite reflectance can be compared with the vitrinite reflectance of fossil plant material (Goodarzi & Norford, 1985, 1989). Graptolite reflectance data are compared to the CAI (color alteration index) in conodonts and may provide information on the maximum overburden of sedimentary successions through the known depth temperature gradient (Bergström, 1980). Therefore, the graptolite fusellum provides important information on the burial history of sedimentary basins through changes in the optical properties of the organic material. Through paleo-temperature evaluation and thermal alteration, the metamorphism and overburden of the sedimentary succession can be evaluated. Important information for basin evolution and tectonics can be gained through the investigation of the thermal history as shown by the example of the central Andean Basin in

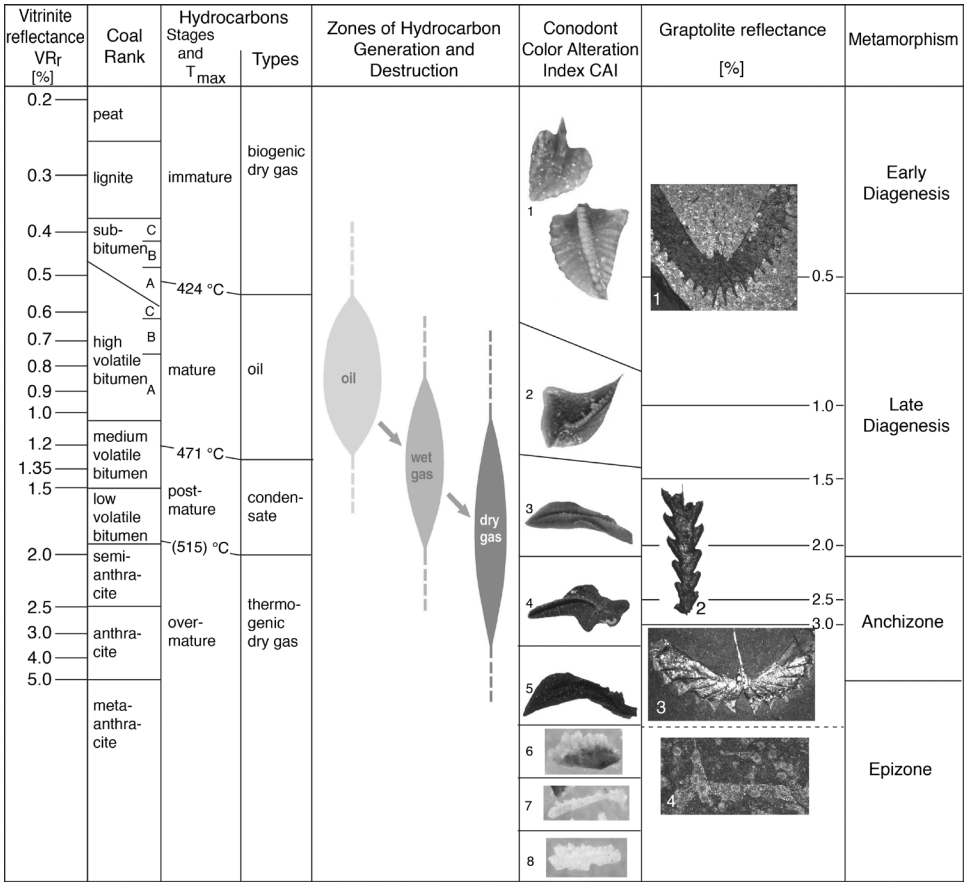


FIG. 87. A comparison of hydrocarbon generation and graptolite reflectance. Conodont specimens from HARTKOPF-FRÖDER and others (2015) to demonstrate CAI values. Graptolites: *1*, *Parisograptus imitatus* (HARRIS, 1933) , GSC 139246, Cow Head Group, western Newfoundland; *2*, *Orthograptus apiculatus* ELLES & WOOD, 1907, PMU 35732, Gullhögen Quarry, Billingen, Västergötland, Sweden; *3*, *Isograptus rigidus* MALETZ, 2011a, PMO 234.063, Slemmestad, Oslo Region, Norway; *4*, *Baltograptus geometricus* (TÖRNQUIST, 1901), LO 1585T, lectotype, Diabasbrottet, Hunneberg, Sweden. Specimens not to scale (adapted from Maletz, 2020a, fig. 6).

Argentina (see HERRERA SÁNCHEZ & others, 2021). The color change of the graptolite tubaria through a temperature gradient is easy to recognize, from dark brown to black (unchanged) to a silvery hue (highly mature) resulting from deep burial or contact and regional metamorphism of the sediments (MALETZ, 2020a). With increasing grade or depth, the original organic material of the graptolite disappears completely.

SCHOVSBO, NIELSEN, and GAUTIER (2014) explored the potential of the Scandinavian Alum Shale Formation as an unconventional gas play in Denmark and provided a geological model that underlies this assessment. They predicted the prospective areas for gas in the Norwegian-Danish Basin. The research is complimented by a discussion by KOSAKOWSKI and others (2017) of the Alum Shale Formation in the Baltic Basin and the Podlasie Depression as important petroleum source rocks.

Hydrocarbon exploration has also been the driving force behind the investigation of Silurian Hot Shales in northern Africa and Arabia in recent years (LÜNING & others, 2000, 2005; LOYDELL, BUTCHER, & AL-JUBOURY, 2013; LOYDELL, BUTCHER, & FRÝDA, 2013).

In these regions, early Silurian (Rhuddanian) successions have been identified as important hydrocarbon source rocks. They represent 80–90% of the Paleozoic hydrocarbons in Arabia and North Africa.

Discontinuous basins filled with organic-rich shales developed on the northern rim of Gondwana, where their thickness was controlled by an early Silurian paleorelief related to the Late Ordovician glaciation event. Extensional and compressional regional tectonics also influenced the distribution of these graptolitic shales. Detailed biostratigraphical correlation of the successions is important for understanding the source potential of these deposits for economic exploration in the regions (Lüning & others, 2000, 2005).

The most important recent development in the exploration for oil and gas comes from the South China Platform. The investigation has concentrated on the Longmaxi Formation (latest Ordovician to basal Silurian) in the Sichuan Basin and also outside this region on the Yangtze Platform. Numerous gas and oil fields have been developed (Hu, He, & Chen, 2012; Chen, Lu, & Ding, 2014; Chen & others, 2014; Guo & others, 2014; Jiang & others, 2015; Shan & others, 2015; Tang & others, 2015; Zou & others, 2015; Ma, 2017; Sun & others, 2020).

BIOSEQUENCE STRATIGRAPHY

Evolutionary studies on graptolites have often included origination and extinction events and their effects on the diversity of the faunas (see p. 138–140), but the connection with sedimentological research has usually been neglected even though it is urgently needed (see Holland & Allen, 2008). It is well known that graptolites are preserved more commonly and much better in certain sediment types, especially in black, anoxic shales (Maletz, 2020a). This knowledge clearly indicates the need for closely connected sedimentological and paleontological research. Sedimentological research can indicate the effects of sea-level changes in fossiliferous successions, and the faunas provide a deeper insight into the amount of paleontological change and also allow an interpretation of the reasons behind this change. The effect of sea-level changes on the preservation of graptolite faunas, and especially their effect on the preservation of shallow-water and deep-water faunal elements in the successions, can help us understand graptolite distribution through time. Egenhoff and Maletz (2007) investigated the use of graptolites as indicators for maximum flooding surfaces in monotonous deep-water shelf successions in the Diabasbrottet section in Västergötland, Sweden. The authors noted the migration of shallow-water endemics and pandemics landward and the increasing frequency of deep-water pandemics in the succession. At the peak of the transgression, the deep-water pandemics dominated the faunas but were in turn replaced by endemic faunas when the sea level fell. Egenhoff and Maletz (2007) thus recognized four levels of deep-water faunas as maximum flooding surfaces in the Diabasbrottet section, combining a sequence stratigraphic approach with graptolite biostratigraphy and diversity studies.

EVOLUTIONARY HISTORY

Jörg Maletz

The interpretation of evolutionary relationships is one of the most important aspects of modern biology and also connects biology and paleontology in the genealogical interpretation of extant and extinct organisms, combined in a unified biological system comparable to the family trees of humans. The taxonomical concept of Linnaeus (1735, 1758) combined organisms based on shared characters, as does modern cladistics (Hennig, 1950, 1965, 1999). Shared homologies or synapomorphies are employed to understand evolutionary relationships, and early on, characters were often used in a kind of trial-and-error method before a better understanding of evolutionary connections was established. Clearly, the concentration on extant organisms can only produce an unfocused and biased view, but often this is all we have. The inclusion of the fossil record may provide much-needed additional information for evolutionary interpretation, and luckily some fossil material of the Hemichordata is available to help demonstrate the origin and early evolution of this group in the deep time of the early Paleozoic (Maletz, 2019a).

Investigation of the evolutionary history of the Hemichordata, based on the fossil record, highlights the dilemma faced when combining extant and extinct groups of organisms. Bateson (1885a) introduced the Hemichordata to science and suggested that they were closely related to the Chordata due to the presence of a notochord, the precursor of the backbone of the vertebrates. The Hemichordata are now regarded as a sister group to the Echinodermata, and some of the early interpretations have been revised considerably (e.g., Halanych, 1995; Cannon & others, 2009; Philippe & others, 2011; Maletz, 2014a).

The Enteropneusta is a group with an extremely poor fossil record. Only in recent years has it been possible to relate a few of the fossil enteropneusts to the four extant families (Cameron, 2016, 2018). A stem-group taxon from the Burgess Shale of British Columbia, Canada apparently produced a possible housing construction (Nanglu & others, 2016) that has been linked to the pterobranch tubarium formation. However, the crown group Enteropneusta has been verified only from the late Paleozoic onward; and except for five taxa, all known species are extant.

Due to the lack of information on the Enteropneusta, the discussion on the evolutionary history of the Hemichordata will herein be focused on the Pterobranchia. The pterobranch tubaria form extremely important fossil remains for geological research and render them ideal for evolutionary studies. However, these housing constructions provide only a limited insight into the evolutionary history of the clade. The soft-bodied zooids did not leave an interpretable fossil record, and we do not know how much evolutionary change has been involved in the organization of these animals since their first fossil appearance during the early Palaeozoic. It is unknown when and how the pterobranchs started to develop their typical clonal reproduction method and why they became the leading planktic organisms in the early Palaeozoic but then largely disappeared during the late Paleozoic.

Because graptolites (fossil Pterobranchia) are thought to be common and widely distributed, it may be reasonable to assume that their evolutionary history is well known. However, only the general picture is outlined from the fossil record, and numerous questions still remain. The story began with the origin of this fascinating group of organisms, probably somewhere during the early Cambrian time interval and led to the few members that are still around today.

EVOLUTIONARY INTERPRETATIONS

The differences in the tubarium construction have been used to interpret evolutionary relationships of the graptolites, and early discussions go back to Nicholson and Marr (1895) and Elles (1898), who were clearly aware of the polyphyletic concept of many of the established genera at their time. They understood that many characters used to define taxa evolved independently in unrelated lineages, even though they did not yet use the term convergent evolution as did Lenz and Melchin (2008) when comparing the Silurian monograptids *Cochlograptus* Obut, 1987 and *Testograptus* Přibyl, 1967a. However, Nicholson (1868**c**) had already discussed the zoological position of the graptolites and looked for homologous characters to connect the group with other organisms.

Elles (1922, p. 174) discussed proximal end development types and a number of trends leading to her "lines of evolution in the Graptoloidea," which provided a fairly simplified concept. A later version of this discussion appeared in Jaeger (1978c). It was also clear to him that the evolution of the graptolites was based on numerous lineages with parallel and convergent evolution due to the constructional limitation of the bausteine [building blocks] of their tubaria. Jaeger discussed eight trends in the evolution of the graptolites and stated (Jaeger, 1978c, p. 8), that "Diese Trends wirken gleichzeitig nebeneinander oder abwechselnd und nacheinander; sie sind miteinander korreliert oder voneinander unabhängig. Sie sind nicht gleichwertig. Die Reihenfolge ihrer Behandlung ergibt sich aus Zweckmässigkeitsgründen der Darstellung. Diese ist kein Kriterium für die Wertigkeit des einzelnen Trends." [These trends act simultaneously and parallel to each other, or after one another. They are not equal. Herein, the succession in their discussion is based on practicality of the demonstration. It does not provide a criterion for the value of the individual trends.]

Thus, patterns of parallel and convergent evolution appear to be a fundamental feature in the evolution of the Graptolithina, implied by the constructional limitations of a tubarium formed from fusellar half rings as branching tubes (see Maletz, 2017a, p. 121). Graptolite evolution can thus be regarded as strongly directional (see Mitchell, 1990).

A large number of studies discussed various aspects of graptolite evolution (e.g., Urbanek, 1966, 1970, 1987; Rickards, 1977; Koren' & Sujarkova, 2004; Urbanek & others, 2012; and many others), generally focusing on individual, short-lived anagenetic lineages, typically expressed by the example of the evolution of the *Demirastrites triangulatus* group (Sudbury, 1958; Štorch & Melchin, 2019) and rarely considering a larger picture (see Rickards, Hutt, & Berry, 1977; Mitchell, 1990; Fortey & Cooper, 1986; Mitchell & others, 2013; Crampton & others, 2016, 2018). These individual studies provide puzzle pieces of important information, and fitted together give us an idea on the way evolution through time modified the tubaria of the graptolites.

Bulman (1958), in a classic study, revised the ideas of Elles (1922) and defined a sequence of four overlapping subfaunas (Fig. 88). These were based on several major characteristics. The anisograptid, dichograptid, diplograptid, and monograptid faunas can easily be recognized by their typical tubarium shapes. However, other tubarium developments of these faunas render differentiation difficult at a closer view. Even in the most recent interpretations of graptolite diversity and evolution (see Sadler, Cooper, & Melchin, 2011; Cooper & others, 2014), these four subfaunas are recognizable and have been defined in a seemingly identical way as high-level taxonomic units (Fig. 88). However, Elles (1922), Bulman (1933b, 1958) and Jaeger (1978c) understood these groups as grades of organization that were progressively replaced as the various lineages evolved nearly parallel to each other through time. Modern cladistic interpretations view the patterns as a number of independently

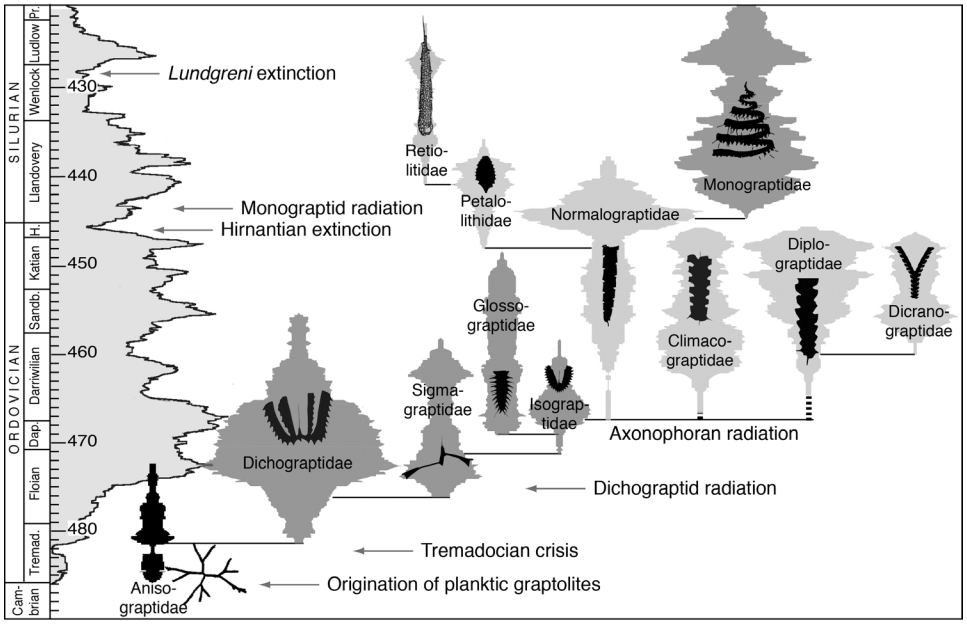


FIG. 88. Graptoloid diversity and the main groups of graptoloids. The anisograptid (*black*), dichograptid (*dark gray*), diplograptid (*light gray*), and monograptid (*dark gray*) faunas can easily be recognized (based on data in Sadler, Cooper, & Melchin, 2011; adapted from Maletz, 2017c, fig. 9). Note: Only some of the events in graptoloid history are marked on the diagram. Pr. = Pridoli; H. = Hirnantian; Sandb. = Sandbian; Dap. = Dapingian; Tremad. = Tremadocian.

evolving clades, but the general picture remains the same.

Detailed information on the evolution of benthic graptolite faunas is not available. Thus, they do not appear in any diversity studies of graptolites. BOUČEK (1957, fig. 75) and CHAPMAN, DURMAN, and RICKARDS (1996) provided some suggestions on the basic evolutionary relationships of the dendroid graptolites. ANDRES (1977, 1980) compared the fusellar construction of Ordovician graptolites and extant pterobranchs and concluded a possible closer relationship of these two groups. MITCHELL and others (2013), in a cladistic analysis, included the modern pterobranchs in their concept of the graptolites but did not analyze the various groups of the dendroids in detail.

More recently, cladistic methods were used to interpret graptolite taxonomy and evolution and to attain information on origination and extinction events that may have shaped the evolutionary history of the group (e.g., FORTEY & COOPER, 1986; MITCHELL, 1987; MELCHIN, 1998; FORTEY, ZHANG, & MELLISH, 2005; MALETZ, CARLUCCI, & MITCHELL, 2009; MELCHIN & others, 2011; MITCHELL & others, 2013; MELCHIN, LENZ, & KOZŁOWSKA, 2017). These cladistic analyses support the main taxonomical concepts of the Graptolithina but cover only some of the recognized clades. A stratocladistic attempt to provide a better understanding of graptolite evolution of a number of Silurian monograptid taxa indicated the need for more detailed morphological investigation for support (WITTINGHAM, RADZEVIČIUS, & SPIRIDONOV, 2020).

SADLER, COOPER, and MELCHIN (2011) noted that the tempo of evolutionary change may have been slower during the Ordovician and faster during the Silurian. Clearly, the data indicate an interconnection to climatic changes; and during colder periods, extinction events may have reduced the diversity of the graptoloids considerably by influencing the equatorial or warm-water faunas more strongly. Over time, a general understanding

of graptolite evolution has been achieved from the origin of the planktonic graptoloids near the base of the Ordovician to their final extinction during the Early Devonian. However, major gaps still exist in the evolutionary understanding of the benthic groups, as their fossil record is relatively poor and incomplete.

ORIGINATION, EXTINCTION, AND DIVERSITY

The macroevolutionary trends in this directional evolution of graptolites have been the focus of diversity studies, indicating a number of extinction, origination, and diversification intervals during the Paleozoic (Fig. 88). A considerable number of extinction events have been established for the graptoloid clade (e.g., Štorch, 1995; Sadler, Cooper, & Melchin, 2011; Bapst & others, 2012; Maletz, 2017a), leading to its near extinction and also to distinct episodes of radiation after a particular extinction event. Various extrinsic factors have been connected to the evolutionary rates of the Ordovician and Silurian planktic graptolites, including climatic conditions and even Milankovitch cycles (Cooper & others, 2014; Crampton & others, 2016, 2018, 2020). Because graptolites are most commonly preserved in black shales, these lithological intervals may have led to an overinterpretation of graptolite diversity due to the better preservation of the specimens in anoxic environments (Maletz, 2018, 2020a). Graptolites are poorly represented in other sediment types, and these faunas are underrepresented, an aspect in graptolite diversity in need of further investigation.

Quantitative methods have recently been employed to understand biostratigraphic distributions and interpret evolutionary relationships and events in the geological history of the graptolites. Foote and others (2019) discussed the completeness of the graptoloid record based on a mathematical model, and Crampton and others (2020) discussed the possibility of sampling bias for the macroevolutionary interpretation of graptolite evolution. Even though sampling is a major factor in the interpretation (see also Boyle & others, 2017), a connection to the sediment type and graptolite taphonomy has rarely been made (Maletz, 2020a).

The Hirnantian event close to the end of the Ordovician (Fig. 89) was one of the largest and best investigated events in graptoloid history (Koren', 1979, 1991; Chen & others, 2003, Chen, Fan, & others, 2005; Štorch & others, 2011). Chen, Melchin, and others (2005) and Finnegan and others (2011) describe the event as a two-step extinction starting with the first step near the Katian/Hirnantian boundary and a second one at the end of the Hirnantian. Also, Bapst and others (2012) discussed two separate extinction episodes during the Hirnantian, associated with the initiation and termination of a global cooling period, located at the base and the top of the Hirnantian interval. Bond and Grasby (2020) recently suggested an early cooling phase and a second phase of warming and anoxia development for the Hirnantian mass extinction, which supports this idea.

During the Hirnantian extinction event, most warm-water graptolite faunas were severely affected, and the Diplograptina went extinct in the second phase, while at the same time, the Neograptina experienced an enormous radiation, suggesting the demise of most warm-water faunal elements (Melchin & Mitchell, 1991; Štorch & others, 2011; Bapst & others, 2012).

A distinct replacement of the Diplograptina faunas by the Neograptina faunas can be demonstrated (Fig. 89). Sadler, Cooper, and Melchin (2011, fig. 13) estimated a diversity of less than 20 species during the Ka4-Hirnantian crisis (circa *Metabolograptus persculptus* Biozone?), but Bapst and others (2012) indicated approximately 25 species in the *Metabolograptus persculptus* Biozone. Goldman and others (2011) listed 39 species of normalograptids from the *Metabolograptus persculptus* Biozone alone (his zone 13, Bo5), but the list does not include the diplograptine faunal elements.

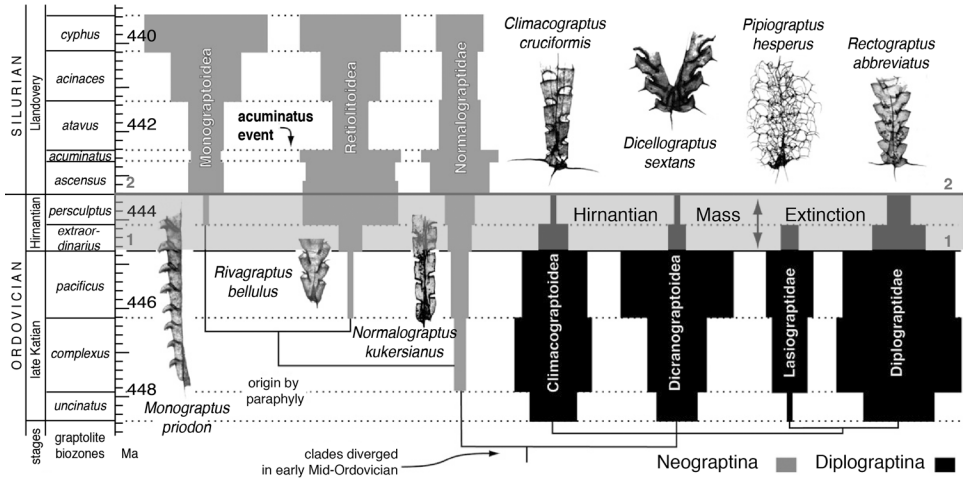


FIG. 89. Interpretation of the Hirnantian extinction and replacement of the Diplograptina (*black*) by the Neograptina (*gray*) (adapted from Bapst & others, 2012, fig. 1).

ŠTORCH and others (2011, fig. 3) regarded a number of the Hirnantian Diplograptina as Lazarus taxa—taxa experiencing an apparent extinction but reappearing later on. As the authors indicated the ranges of these taxa through the supposed extinction interval, the record would not represent a real extinction, and the diversity in the extinction interval may be considerably exaggerated. The faunal change may better be interpreted as a turnover and successive replacement that does not need to be connected to an intense extinction event, as in the *Lundgreni* Event (KOREN', 1987; JAEGER, 1991) in which the diversity of graptolites was extremely reduced. Still, the selectivity of the event suggests that certain graptolite groups were more vulnerable to extinction than others. CRAMPTON and others (2016, p. 1498) suggested that "old species were selectively removed" during the Late Ordovician mass extinction, but SHEETS and others (2016, p. 8380) recognized a "preferential decline in abundance of dysaerobic zone specialist species." The high diversity in the *Metabolograptus persculptus* Biozone could also be based on the increased international attention of the interval due to its being defined as a Global Stratotype Section and Point (GSSP) at the base of the Silurian and the supposed extinction interval in the Hirnantian. This attention led to an extreme splitting of specimens into numerous local graptolite species (SOBOLEVSKAYA, 1974; CHEN & LIN, 1978; NI, 1978; MU & NI, 1983; FANG & others, 1990; LEGRAND, 2001, 2009; MU & others, 1993; CHEN, FAN, & others, 2005; CHEN & others 2007, 2020), possibly masking the real impact of the event on graptolite diversity. However, this suggestion should not downplay the real extinction event that can be recognized in the Late Ordovician and is not restricted to the graptolites.

As earlier discussed, the term Lazarus effect (see FLESSA & JABLONSKI, 1983; WIGNALL & BENTON, 1999), used to describe the cryptic appearance of members of lineages disappearing at an extinction event and reappearing later on (URBANEK, 1993, 1998; RICKARDS & WRIGHT, 2002; ŠTORCH & others, 2011), should not be confused with a genuine extinction. Adding these species to the diversity diagram (ŠTORCH & others, 2011, fig. 5) would lead to a somewhat different interpretation: very few species of the Diplograptina fauna went extinct at the base of the *Metabolograptus extraordinarius* Biozone.

The reappearance of species of the genus *Cyrtograptus* CARRUTHERS in MURCHISON,

1867a as relic elements in the Ludlow of New South Wales (Rickards & others, 1995) could be interpreted as a Lazarus effect. Alternately, they may be based on parallel evolution of main tubarium features, thus needs reinvestigation. This reappearance may not represent a genuine record of the genus *Cyrtograptus* but the emergence of the genus *Formosograptus* Bouček, Mihajlovic, & Vaselinovic, 1976, generally lacking cladia (see Urbanek, 1997a).

The largest extinction event influencing graptolite evolution may have been the Silurian *Lundgreni* Event (e.g., Koren', 1987; Lenz & others, 2006; Crampton & others, 2016) or the Great Crisis of Jaeger (1991) during the early Homerian (Wenlock) (see Fig. 88). During this event, nearly all monograptids and retiolitids disappeared, and the two groups rediversified after a short interval in which only two graptoloid taxa, *Pristiograptus* Eisel, 1912 and *Gothograptus* Frech, 1897, have been recognized as the sole survivors of the previously dominating Silurian neograptine and monograptid clades. Urbanek (1997a, 1998) identified this bottleneck effect of near extinction or survival and recovery with the term oligophyly.

Cooper and others (2014) suggested different causal linkages for the graptolite diversity patterns during the Ordovician and Silurian. They postulated relatively stable marine environments for the Ordovician, but the Silurian appeared to be characterized by more volatile climatic changes leading to a number of distinct extinction events. Cooper and Sadler (2010) discussed the extinction risk of graptolite faunas and came to the conclusion that the facies preference of graptolites predicted their extinction risk. They suggested that species restricted to the deep-water classical graptolite facies (deep-water black shales) had a distinctly lower mean duration than faunal elements also found in shallow-water or platform regions. The analysis, however, does not include the notion that the anoxic black shale facies favors preservation of organic material and thus, superior preservation of graptolite tubaria.

EVOLUTIONARY TRENDS

Evolutionary studies of graptolites can be used to differentiate micro- and macroevolutionary patterns, but the differentiation is not easy, as the fossil record is typically quite patchy, with micro-evolutionary steps nearly impossible to trace. Tracing the change of single species into a different, derived species may be termed micro-evolution. This is exemplified by the work of Sudbury (1958) and Štorch and Melchin (2019), who demonstrated anagenetic change in the genus *Demirastrites* Eisel, 1912. They documented the stepwise generation of changes in faunal populations until differences became large enough to indicate a speciation event. Numerous further examples are discussed in the scientific literature (see an overview for Silurian monograptids in Rickards, Hutt, & Berry, 1977).

Urbanek (1995) discussed the *Wolynograptus spineus* lineage in some detail from chemically isolated material and was able to trace anagenetic changes in the construction of the thecal apertures through a number of species. *Wolynograptus acer* Tsegelnjuk, 1976 evolved through the apertural addition of new characters to the intermediate *Wolynograptus protospineus* (Urbanek, 1995) and finally to *Wolynograptus spineus* (Tsegelnjuk, 1976) (Fig. 90). The paired apertural spines of *Wolynograptus spineus* are reminiscent of the much older *Monograptus priodon* group, but the species cannot be identified as a cryptogenic faunal element or interpreted as a Lazarus taxon. It was a newly evolved taxon with a homoplastic character indicative of parallel or convergent evolution. Thus, tracing the micro-evolutionary changes in a single lineage was used to understand macroevolution in monograptids and to determine characters as homoplastic and not homologous.

DIRECTIONAL EVOLUTION AND HOMOPLASY

Larger-scale differentiations or macroevolutionary patterns occurred in the evolution of groups such as the Dichograptina, Axonophora, or Neograptina, and eventually

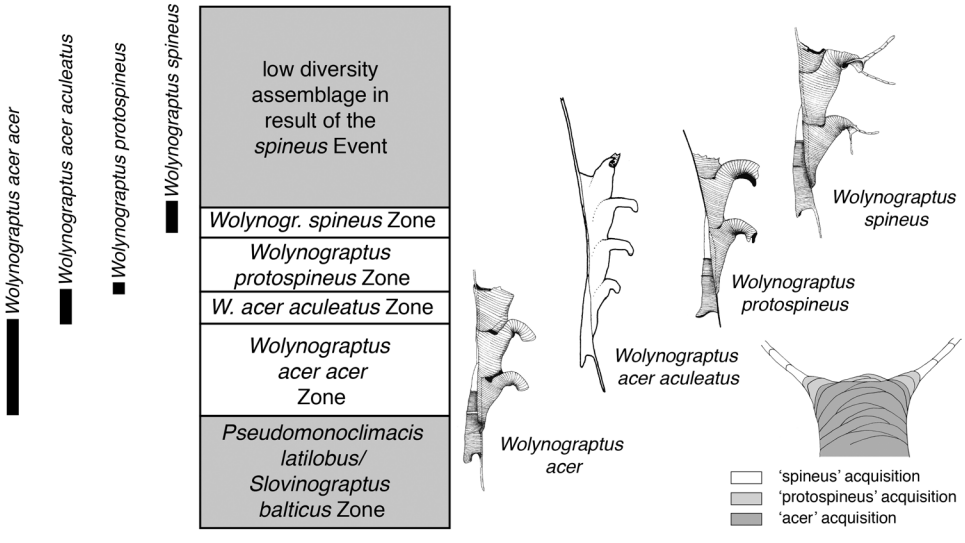


FIG. 90. Phyletic evolution in the *Wolynograptus spineus* (TSEGELNJUK, 1976) lineage based on URBANEK (1995) (adapted from Maletz, 2017a, fig. 7.7).

the Monograptidae, and correspond to the trends in graptolite evolution as suggested by ELLES (1922). These trends have invariably been understood as polyphyletic and not strictly interpretable in a phylogenetic way.

Due to the constructional limitations imposed by the formation of thecal tubes by fusellar half rings, "many tubarium features evolved again and again independently during the evolutionary history of the graptolites" (MALETZ, 2017a, p. 121), a factor identified as directional evolution and discussed for Ordovician axonophorans by MITCHELL (1990). Numerous characters of graptolite colonies cannot be used to simply postulate phylogenetic relationships and explain evolutionary lineages. These characters should be interpreted as homoplastic, and morphological similarities are based on convergent evolution (see LANKESTER, 1870). Thus, real homologies are difficult to detect in graptolites, and a detailed morphological analysis is needed to trace them (Fig. 91).

Excellent examples of this directional evolution and convergence occur in a large number of groups (MITCHELL, 1990). The decrease of the number of stipes was regarded as of prime importance initially, but NICHOLSON and MARR (1895, p. 531) had already stated, that "the number of stipes in the polypary is a character of minor importance." Thus, translated into modern terms, the number of stipes is not a homologous character (Fig. 91.1–91.2). This statement may be supported by the modern inclusion of single-stiped tubaria into several unrelated clades (e.g. *Azygograptus* NICHOLSON & LAPWORTH in NICHOLSON, 1875 in Sigmagraptidae; *Nicholsonograptus* BOUČEK & PŘIBYL, 1952a in Sinograptidae; Monograptidae as a Silurian clade). MALETZ (2017a, fig. 7.6) illustrated the situation as a prime example of convergent evolution (Fig. 91.3–91.4). It is also supported by the recognition of cladia forming secondarily multiramous tubaria (Fig. 91.1–91.2) in various clades of the Graptolithina. As we now know, cladia evolved independently in the Pterograptidae (SKWARKO, 1974; MALETZ, 1994a), the Dicranograptidae (MALETZ, 2020b), the Nemagraptinae (FINNEY, 1985a), and in a number of monograptid genera (STRACHAN, 1952; URBANEK, 1963).

The repeated origination of retiolitid-type developments in the graptolites may be one of the most stunning and easily recognizable examples of convergent evolution. The retiolitid-type development is characterized

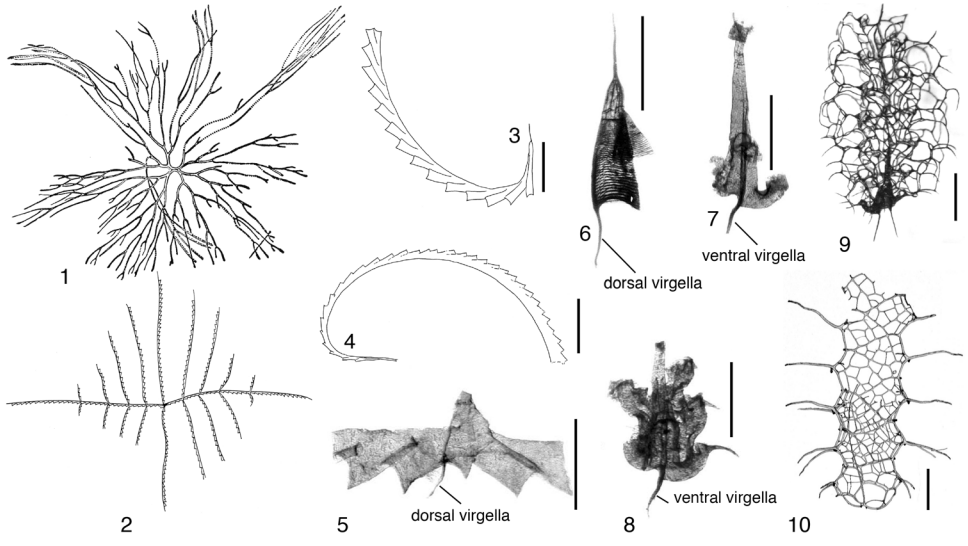


FIG. 91. Examples of directional evolution and homoplasy. *1*, *Clonograptus flexilis* (HALL, 1865), multiramous tubarium with dichotomous branching (Hall, 1865, fig. 8); *2*, *Abiesgraptus multiramosus* HUNDT, 1935a, multiramous tubarium with cladial branching (adapted from Jaeger, 1959, fig. 25); *3*, *Cymatograptus validus* (TÖRNQUIST, 1904), strongly curved taxon with single stipe (reconstructed from Beckly & Maletz, 1991, fig. 19B); *4*, *Coronograptus cyphus* (LAPWORTH, 1876b), strongly curved single stiped monograptid (reconstructed from Zalasiewicz, Williams, & Akhurst, 2003, fig. 2A); *5*, *Xiphograptus lofuensis* (LEE, 1961), showing dorsal virgella (Maletz, 2010a, fig. 8C); *6*, *Phyllograptus typus* HALL, 1865, dorsal virgella (Maletz, 2010a, fig. 6C); *7–8*, *Levisograptus sinicus*, ventral virgella (Maletz, 2010a, fig. 5); *9*, *Pipiograptus* sp. showing meshwork of external bars (Maletz, 2017a, fig. 11.8J); *10*, *Spinograptus spinosus* (WOOD, 1900), retiolitid graptolite with meshwork of ancora sleeve (Maletz, 2010b, fig. 5A). *1, 3, 5–8:* Ordovician; *2:* Devonian; *4, 9–10:* Silurian. Scale bars, 1 mm, with the exception of *4,* which is 5 mm.

by the independent extrathecal development of a meshwork of lists as in the Ordovician Lasiograptidae (Fig. 91.9) and especially in the Silurian Retiolitidae (Fig. 91.10), in which the precise development had a very different origin of comparable features (LENZ & others, 2018).

Another prime example of directional and convergent evolution involves the formation of the virgella spine (Fig. 91.5–91.8), initially regarded as a character used to define the Virgellina as a monophyletic group (FORTEY & COOPER, 1986). At least three instances of independent origin and evolution of a virgellar spine have been identified, and MALETZ (2010a) differentiated a dorsal and a ventral virgellar spine in the Graptolithina. The loss of bithecae in the late Tremadocian appeared even more complex than expected to FORTEY and COOPER (1986). A polyphyletic loss of the bithecae has been suggested by a number of authors (BULMAN, 1960; ERDTMANN, 1982a; LINDHOLM, 1991) and can be supported by the presence of at least a sicular bitheca in the sigmagraptine *Paradelograptus* ERDTMANN, MALETZ & GUTIÉRREZ-MARCO, 1987 (see MALETZ, ZHANG, & VANDENBERG, 2018).

Numerous further characters may be identified as independently evolved in widely separate clades, making cladistic interpretations difficult without the detailed morphological knowledge of the tubarium construction of the graptolites. The instances of homoplasy in the Pterobranchia discussed herein can also be described in the terms of convergence and parallel evolution in various graptolite groups.

RIGBY and MILSOM (1996) suggested neoteny or paedomorphosis as the motor for the evolution of planktic graptolites. It is, however, difficult to use the concept for the development of the colonial astogeny of the graptolite colonies or, in fact, for

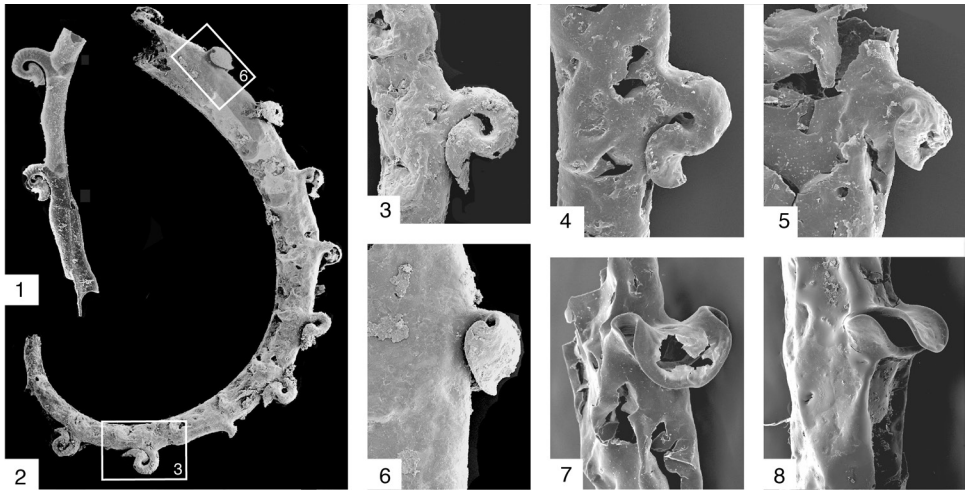


FIG. 92. *Paramonoclimacis sidjachenkoi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA & BONDAREV, 1965) showing thecal gradients. *1*, proximal end with two thecae; *2*, strongly curved proximal fragment lacking sicula; *3–4*, proximal thecae; *5–6*, median thecae with wide hood; *7*, thecal hood reduced in width; *8*, slender thecal hood and lateral lobes of distal theca (new; details of specimens in MALETZ & others, 2019). Not to scale.

colonial organisms in general. RICKARDS (1977) discussed a number of cases that may indicate paedomorphosis, including the evolutionary change from *Petalolithus* SUESS, 1851 to *Cephalograptus* HOPKINSON, 1869. In this example, RICKARDS (1977) interpreted the elongation and reduction of the number of thecae in the tubarium as a possible example of neoteny. There is no change in the size and development of the sicula in these forms. He also regarded the Ordovician genus *Corynoides* NICHOLSON, 1867a as a possible paedomorphic derivative of the isograptids, achieved through the loss of the unrestricted growth of the graptolite colony.

In the Dichograptina, the first few thecal pairs are typically fairly slender as are the stipes. Through the astogeny, the stipes widen considerably distally as in *Tetragraptus* SALTER, 1863a or in *Didymograptellus* COOPER & FORTEY, 1982 (see WILLIAMS & STEVENS, 1988, fig. 44) but also in many other taxa. This can be regarded as a simple expression of morphological gradients in graptolite colonies, even though changes in thecal construction are minimal. Morphological gradients are most commonly described from Silurian monograptids (e.g., BULMAN, 1958; HUTT, 1974b) and are often easily visible even in flattened shale material. MALETZ and others (2019) described the dramatic change of the thecal style in *Paramonoclimacis sidjachenkoi* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & BONDAREV, 1965 from chemically isolated material (Fig. 92). The proximal thecae of this taxon bear strongly coiled thecae with a streptograptid nozzle (Fig. 92.3–92.4), changing distally to dorsal hooks associated with two lateral lobes (Fig. 92.8) through a number of intermediate thecal stages (Fig. 92.5–92.7). Similar thecal gradients are present in genera such as *Torquigraptus* LOYDELL, 1993, *Pernerograptus* PŘIBYL, 1941, *Pribylograptus* OBUT & SOBOLEVSKAYA, 1966, and to a lesser degree in *Coronograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVESKAYA, & MERKUREVA, 1968 (HUTT, 1974b; LUKASIK & MELCHIN, 1997).

BULMAN (1958) and URBANEK (1960) discussed and illustrated thecal gradients of a number of examples of Silurian monograptids. They explained the development of *Cyrtograptus* in which cladial branches have initial thecae that are quite different from the thecae of the main stipe at which the

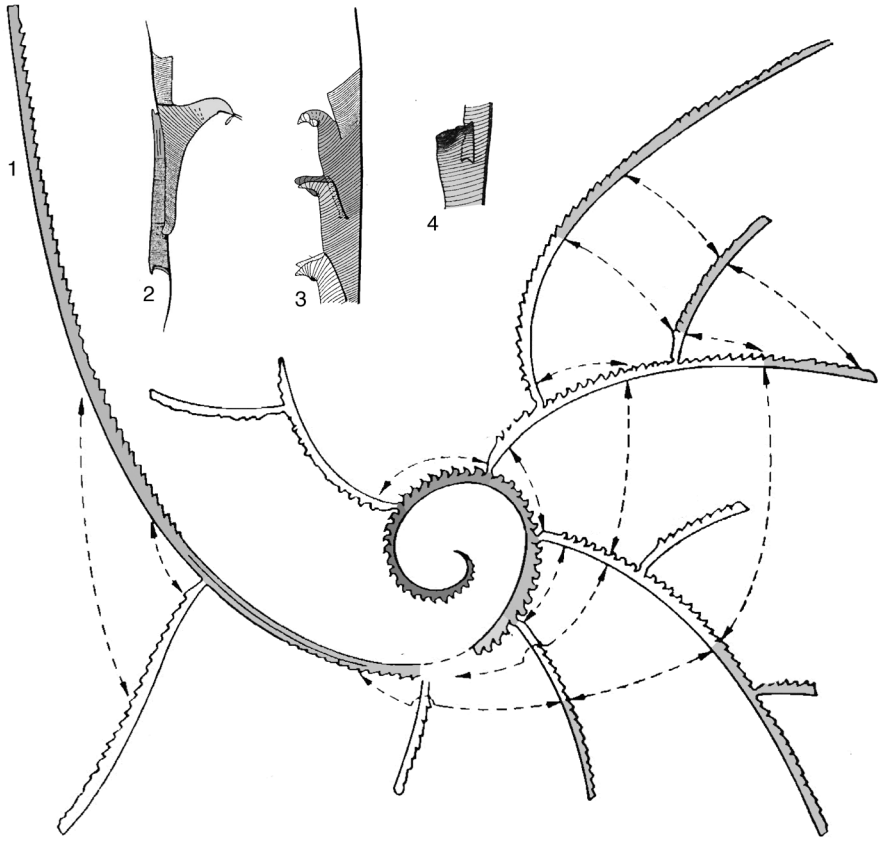


FIG. 93. Thecal gradients in cladial stipes. *1, Cyrtograptus murchisoni* CARRUTHERS, 1867a (new; based on Bulman, 1958, fig. 7 and URBANEK, 1960, fig. 10); *2–3, Cyrtograptus perneri* BOUČEK, 1933, proximal end and thecae from median part of colony (adapted from Thorsteinsson, 1955, fig. 1–2); *4, Cyrtograptus hamatus* (BAILY, 1862), distal theca (Teller, 1976, fig. 12). Illustrations not to scale.

cladium is developed but can be compared to much more distal thecae (Fig. 93). In this example, a thecal gradient is combined with cladial branching, allowing recognition of the exact point during astogeny of initiation of the growth of the cladial branch. They interpreted a delay in the initiation of the growth of cladial branches following the suggestion of THORSTEINSSON (1955), who first described this delay in *Cyrtograptus perneri* BOUČEK, 1933 (see revision of taxon in LENZ & others, 2012, p. 32). However, BULMAN (1958) and URBANEK (1960) illustrated a specimen of *Cyrtograptus murchisoni* CARRUTHERS IN MURCHISON, 1867a as an example in which the thecal gradient has not yet been described in detail (Fig. 93.1). Information of the thecal differentiation can be taken from other taxa of the genus (Fig. 93.2–93.4). The phenomenon was called retardation and was explained by the observation that "before the first signs of the growth of the first cladial theca, some 3–4 next thecae have appeared on the main stipe" (URBANEK, 1960, p. 158). URBANEK (1963, p. 230) suggested that this delay may be described by the "law of morphological equivalence of simultaneously budding thecae, established by THORSTEINSSON (1955)." The "distribution of suitable morphogenetic substances" produced by the oozoid (siculozooid) may be the mechanism behind this delay and lead to the different thecal styles (URBANEK, 1963,

p. 230). It could also help to understand bipolar stipes as the regeneration of stipe fragments, in which the theca growing to one side is often different in size and shape to the one on the other side. Oldest bipolar tubaria without the presence of a sicula were recognized in the Middle Ordovician and described as *Janograptus* Tullberg, 1880a, but are more common in Silurian monograptids (see Rickards, Hutt, & Berry, 1977). Albani and others (2001) illustrated a Darriwilian (Middle Ordovician) janograptid specimen with the first thecal apertures on the two stipes of the bipolar tubarium distinctly different in size. Jaanusson (1973) discussed morphological discontinuities in the evolution of graptolites and the possible presence of polymorphic populations. He suggested that this was commonly involved in the change of number of stipes in graptolite colonies and provided a number of examples, including the three- and four-stiped specimens of *Tshallograptus fruticosus* (Hall, 1858) (see VandenBerg, 2017, for a modern taxonomic approach). He expected that, in these cases, both morphological types would coexist for some time as genetic polymorphs. Skevington (1966, 1967) elaborated on the concept of genetic polymorphism in the case of *Holmograptus* Kozłowski, 1954 and *Nicholsonograptus,* suggesting that both were likely to be intraspecific variants of a single species. However, both genera are now regarded as separate members of the Sinograptidae (Maletz, Zhang, & VandenBerg, 2018), and the concept of evolutionary change through polymorphy has not been proven for graptolites.

Biogeography was also involved in the evolutionary differentiation of graptolite faunas and was important for the formation of biogeographically distinct regions (see *Paleogeography of the Hemichordata,* p. 119–126).

GRAPTOLITE PREPARATION AND ILLUSTRATION TECHNIQUES

Denis E. B. Bates, Jörg Maletz, and Jan Zalasiewicz

INTRODUCTION

The collection, preparation, and illustration techniques for graptolites—as for all fossils—have changed considerably during the last 150 years to enable increased precision in collection and documentation of scientific material, and it will undoubtedly continue to change during the coming decades. Nonetheless, certain basics are still followed and have remained unchanged. New discoveries may be made in museum collections, but the most important source of material remains the tireless fieldwork of geologists and paleontologists. The value of collections is enhanced if their exact origins are carefully noted prior to deposition in public repositories of national museums and geological surveys.

With the change in collection methods, documentation of the material in scientific publications has also changed dramatically. In earlier publications, woodcuts and line drawings were the common method of illustration. The photographic illustration of fossil specimens in scientific books and other publications was rare at the time of Joachim Barrande, James Hall, Hanns Bruno Geinitz, Charles Lapworth, Sven Leonhard Törnquist, Gerhard Holm, and others, because graptolites were just too small to photograph with existing technology. The eventual use of camera lucida (see p. 157) greatly improved the accuracy of drawings. The quality of the scientific illustrations, therefore, is quite variable in earlier publications and can be unreliable, hampered by lack of understanding of the fossils investigated and their construction and preservation (see, for example, *Nautilus veles* Richter, 1871, now *Cochlograptus veles* in Maletz, 2001a). This situation has sometimes resulted in uncertain identification of type specimens and subsequent taxonomic attribution. Techniques such as scanning electron microscopy (SEM) and transmission electron microscopy (TEM) investigation as well as computer techniques, e.g., computer tomography (CT) and X-ray imaging have provided new insights into graptolite research and will likely provide some unique perspectives on these enigmatic fossils.

COLLECTING GRAPTOLITES

Collecting graptolites does not require any special techniques that are not common to most paleontological collecting. Care should be taken to collect with a precise knowledge of the individual horizons and to document the faunal assemblages. Faunas can change considerably from horizon to horizon, not just in terms of biostratigraphical changes, but also in terms of ecological influences. All available data (e.g., enclosing lithology) concerning these factors should be collected.

Detecting graptolites in rock may require astute attention. Although the classic graptolitic facies is marine black shale, the fossils can occur in various rock types, such as greywackes, sandstones, or carbonates in which the tubaria may not be orientated parallel to bedding planes. Graptolites may be more apparent on weathered surfaces than on fresh rock where they may appear whitish from clay coatings or reddish from iron oxide formation. Graptolites that are clearly visible in newly broken fresh rock may become less visible as the inherent moisture dissipates from the surface. Wetting surfaces with alcohol (isopropyl is recommended) usually enhances graptolite definition on both fresh and weathered rock and sometimes reveals otherwise undetected specimens.

Where possible, counterpart pieces should be collected. These can include fragments of

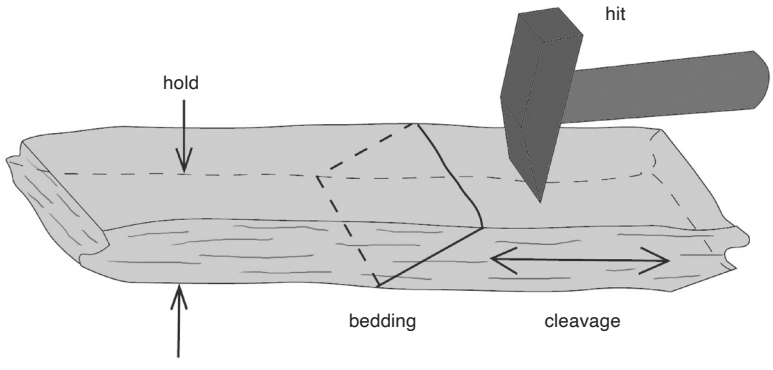


FIG. 94. Splitting tectonized rock slabs to gain fossil specimens (new).

the tubarium material on both parts, as well as molds. Material in friable shales should be particularly protected from abrasion of the surface. Wrapping is best done using pliable paper, such as newspaper or paper towels. Packages of specimens can be held together using tape and put into bags that are labeled with indelible pens. The orientation of material may be recorded; for example, where there appears to be an alignment of specimens. Bulk material, collected for subsequent splitting or acid digestion, is usually more robust. If appropriate, the geologic sections from which specimens are collected should be carefully logged. Both local and national rules on collecting should be obeyed and appropriate permissions obtained to access private property and other sites.

Splitting shale samples with a bladed hammer or with the help of a chisel is usually easily achieved. In tectonized areas, however, it can be difficult to split the rock along bedding rather than cleavage planes. After extracting a piece of rock, one needs to identify a bedding plane going through it, which may have graptolites on it. A good technique would be to hold the rock in one hand, with the bedding plane dipping toward the hand (Fig. 94) and hit the other end of the rock with the chisel end of a hammer, with the chisel held parallel to the bedding (PALMER & RICKARDS, 1991, p. 61).

The immediate marking or labeling of the rock slabs collected is very important. In the past, much care was exercised and scientists labeled each individual slab with the name of the locality and a mark to recognize the important fossil specimens (Fig. 95). Proper labeling is often neglected, and samples are sometimes just placed in boxes with paper notes. Misplacement of these samples in the wrong boxes can easily go unnoticed and may lead to misinterpretations. In Germany, many samples were rendered useless during World War II, when samples and labels were separated and partly lost, leaving the curated material without essential locality data.

PHYSICAL PREPARATION OF GRAPTOLITES

Developing is the term given to the physical excavation of graptolites by removing rock matrix that overlies and obscures the fossil. Such work is not always necessary. If graptolite-bearing rocks split cleanly along the bedding, the graptolites (particularly when flattened in fine-grained and well-laminated shales) can emerge more or less entirely visible, and no further work is needed. However, when graptolites occur in more massive lithologies or, particularly, in tectonically cleaved rocks that do not split easily along the bedding, then all that may initially be seen is the fractured end of a graptolite that seems to disappear into the rock (Fig. 97.1, Fig. 97.5). In such cases, a good deal of work must follow to reveal the remainder of the fossil.



Fig. 95. Labeled fossil slab, with specimen of *Demirastrites urceolus* (Richter, 1853), NMG 10015; labels indicate the locality (14. Mittelsilur Raitzhain/Ronneburg) and identification (*Demirastrites urceolus* Richter) of specimen (marked with red arrow) on upper side (*1*) of slab, as well as its scientific value (Original Exemplar) on back side (*2*) of slab, indicating that the specimen was illustrated in a scientific publication (Eisel, 1912, pl. 2,25).

The typical implement used to develop these fossils is a strong needle mounted in a handle such as a pin vice (available from some hardware stores) or an engineer's scribe. A typical sewing needle is usually too flexible to be effective. An old-fashioned steel gramophone needle (admittedly hard to find) or something similar is nearer to the ideal. The needle point is best kept very sharp (using an emery stick), though some workers also shape them into tiny, very sharp chisel ends. One may also use a small mechanical drill with a grinding wheel or an electric engraver (vibro-tool)—particularly for graptolites encased in very hard rock such as chert (although the approach here is a little different to that described below).

Some workers prefer to use a scalpel or a razor blade for preparation. A scalpel is best, because it is easier to handle than a razor blade that has to be mounted for this purpose. These tools work well for softer rocks, such as shales that are not overly tectonized or thermally altered. Very precise excavation work can be done with a scalpel, and even larger specimens are easily and cleanly prepared.

Preparation should invariably be carefully done while using a binocular microscope under good light to follow the work exactly. The specimen should be comfortably and firmly held in place, either simply by hand or with the help of wooden blocks or small sandbags.

Many graptolites are far more delicate than the enclosing rock, although this varies, depending on the nature of the rock and the type of preservation of the graptolite (e.g., a pyrite-filled, weathered, flattened film of organic material). The technique, however, remains essentially the same in all cases (Fig. 96). Where the rock matrix cover is thin, the needle is simply pressed down—firmly but carefully—vertically into the rock above, or just adjacent to, the graptolite; scraping laterally is not recommended. This should

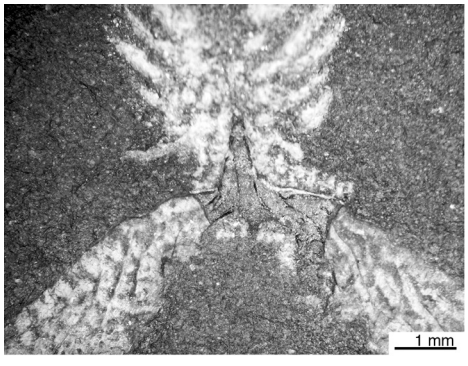


Fig. 96. *Baltograptus jacksoni* Rushton, 2011, holotype, BGS Ht 1260a; proximal end excavated from rock matrix with the help of a preparation needle; proximal end with preserved fusellum (dark gray), distal stipes preserved as imprint outlined with orange-colored pressure shadow minerals. Color image available in *Treatise Online* 65.

free a small flake of matrix from the graptolite, exploiting the plane of weakness that almost always exists between graptolite and matrix. One then works progressively along the graptolite, theca by theca (Fig. 96). If the rock matrix above the graptolite is thick, then one can more quickly excavate a small quarry-like hollow area above the graptolite before proceeding more carefully to break through its floor to the graptolite beneath. Careful work is slow, with many breaks to blow or wash away (using alcohol) the dust and rock chips produced from the graptolite; excavating a single graptolite may take a couple of hours or more.

Accidents do happen and many museum specimens, including type specimens, have all too obviously been severely damaged by hasty and careless excavation; it is all too easy to push the needle through the rock into the graptolite itself. Even in these instances where the fossil is accidentally damaged, the organic material of the graptolite almost invariably breaks away, leaving an impression or a pyrite internal cast (that is still taxonomically useful) beneath. Graptolites are often coated with pale phyllosilicates, commonly regarded as pressure shadow minerals formed during the tectonic deformation of the surrounding rocks (Underwood, 1992). One may aim to retain this coating (for example, in the case of flattened, white graptolites on black shale, this essentially represents the graptolite itself) or remove it (as in the case of the so-called chlorite sheath around pyritic Welsh graptolites, although the surface of this coating typically mimics the external outline of the graptolite).

Practice is essential to graptolite preparation, and best done on spare graptolite fragments. Repairs are sometimes possible. A fragment of an accidentally broken graptolite may be put back in place with a drop of glue, carefully applied from the tip of a fine brush or needle (for this, it is best to use water-soluble glue, strongly diluted with water to make it very runny). However, it may be better to keep specimens flaked off a slab in a separate container (glass bottle, etc.) in glycerin or dry on a slide, so they can be viewed from both sides (Fig. 97.3–97.4).

One can almost never entirely free the graptolite from its matrix—and should not try. The idea is to expose as much of the graptolite as possible, and as needed for identification of relevant characters, while leaving it firmly bound into the rock slab. The needle technique works for most graptolites and is mostly done dry, though occasionally it may be best done under alcohol, which necessitates frequent washing of the specimen with the same fluid.

Mechanical drills are best used on very hard rocks, too tough to yield to pressure from a hand-held mounted needle. These drills require care, as it is more difficult to have the same fine control as in the hand-held excavation. It is important to use ear protection, as most such drills are painfully loud. Typically, the most effective drill bit is the sharpest and finest one, which is used to slowly excavate through enclosing matrix, with special care at the interface with the graptolite (at which point, it may be advisable to revert to using the hand-held mounted needle).

Although friable material has often been fixed by varnishing the surface, varnish is difficult to remove, may darken, and invariably cracks with age, so this method is not recommended. An alternative is gum tragacanth. Another material, which can be removed using acetone, is an ethyl methacrylate copolymer, Paraloid/Acraloid B72, diluted to a 20% w/v concentration. Removing specimens that are in the state of separating from the shale surface (Fig. 97.2) is recommended, and they can be kept in separate bottles or on slides. In these instances, latex casts can be taken from the imprint left in the shale if the shale is hard enough. A small glass bottle can be used to keep the separated specimens in glycerin, as it prevents them from being broken on transport. Loose, shifting specimens on slides may easily be damaged, as evidenced by the isolated specimens in the Holm collection, Naturhistoriska Riksmuseet

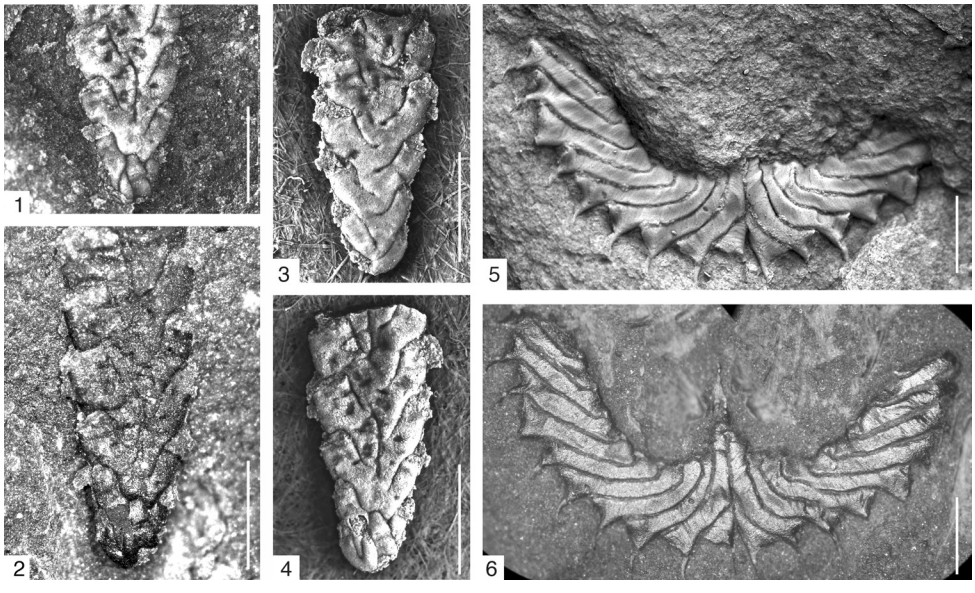


FIG. 97. Preparation of graptolites; specimens from the Lerhamn and Krapperup drill cores of Scania, Sweden. *1–4, Skanegraptus janus* MALETZ, 2011b, LO 11196T, holotype (Maletz, 2011b); *1,* unprepared specimen, coated for photography; *2,* prepared specimen becoming loosened on slab (see shadow on lower left side); *3–4,* specimen separated from slab and coated for photography to show reverse (*3*) and obverse (*4*) views of the same individual; *5–6, Arienigraptus geniculatus* (SKEVINGTON, 1965), LO 10601t; *5,* unprepared, coated specimen (new); *6,* prepared, uncoated specimen (Maletz & Ahlberg, 2011a, fig. 6L). All scale bars, 1 mm.

(Natural History Museum) in Stockholm, Sweden. Many weathered slabs with graptolites from Victoria, Australia, have been completely destroyed by covering the specimens with varnish, which later cracked and started to flake off, as the shale is very soft and deeply weathered.

Serial sectioning (cutting original specimens into very thin slices) has long been used to reconstruct the internal structure of isolated three-dimensional material. Pioneered during the nineteenth century by HOLM (1890, 1895) and WIMAN (1895, 1897a, 1897b, 1901), it was used to great effect during the twentieth century by BULMAN (1944–1947) and KOZŁOWSKI (1949). HOLM used paraffin wax, and BULMAN used collodion and paraffin wax. However, a low-viscosity epoxy resin, such as that used to embed material for TEM sectioning, is a better material. The serial sections are now commonly reasembled using computer programs. Although sectioning has, to some extent, been superseded by SEM examination of isolated specimens, it is still a useful, if time-consuming, technique (see DUMICAN & RICKARDS, 1985). Modern techniques include the use of computer programs to reconstruct the sections (SUTTON & others, 2001). However, a disadvantage of the method is the destruction of the original specimen, which can be avoided using CT scans, as was done by WANG and others (2020) for Upper Ordovician climacograptids.

TÖRNQUIST (1893, p. 2) described a simpler, but highly effective, method for the preparation of sections for graptolite specimens filled with pyrite in hard shales. He ground the slabs down on a slab of sandstone to the desired level and subsequently polished it. The results are beautiful sections of pyritic graptolites showing the internal features (Fig. 98). LOYDELL and MALETZ (2009) used a similar method to investigate the internal features of *Normalograptus scalaris* (HISINGER, 1837) (see Fig. 106.2, 106.3). Chemically isolated specimens were embedded in epoxy resin, ground down on one side, mounted

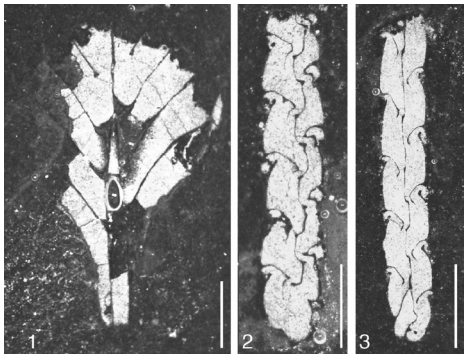


FIG. 98. Specimens from Tommarp, Scania, Sweden, preserved as polished sections on dark shale slabs; sections prepared and illustrated as drawings by TÖRNQUIST (1893). *1, Petalolithus palmeus* (BARRANDE, 1850), LO 1119t, obverse view (Törnquist, 1893, fig. 35); *2, Metaclimacograptus internexus* (TÖRNQUIST, 1890), LO 1111t, reverse view (Törnquist, 1893, fig. 27); *3, Metaclimacograptus internexus* (TÖRNQUIST, 1890), LO 1110t reverse view (Törnquist, 1893, fig. 26). Scale bars, 1 mm.

on a glass slide, and ground down from the other side to get sections of the specimens.

Natural molds of graptolites (Fig. 99.1, Fig. 99.3), commonly the result of pyrite oxidation or weathering, can be studied by making latex replicas to improve the visibility of important features (Fig. 99.2). These latex replicas are sometimes good enough to be examined by SEM. Because latex dries clear, a few drops of Indian Ink can be added to the latex before applying. This will produce a matt black peel that, after whitening, photographs well. The application of liquid latex must be preceded by wetting the slab. This lowers the surface tension of the latex and allows it to seep into every small surface feature to form a perfect cast without producing air bubbles.

Latex can also be used to clean weathered surface areas of shales and make graptolites more easily visible. A first latex cast can be used for cleaning of the shale surface, while a second one provides the useful casts of specimens.

In some instances, the latex (dyed black) slightly dyes the specimens, but not the surrounding shales, and enhances the contrast of the graptolite specimens. Conversely, it may dye the shale and not the smooth surface of the graptolite imprints. Thus, applying latex typically makes the specimens more easily visible on the shale surfaces.

Loss of paleontological specimens by pyrite oxidation is common in geological collections. It may be a serious problem for fossil collections that include pyritic specimens and considerable effort is necessary to preserve these (NEWMAN, 1998). Pyritic internal molds of graptolites often suffer from mineral decomposition and can easily be lost completely (BIRKER & KAYLOR, 1986). Pyritic specimens in shale should be kept in dry conditions; in the presence of oxygen they break down to ferrous sulfate ($FeSO_4$) and sulfur dioxide (SO_2). If water is present, sulfuric acid (H_2SO_4) is also produced, which can cause damage to labeling and storage containers. The most effective method of preventing rapid decay from pyrite oxidation is to store specimens within a moisture and oxygen barrier containing an oxygen scavenger. Further oxidation can be reduced or eliminated by storing specimens in an environment with a humidity level below 30%. Ammonium gas and ethanolamine thioglycollate treatments neutralize sulfuric acid and remove ferrous sulfate, and they are reportedly effective in partly or completely removing oxidation reaction products (SHINYA & BERGWALL, 2007). HUTT and RICKARDS (1967) suggested a transfer method to preserve pyritic graptolite specimens in polyester resin.

CHEMICAL ISOLATION OF GRAPTOLITES

Detailed information about the structure and development of graptolites is obtained almost entirely from specimens that have been isolated (dissolved) from their matrix and, in some cases, rendered more or less transparent by the use of various oxidizing agents (Fig. 100). The actual processes and reagents employed depend, of course, on the degree of carbonization of the fossil. Not only is it possible to isolate three-dimensionally

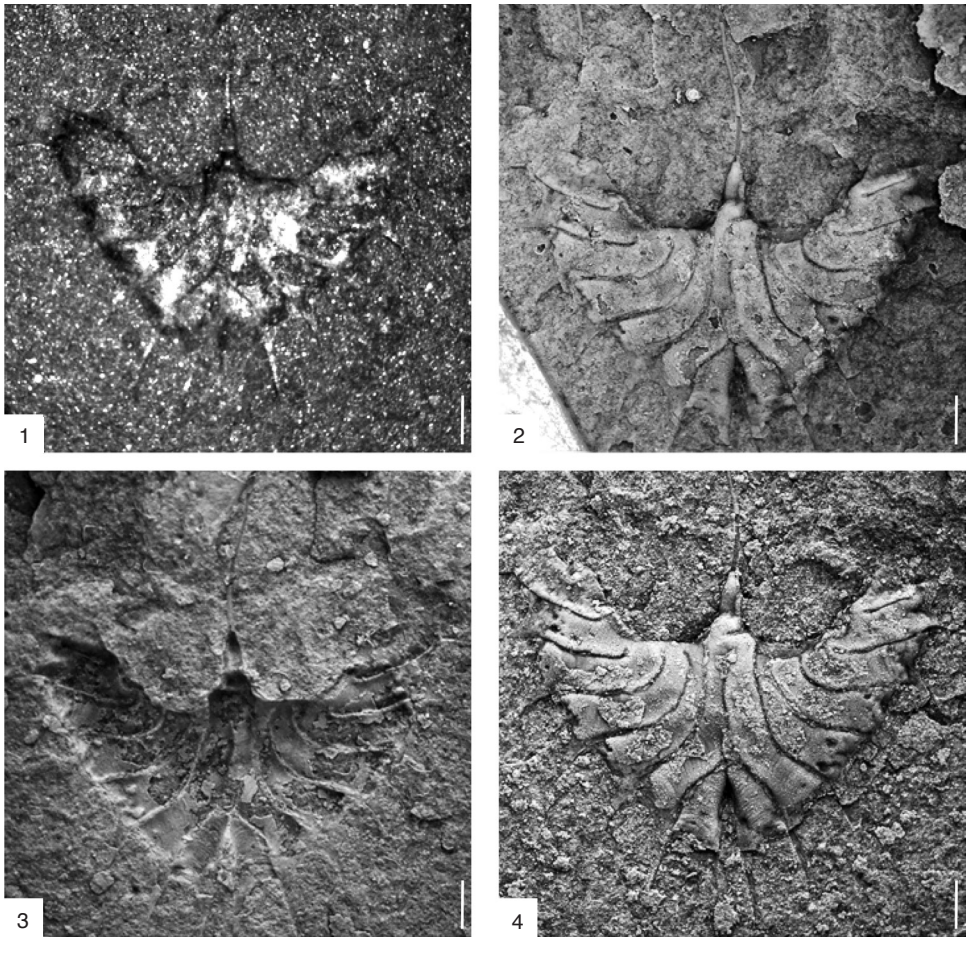


FIG. 99. *Arienigraptus zhejiangensis* YU & FANG, 1981a, Krapperup drillcore, 59.30–59.35 m, LO 12247t. *1,* mold of specimen; *2,* latex cast of mold; *3,* coated mold; *4,* counterpart, relief specimen for comparison. Specimens in *2–4* lightly coated with ammonium chloride to enhance visibility of features; scale bars, 1 mm (new).

preserved specimens, but also flattened ones, as, for example, from shales using hydrofluoric acid (HF); see, for example, ALBANI and others, 2001. Chemical isolation produces the best and most complete assemblages, allowing for recovery of small specimens and delicate forms not easily recognizable on rock surfaces. GÜMBEL (1878) first attempted the chemical isolation of graptolites, but HOLM (1890, 1895) deserves much credit for successfully isolating numerous graptolites and describing them in great detail. Pure limestone matrix containing graptolites can be readily dissolved with hydrochloric acid (HCl) or acetic acid (Fig. 100.1). For fragile material, acetic acid is preferable because of its more gentle action. Dolomite can only be dissolved using HCl, and the concentration should be adjusted so that effervescence is very gentle and is maintained by the repeated addition of drops of concentrated acid. If the concentration of acid becomes too dilute, there could be access to the container and a danger of fungal growth occurring and entangling with the specimens. This can be counteracted by adding thymol.

The physical preservation of the graptolite's organic material is an important factor.

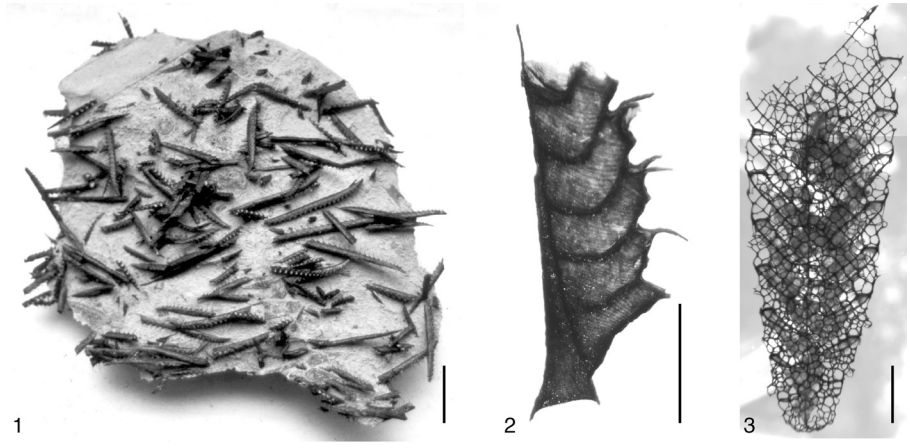


FIG. 100. Chemical isolation of graptolites. *1–2, Saetograptus leintwardinensis* (HOPKINSON in LAPWORTH, 1880a). *1,* numerous specimens partially isolated from limestone, glacial boulder, northern Germany, FGWG 125, scale bar, 10 mm (new); *2,* SMF 68 294, individual specimen from the sample, scale bar, 1 mm (Maletz, 1997d, fig. 4,*12*); *3, Retiolites geinitzianus* (BARRANDE, 1850), isolated specimen, SMF XXIV450, scale bar, 1 mm (Maletz, 2008, fig. 1a).

Some limestone material, otherwise seemingly suitable, should not be subjected to chemical isolation if the graptolite remains are too highly carbonized. Moreover, some graptolites are so brittle that they crumble to a powder when freed from matrix. It is often impossible to know this in advance, and a trial is invariably useful. Before examination by SEM, it is advisable to treat already isolated specimens with hydrofluoric acid (HF), which can remove any fine clay or siliceous material adhering to them. Some graptolite material, however, is surrounded by diagenetic silica and dissolution of this mineral growth will destroy the specimens, as the silica helps to keep the broken graptolite fragments in place (see MALETZ, 2009); in these instances, it is advisable to check whether the specimens show broken tubarium walls or are well preserved.

Impure limestone generally requires a double treatment, involving the solution of the calcareous matter first and then, after washing out all trace of HCl, the solution or disintegration of the arenaceous or argillaceous remainder with HF. Non-calcareous material, such as shale or chert, can be treated directly with HF. Repeated washing and decanting is necessary to remove all HF before the graptolite remains can be picked out with a pipette or a small brush under a low-power binocular microscope. Much of the fine mud can be removed by elutriation. Some workers wash the insoluble residue through one or a series of sieves, although this risks greater breakage of specimens.

JAROCHOWSKA and others (2013) described a new, acid-free method of extraction of graptolites and other fossils from clay-rich sediments. The surfactant Rewoquat® can be used to disintegrate samples and to isolate fossils from sediments with little damage. It is a very gentle method that can produce excellent results and even preserve features, such as the delicate membranes in retiolitids.

A bleaching agent can be used to render material more or less transparent (Fig 101.1, 101.3). Graptolites that have been dissolved out of calcareous rocks may contain bubbles of CO_2, which should be removed in a vacuum dessicator before further treatment. Clearing is most usually done in a watch-glass with potassium chlorate and concentrated nitric acid, though bleaching agents (e.g., eau de Javelle) have been used. The treatment time varies with the thickness of the fusellum and the degree of carbonization and can only be judged individually by

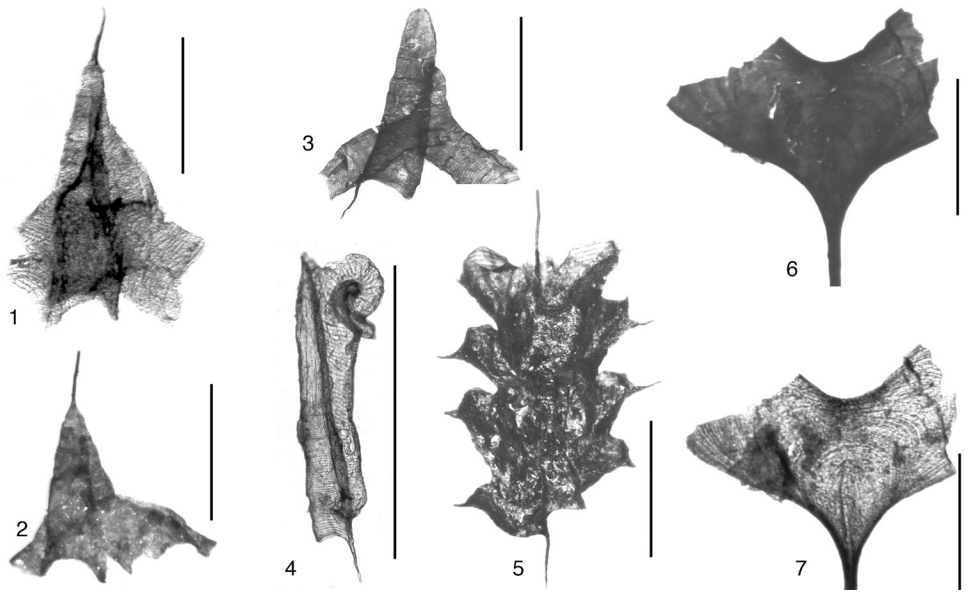


FIG. 101. Photography of isolated specimens (new). *1, Tetragraptus* sp., chemically bleached flattened specimen, showing some fusellar construction; *2, Tetragraptus* sp., unbleached, flattened, not showing fuselli; *3, Xiphograptus primus* MALETZ, 2010a, bleached, flattened specimen, showing well-preserved fuselli; *4, Streptograptus* sp., 3D specimen, IR-photo; *5, Oepikograptus bekkeri* (ÖPIK, 1927), isolated 3D specimen, fuselli visible on distal thecae, unbleached; *6–7, Archiclimacograptus decoratus* (HARRIS & THOMAS, 1935), nematularium, transmitted light photo (6) and IR-photo (7) of same specimen. All scale bars, 1 mm.

constant observation through a low-power binocular microscope. In general, the treatment cannot be prolonged much beyond 20–30 minutes without the specimens becoming too brittle to handle; however, some workers use a much lower concentration of bleaching agent and a correspondingly greater period of time. After bleaching, clove oil can be used to neutralize the acids. Quite a high proportion of material successfully dissolved from its matrix proves unsuitable for further treatment of this kind. The process of bleaching has now been largely superseded by Infrared (IR) photography (Fig. 101.4, Fig. 101.7). If IR photographs do not reveal details such as growth lines, bleaching will not help.

All chemical treatments should be carried out in controlled conditions, with due regard for safety. These activities should be done in appropriately ventilated spaces equipped with fume hoods; protective clothing and eye goggles should be worn; and all written safety instructions consulted and followed.

Long-term preservation of chemically isolated specimens is problematic, because the specimens are generally fragile and can easily break during handling if kept dry. Various methods have been used in the past to ensure their preservation. Robust specimens can be mounted dry, because surface features are more easily seen than when mounted in a relatively high-refractive index medium. Gerhard HOLM mounted specimens between glass slides so they could be observed from both sides. He left enough space between the two slides so the specimens were not damaged (Fig. 102.1). Specimens can be affixed between two glass slides with a minute drop of gum Arabic. These specimens are generally in good shape, even after more than 100 years of museum storage. Roland SKOGLUND used a similar method for flattened graptolite specimens

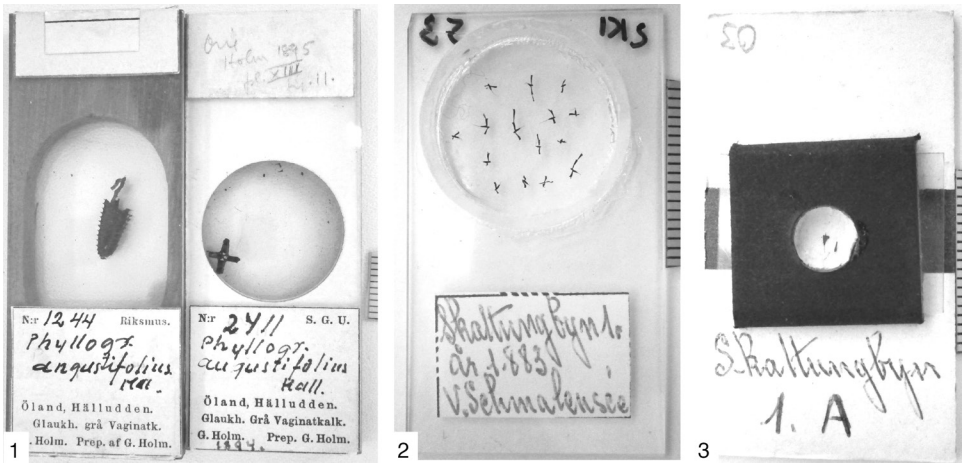


FIG. 102. Isolated and dry-mounted graptolites. *1, Pseudophyllograptus angustifolius* (HALL, 1865), NRM Holm Nr. 1244 and SGU Holm 2411, both specimens mounted by Gerhard HOLM (new, possibly originals for HOLM, 1895, pl. 13–14); *2, Acrograptus* sp. specimens, SGU-SK 1.23, originally mounted by Roland Skoglund in liquid (alcohol or glycerin), which has now evaporated; *3, Pseudophyllograptus* sp., juvenile, SGU-SK 1A.03, mounted dry by Roland SKOGLUND (Skoglund material is unpublished).

from Dalarna. He mounted individual dry specimens on cardboard, covered with a thin glass slide (Fig. 102.3). More problematic is the preservation of his numerous specimens in small containers glued on glass slides (Fig. 102.2). As the liquid in the containers dried out over time, the specimens started to break apart and acquire considerable damage (see also MALETZ & SLOVACEK, 2013, fig. 1).

Transparent specimens may be mounted in Canada balsam. Euparal is an alternative to Canada balsam, which has the advantage of not requiring perfect desiccation in absolute alcohol, thus eliminating processes in which damage to the specimen may occur.

Most specialists agree that graptolites are best kept in glycerin (glycerol) for long-term storage, which allows the specimens to be moved and viewed from all sides. They can also be removed from the glycerin and washed with warm water prior to SEM photography of the dry specimens; thorough removal of the glycerin is necessary, as surface features may be covered by residual fluid. However, ALLINGTON (2006) provided a warning and suggests the use of silicone oil instead.

Graptolites in the Natural History Museum (formerly the British Museum [Natural History]) that were stored in glycerin to prevent pyrite decay apparently allowed pyrite oxidation and deterioration of the material. The containers with graptolite specimens should invariably be tightly closed to prevent absorption of water from the atmosphere by the hygroscopic medium.

Other liquids, such as alcohol, formalin and thymol, can be used for long-term storage. However, long-term preservation in alcohol requires special care because the alcohol needs to be refilled from time to time due to evaporation, even in the most tightly sealed containers.

Special care is also necessary to preserve the delicate and fragile graptolite specimens on SEM stubs. These have to be kept in a dry place and need to be protected from dust. Plastic boxes in which the SEM stubs are mounted securely is one option.

ILLUSTRATIONS

During the nineteenth century, graptolites, like other groups of fossils, were originally illustrated with drawings or paintings. Even with the advent of light photography, there was no major change to illustration methods—the nature of preservation of most

material did not lend itself to photography. As a result, freehand drawing or painting has continued to be a standard method of illustration to the present day.

The illustrations by the Scandinavian authors HOLM and WIMAN and the British authors ELLES, WOOD, and BULMAN mark the high point in freehand graptolite illustration. In HOLM's publications, the illustrations were by Georg Gideon LILJEVALL (1848–1928) (Fig. 103.1). However, such standards are impossible to achieve for most people, and many papers are illustrated with outline drawings, often with use of a camera lucida.

Illustrations should be at as large a scale as possible to show all necessary information. Overall illustrations of most graptolites should be at a smaller scale, whereas details should be shown at greater magnifications. Early scientific works typically have small illustrations at original size that are inadequate in detail for modern use, considering the amount of available detail in many specimens that is necessary for modern identifications (e.g., LAPWORTH, 1876c; ELLES & WOOD, 1901–1918). However, even some earlier authors (e.g., WIMAN, 1893a) provided incredible insight from drawings of highly magnified specimens (Fig. 103.4–103.5). The drawings by Ethel Wood (in ELLES & WOOD, 1901–1918), finely reproduced on the plates (at original scale), remain useful today to understand colony shapes, though they often lack the detail necessary for a proper taxonomic identification.

DRAWINGS

Most non-isolated and matrix-bound graptolites can be drawn using a binocular microscope with a camera lucida attachment, essentially a drawing mirror. The image of the specimen under the microscope is superimposed by a split screen onto a sheet of paper on the side under a mirror, and the fossil outline can be traced directly (see Fig. 104). The results obtained can give a clearer and cleaner image of the graptolite than can be obtained even by careful close-up photography. This is because the photograph (if not heavily retouched) will have every visible feature, petrological as well as paleontological, regardless of its taxonomic significance. In drawing a graptolite, the illustrator should focus on the morphology of the graptolite, although it is useful to include such features as fractures and compactional or tectonic crumples that are deemed significant. Thus, the drawing is an interpretation, albeit one that is tightly constrained by the physical evidence and dimensionally accurate.

It is best to draw at as high a magnification as is practically possible—considerably higher than is intended for the final published figure. To start, one needs to balance the lighting on both the graptolite and on the sheet of paper (the latter provided by a separate lamp), so that both graptolite and paper (and the moving pencil point) can be clearly seen. For some makes of camera lucida, there is some distortion near the edge of the field of view; therefore, it is best to work in the middle three-fourths or so of the field of view.

A scale must be added to each drawing. This can be done at the time of drawing by placing a scale (e.g., a ruler with millimeter divisions) against the graptolite and then drawing a few of the millimeter divisions using the camera lucida.

For final publication, most illustrators (and publishers) now use computer programs that can assist a rendering of the original pencil or ink drawing by digital means. Digital drawings can be made from a photograph that itself might be unusable. BULMAN's early line drawings were produced from photos (STRACHAN & others, 1991, p. 66), a method still used by some workers. The lines were inked on a highly magnified photo and the photo was subsequently bleached. That process can now be easily achieved digitally.

VISIBLE LIGHT, ULTRAVIOLET, AND INFRA-RED PHOTOGRAPHY

Flattened specimens can be very difficult to photograph, unless there is a good

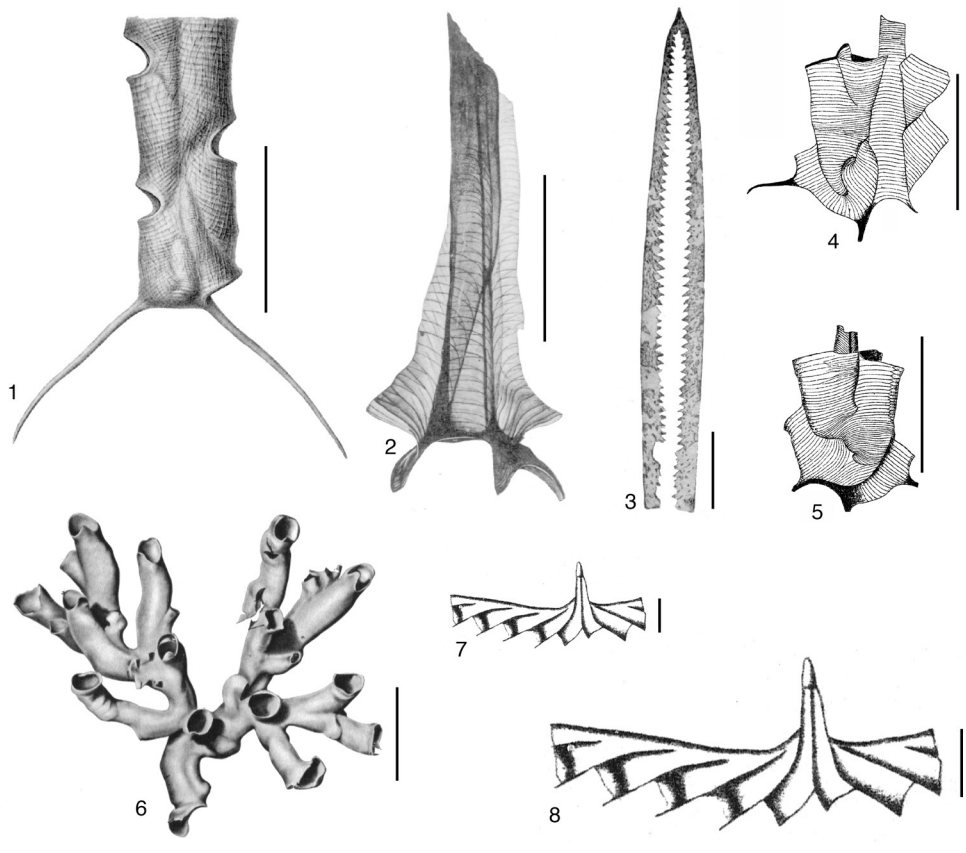


FIG. 103. Illustrations of hand-drawn graptolites with fine detail. *1, Diplacanthograptus spiniferus* (RUEDEMANN, 1912), drawn by G. Liljevall, note even the presence of cortical bandages on the surface of the thecae is drawn, scale bar, 1 mm (Bulman, 1932a, pl. i,*7*); *2, Corynoides* cf. *calicularis* NICHOLSON, 1867a, drawn by O. M. B. Bulman, scale bar, 1 mm (Bulman, 1945 in 1945–1949, pl. *ii*,*12*); *3, Didymograptus murchisoni* BECK, drawn by E. M. R. Wood, scale bar, 10 mm (Elles & Wood, 1901, pl. iii,*1f*); *4–5, Rectograptus gracilis* (ROEMER, 1861), line drawings of specimen showing growth lines and proximal development in all available detail in obverse (*4*) and reverse (*5*) views (identified as *Diplograptus* sp. in WIMAN, 1893a, fig. 7), corrected from WIMAN's (1893a, p. 104) originals, as he stated that the plate was accidentally prepared as a mirror image of the original drawings, scale bars for *4* and *5,* 1 mm (adapted from Wiman, 1893a, fig. 7); *6, Rhiphidodendrum samsonowiczi* KOZŁOWSKI, 1949, scale bar, 1 mm (Kozłowski, 1949, pl. 10,*1*); *7–8, Expansograptus latus constrictus* (HALL, 1865), originally magnified ×4.5, even showing the differentiation of the prosicula in a relief specimen in black shale, scale bars, 1 mm (Törnquist, 1901, pl. 2,*15*).

contrast between specimen and matrix. Flooding by alcohol, commonly isopropyl alcohol or industrial methylated spirits, can increase contrast, and also reduce unwanted reflections, although it evaporates quickly. An alternative is a mixture of 50% alcohol and 50% glycerin (Loven's reagent). This can be washed off using alcohol. Wetting the surface can improve the contrast between matrix and graptolite, but it may cause the clay minerals to swell and the organic material of the graptolite to flake off.

For specimens in relief, including latex peels and even isolated pyritic specimens, the material can be whitened using either MgO ribbon burning or ammonium chloride, applied as a sublimate. This method improves the visibility of structural details in relief specimens (Fig. 105). Great care must be used for the process.

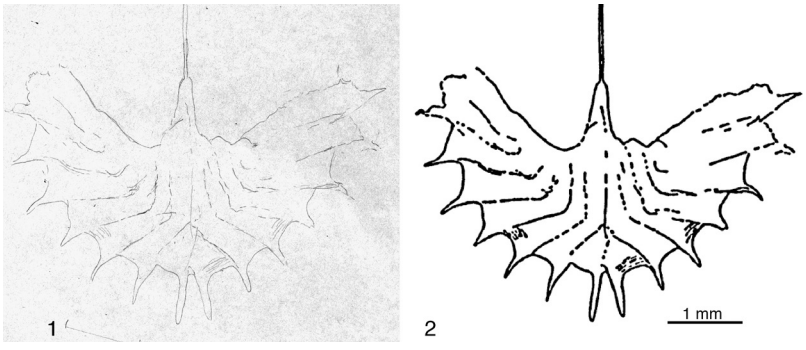


FIG. 104. Example of camera lucida pencil drawing (*1*) and ink drawing (*2*) of *Arienigraptus angulatus* (GEH & YIN in MU & others, 1962), reverse view, from *Levisograptus dentatus* Biozone, Côte Fréchette, Québec, Canada, GSC 102702a (new).

The documentation of internal details of the graptolite colonies has always been difficult, and a number of methods have been used, including various measures of preparation and photographic experimentations (Fig. 105). Good results are achieved by using infrared (IR) photography of chemically isolated graptolites. Infrared photography was explored by EISENACK (1935) to investigate graptolites, though it presented too many difficulties to be a successful method at that time; it was reintroduced by MELCHIN and ANDERSON (1988) using a modern IR-video camera (Fig. 105.1). Infrared video microscopy (IVM) uses a relatively inexpensive video camera that is sensitive through the visible and near IR range, up to wavelengths of 1300 nm. This camera can be connected to a normal biological or petrographic microscope. The best results are obtained when visible light is filtered with a 1000 nm, long-pass filter, although the crossed polarizers on a petrographic microscope can serve a similar function. The images obtained can be viewed on a video monitor, printed by direct connection to a video printer or electronically stored using a computer video image capture system. The stored images can then be analyzed using image analysis software.

Provided the specimens are not of high thermal alteration or very thickly covered in cortical tissues, and are not covered or infilled with IR-opaque mineral material, the resulting images reveal surface morphology, fusellar banding (and occasionally cortical bandages), as well as all internal walls and structures (Fig. 106.1). Optimum image quality requires that the specimens be immersed in a very high refractive index liquid, preferably 1.76, the refractive index of the graptolite fusellum. The best visualization of internal structures can be achieved using stereo-pairs of prints of the video images. These can be obtained

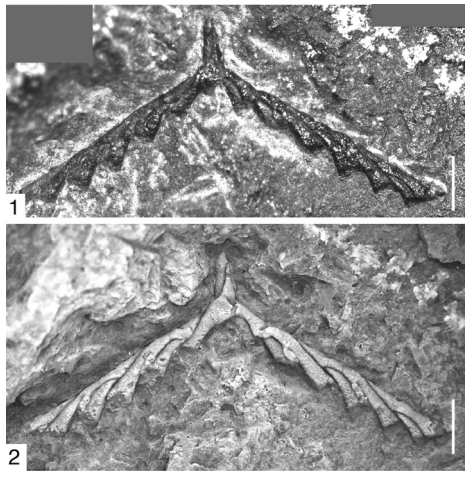


FIG. 105. *Kiaerograptus* (?) *supremus* LINDHOLM, 1991, LO 5970T, holotype; scale bars, 1 mm. *1,* original specimen showing traces of preparation on rock (light color); *2,* same specimen coated with ammonium chloride for photography, showing the tubarium construction more clearly.

by using a universal stage and tilting the specimens approximately 8° between prints. Stereo-pairs are useful for relief material, but flattened specimens can also be examined with IR light and provide useful data (Maletz, 2010a). Cross-polarized light has recently been used as an imaging technique for graptolites showing low contrast on shale surfaces (Muir, McCobb, & Zhang, 2021).

With the advent of digital photography and the use of computers, it has become much simpler to improve the quality of images. Contrast can even be improved selectively, for example in the darker areas of the image. Unwanted backgrounds can be removed electronically, instead of physically. This is particularly effective for SEM photographs. Tectonic distortion can be removed easily using an appropriate computer program.

SCANNING ELECTRON MICROSCOPY

Scanning electron microscopy (SEM) has become, since the early 1970s, a widely used method for illustrating complete tubaria and revealing ultrastructure in three dimensions (see examples, Fig. 107). It is applicable to isolated material and to fossils on rock surfaces where there is relief present or where the graptolite wall material is still preserved. SEM can even be used on artificial molds or casts. The SEM reveals only surface features (Fig. 107), not internal details, unless the specimens are broken open. SEM photography is especially important to show the delicate and complex meshwork of the retiolitids (Fig. 107.3).

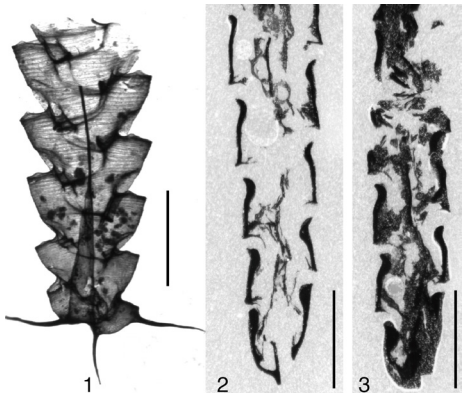


Fig. 106. Documenting internal details of graptolite colonies. *1, Rectograptus intermedius* (Elles & Wood, 1907), USNM 542831, infrared photo of relief specimen with internal structures (Štorch & others, 2011, fig. 17C); *2–3, Normalograptus scalaris* (Hisinger, 1837), showing internal thickenings close to the thecal apertures in sectioned specimens (Loydell & Maletz, 2009, fig. 2). All scale bars, 1 mm.

In preparation for SEM photography, isolated material, which may be stored in glycerin, water and formalin, or dilute acid, should first be transferred to a small container and then washed in several changes of distilled water. This is best done using a pipette to draw off the liquid and then add distilled water. After washing, the specimens can either be directly placed on the stub or coated in liquids, either pure alcohol—industrial methylated spirits (IMS) is satisfactory—or acetone before placing on the stub. Because these liquids have a lower surface tension than water, they may cause less damage to the specimens when being transferred to the stub. If the specimens are small, they can be lifted and transferred in a pipette: it may be possible to manipulate a specimen on the stub surface, before the liquid evaporates.

A fine artist's brush may also be used to lift a specimen. The specimen will adhere to the brush while the liquid evaporates (holding it above an electric bulb will speed up evaporation), and it can then be gently lowered onto the stub. For very large specimens, it is possible to submerge the stub in the container of liquid and specimen, manipulate the specimen onto the stub with a brush, and then pipette off the liquid until the stub emerges from it.

Specimens may also be completely dried before mounting on SEM stubs. Specimens originally preserved in glycerin can be cleaned using warm water and then dried. A small brush with very few hairs can be used to transfer the specimens to an SEM stub. Rubbing the brush slightly on one's skin provides enough moisture for the specimen to stick to the brush.

A variety of adhesive surfaces can be used to attach the specimens to the stub. Double-sided tape is clean and efficient, and can be cut from a roll. However, it can release vapor under vacuum, which may affect the working of the instrument. Alternatively, circular patches of tape are specially made to apply to the stubs. Other liquid glues can be used, such as fingernail polish, spread on the stub and allowed to become tacky before mounting the specimens. In this case, check that the glue used will not react with any liquid remaining on, or in, the specimens.

The standard stub for most instruments has a diameter of about 12 mm, and this will suffice for much material. Indeed, a great number of siculae can be attached to a single stub. If the specimen is larger, bigger stubs can be bought or made using a lathe. An alternative method is to glue a piece of thin sheet metal, such as brass or nickel silver, to a standard stub, using an epoxy glue. Conductive paint should be applied to the underside of the metal to ensure good electrical contact with the stub.

To view a specimen from as wide a range of directions as possible, it may be possible to mount it on a wire, which is glued to the stub. It is not possible to use double-sided tape, but the wire can be smeared with a suitable glue, and the specimen stuck to it.

Material on rock can easily be glued to a stub using epoxy resin, after trimming to size. Bates (1996) used a pair of carpenter's nail pincers to break up pieces of the Viola Limestone from Oklahoma, USA, fracturing it along bedding planes to give counterpart specimens, and also trimming the pieces to size.

Material that was fossilized in anaerobic conditions is commonly infilled with and/or coated in pyrite. In these conditions, the actual wall material of the tubarium may still be present, showing up as a thin brown-to-black coating on the surface of the pyrite. Where the tubarium wall is not present, the pyrite surface may bear the extremely fine mold of the internal surface, including that of the cortical fibrils.

For most work, specimens will be coated, usually with a gold-palladium target in the coater. Occasionally (e.g., where it desired to remove the specimen from a stub, and return it for storage in glycerin), it may be better to view the specimen uncoated, with a low accelerating voltage. Some field emission microscopes can also be used with uncoated material.

The SEM can be used to take stereopair photographs, particularly useful in illustrating retiolite graptoloids (e.g., Bates, 1996; Lenz & Kozłowska, 2006). The specimen can be rotated by about 5° between photographs. The resulting stereopair is

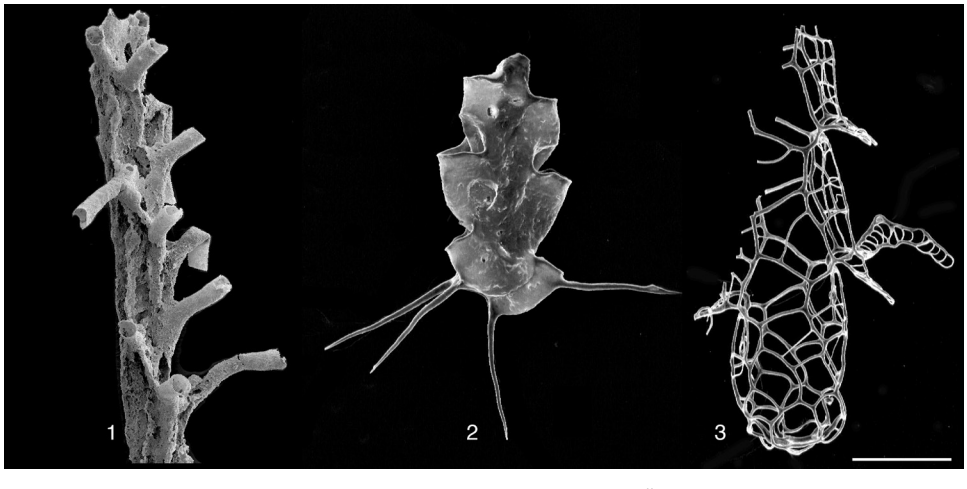


Fig. 107. SEM photos of specimens. *1, Acanthograptus* sp. in obverse view. Öland, Sweden, LO 11412t (new); *2, Rectograptus* sp., Viola Limestone, SMF 75824 (new); *3, Neogothograptus ornatus* Maletz, 2008, glacial boulder, northern Germany, MB.G. 1079.4; scale bar (applies to all), 600 µm (Maletz, 2008, fig. 10M).

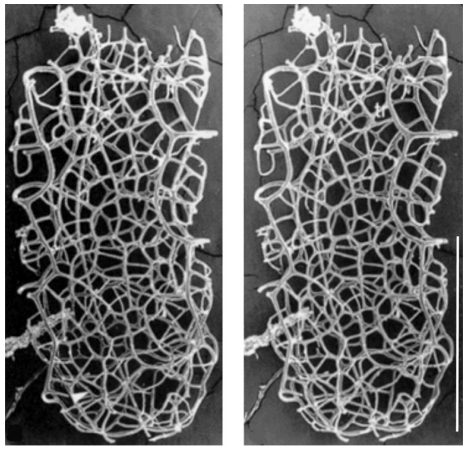


FIG. 108. Stereopair photographs of retiolitid *Sagenograptoides arctos* (LENZ & KOZŁOWSKA-DAWIDZIUK, 2001), scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2001, pl. 8). Color image available in *Treatise Online* 65.

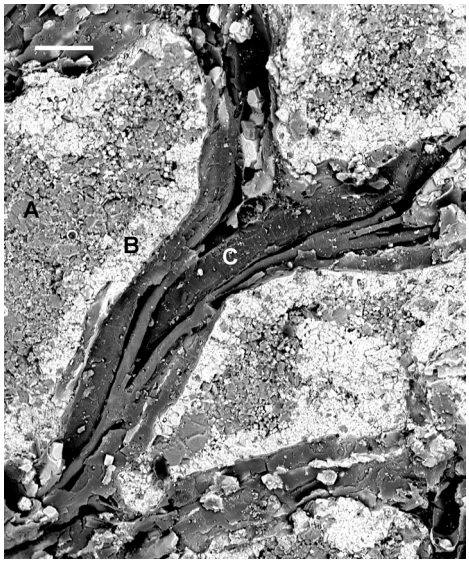


FIG. 109. SEM back-scatter image of *Desmograptus micronematodes* (SPENCER, 1884), FMNH PE60371; *A,* limestone matrix, *B,* pyrite coating of the tubarium, *C,* graptolite; scale bar, 100 µm (Saunders & others, 2009, fig. 3).

normally illustrated using two small prints, with a separation of 60 mm between the images (Fig. 108). It can be viewed through a pocket stereoscope. An alternative method of reproduction uses anaglyph images, typically red and green for the left and right images, the printed image being viewed with green and red spectacles (see color image in *Treatise Online* 65, p. 16, fig. 15.1).

Although the SEM normally shows surface detail, the electron beam does penetrate beneath the surface: the amount of penetration depends on the nature of the specimen, the angle of tilt in the microscope, and the accelerating voltage. In particular, if the fusellum is particularly thin, it may be possible to see such features as fuselli, bandages and even stolons (e.g., BATES & KIRK, 1997, fig. 99a,d).

To obtain SEM images at a higher power than normal, specimens can be examined using a transmission electron microscope in scanning mode. Material, however, must be very small (about 4 mm wide by 3 mm thick by 13 mm long), and it can be tilted to about 60°.

If the back-scattered electron signal is used, an image with mean atomic number contrast is produced. Michael STEINER (described in MALETZ, STEINER, & FATKA, 2005) first used the method for graptolites. MALETZ, STEINER, and FATKA (2005, p. 78) stated that the method worked best with wall thicknesses of less than 5 µm. Thicker wall material did not produce sufficient information and fuselli were not visible. ZHANG and ERDTMANN (2004a) have also applied the back-scattered electron microscopy (BSEM) technique to study graptolites. BSEM images illustrate both the chemical compositional differences on the surface layer and the surface morphology of the sample. On the BSEM pictures of *Psigraptus jacksoni* RICKARDS & STRAIT, 1984 (ZHANG & ERDTMANN, 2004a, fig. 11), the carbonized fuselli are marked as dark lines, whereas the rock matrix is brighter because of the dominance of silicon and heavy elements. The surface morphology of those areas, where the fusellum has broken off and only films have remained, has also been illustrated in the BSEM images. The method also shows the composition of the surrounding sediment and of the pyrite growth (Fig. 109).

TRANSMISSION ELECTRON MICROSCOPY

The use of TEM started with the work of Wetzel (1958) and Kraatz (1964, 1968), though the seminal work in this field comprises the two monographs by Urbanek and Towe (1974, 1975). Standard TEM techniques have been described in a number of papers and books in the biological field (e.g., Hunter, 1993) and can be readily applied to graptolites (Fig. 110). However, graptolite wall material is harder than most biological tissue, so that a diamond knife is essential for good results. In general, a high degree of skill is needed in cutting the sections.

Isolated material is needed for production of sections, using the techniques described above. Unbleached specimens are embedded in a resin such as Durcupan. Blocks are then sectioned using an ultramicrotome provided with a diamond knife. Sections of ~900 Å are suitable. They are then placed on copper grids, which have been coated with a film of paralodion and carbon.

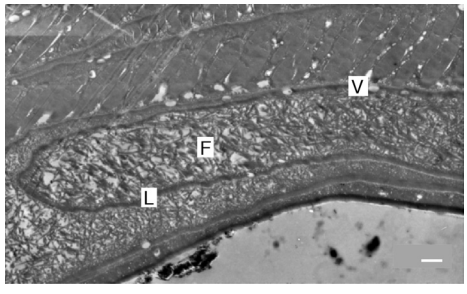


Fig. 110. ?*Dendrograptus* sp., TEM longitudinal section of the closure of a fusellus; parallel fibrils *(F)* of the cortical fabric of the lamella bounding the fusellus are seen as elliptical cross sections that are thicker than the fusellar fibrils but thinner than those of the cortex itself; *L,* basal granular fabric; *V,* vesicles; scale bar, 1 µm (adapted from Bates, 1997, pl. 5).

The TEM work provides ultrastructural details of the tubarium material, showing the development of fibrils in the fusellum and cortex. It offers information on very fine details and helps to compare fossil tubarium material with the tubaria of extant pterobranch specimens.

GLOSSARY OF THE HEMICHORDATA

Jörg Maletz, Denis E. B. Bates, Edsel D. Brussa, Roger A. Cooper, Alfred C. Lenz, John F. Riva, Blanca A. Toro, and Yuandong Zhang

PREFACE

The terminology of the Hemichordata used herein differs considerably from the terminology in the previous versions of the two Graptolite *Treatises* (Bulman, 1955, 1970), which were focused entirely on the fossil members of the Graptolithina and the few known tube-bearing extant and extinct Pterobranchia. Both classes were regarded as independent groups of the Hemichordata, but they are now included as a single taxon, the Pterobranchia, with the Graptolithina and the Cephalodiscida as two subclades (Mitchell & others, 2013). A number of terms are changed herein due to better understanding of the construction of the graptolite tubarium and the phylogenetic relationships within the Pterobranchia, the main group of fossilized hemichordates. These changes reflect an attempt to homogenize the terminology of these previously separated groups.

The term tubarium, for example, is reintroduced to the pterobranch terminology to describe the organic housing or domicile of all Pterobranchia, instead of using the term rhabdosome for the fossil Pterobranchia (Graptolithina in Bulman, 1955, 1970) and the coenecium for the extant members (Pterobranchia *sensu* Bulman, 1955, 1970). Lankester (1884) initially introduced the term tubarium to describe the housing of the extant Pterobranchia, as he considered the terms coenecium or zooecium inappropriate because they described the housing construction of bryozoans, to which the Pterobranchia were referred initially. Tubarium describes the housing construction of extant and extinct Pterobranchia more independently; it also describes it more precisely as being formed by glandular secretions and can easily be used for all members. It is therefore extended herein to include the homologous glandular constructions of the domiciles of fossil graptolite taxa, as was already suggested by Urbanek (1994, p. 324).

Other terms, such as the periderm, have been eliminated due to constructional considerations. The term periderm, introduced by Törnquist (1894), suggests a dermal construction of the tubarium, which is now known to be incorrect. The tubarium is formed from glands on the head shield of the zooids and is not a dermal construction as is the coenecium of a bryozoan. The tubarium can perhaps be compared with the formation of a hornet's nest, though a hornet's nest is largely constructed with foreign material. A comparison with hydrozoan colonies also falls short, as these are often covered by an organic exoskeleton, the perisarc (also identified as the periderm in Hyman, 1940, p. 400), which is secreted by the epidermis of the advancing stolon (e.g., Berking, 2006).

Early graptolite literature is written in a number of languages, including Chinese, Czech, English, French, German, Latin, Norwegian, Spanish, and Swedish. Thus, paleontological terms describing graptolite features were created in a variety of languages. Many terms originally proposed in other languages were translated into English before they became the standard, although a few kept their original form. Reference is given herein to the various terms translated from other languages to indicate the historical origin and evolution of the hemichordate terminology.

A number of papers were entirely dedicated to terminology (e.g., Törnquist, 1894; Wiman, 1893a, 1896c) or included chapters on terminology (e.g., Ruedemann, 1904; Jaanusson, 1960; Cooper & Fortey,

1982). However, the authors am not aware of any glossary for graptolite or pterobranch terminology, except for a German one (KRAATZ, 1978), providing a compilation of graptolite terms in languages other than the English in the former versions of the Graptolite *Treatise* (BULMAN, 1955, 1970). The German glossary (KRAATZ, 1978) provided some translations of the terms of the English terminology, but no additional original useful terminology has been proposed and, in general, the terms are not included herein.

References are provided for all morphological terms listed in cases in which the terms were originally created for graptolites. The most recent revision is quoted and discussed. General paleontological or biological terms not restricted to graptolites are not referenced. Terms related to Enteropneusta are not included herein unless they are used in the various chapters dealing with taxonomy. However, they are defined and illustrated on p. 5–7.

Precise terminology can have considerable effect on the taxonomic and evolutionary understanding of graptolite phylogenies and evolution. A good example is the use of the term virgella, long considered to be important for graptolite taxonomy and identified as a homologous character in all later graptoloids (COOPER & FORTEY, 1982: Virgellina). However, as BULMAN (1963a, p. 404) stated, "it is likely that the virgella spine has evolved more than once," a statement that was supported by the analysis of the dorsal and ventral virgellar spines by MALETZ (2010a). Therefore, a differentiation of types of virgellar spines is necessary for the understanding of graptolite taxonomy and evolution and should be reflected in the terminology.

General descriptive terms that have been used in the past to describe thecal form (dichograptid, glyptograptid, climacograptid) are not included herein and should no longer be used. These terms should be replaced by a more precise constructional terminology. The climacograptid thecal style, for example, is based on a geniculate theca, but many apertural features in these thecae are not considered in this terminology (e.g., geniccular additions, thecal apertural features, thecal overlap, local thickenings). Climacograptid thecae, in a very generalized sense, are present in *Archiclimacograptus, Climacograptus, Amplexograptus, Monoclimacis, Pseudomonoclimacis,* and other taxa and do not indicate a precisely defined term. These features are clearly developed independently in the listed genera.

Terms describing proximal development types (e.g., dichograptid, isograptid, diplograptid, and monograptid) are not included here as they are generalizations, initially used to describe the precise development of certain genera. They are now known to consist of numerous independently changing characters and are quite variable. Proximal development types, as long as they are used in graptolite taxonomy, are described in the individual chapters dealing with taxonomy.

Terms in bold type are recommended for use. Terms combining italic with nonbold type are not recommended for use.

MORPHOLOGICAL TERMS

Abapertural ring (URBANEK, 1959, p. 287). Thickened rim around the primary opening for a new emerging theca. The abapertural ring may be reduced to a crossbar (see GOLDMAN & others 2011) or lacking completely.

abiesgraptid budding (URBANEK, 1963, p. 148). Mode of budding of thecal cladia in monograptids producing two daughter thecae symmetrically placed on either side of the mother theca and producing paired cladia.

abiesgraptid stage (URBANEK, 1963, p. 148). Stage of phylogenetic modifications in the development of a monograptid colony in which the procladium and the sicular cladium have acquired the ability to generate cladia.

aboral list (BATES, KOZŁOWSKA, & LENZ, 2005, p. 710). Thickened dorsal list at the base of the interthecal septum in axonophoran graptolites. Homologous with the transverse list of the Retiolitinae.

adapertural plate (URBANEK, 1963, p. 147). The expanded base of the first theca of the second and subsequent sicular cladia in *Linograptus,* shaped as a subtriangular platform with the true thecal tubule rising on it.

anastomosis. A biological term used in pterobranch terminology to describe the temporary fusion of adjacent branches to form an ovoid mesh. BULMAN

(1945, p. 8) differentiated true anastomosis as a mere touching of stipes. Anastomosis that includes a thecal transfer is defined as pseudanastomosis by Rickards and Lane (1997, p. 173).

ancora (pl., ancorae) (Bouček & Münch, 1952, p. 4, fig. 1; Bates, Kozłowska, & Lenz, 2005, p. 706). Structure of four-branched lists formed at the end of the virgella in the Retiolitidae (Eisenack, 1951, p. 134). It includes the initial part of the ancora umbrella and the ancora sleeve.

ancora stage (Eisenack, 1951, p. 134). Development of the ancora as the first stage in the growth of the ancora sleeve.

ancora sleeve (Bates, Kozłowska, & Lenz, 2005, p. 706). Prolongation of the ancora umbrella of the Retiolitida to enclose the thecae on both the obverse and reverse sides of the tubarium, formed of a fusellar wall (usually not preserved) with bandaged lists secreted on one or both sides. Contact with the thecal framework is only along the lateral apertural list (septal bar) portions of the apertural lists of the thecae.

ancora umbrella (Bates, Kozłowska, & Lenz, 2005, p. 706). Umbrella-shaped structure of lists developed from the ancora that comprises fusellar walls (not usually preserved), initially forking lists and subsequent spiral or polygonal lists, and, in some taxa, a circular rim with or without further looping lists.

ancora umbrella hub (Bates & Kirk, 1992, p. 6). Initial part of the ancora umbrella, formed from the two first branching divisions of the virgella, before dividing again to form four secondary ribs which extend to the rim of the ancora umbrella.

angle of divergence (Herrmann, 1885, p. 43; Elles & Wood, 1901, p. 5, fig. 3); originally Divergenzwinkel (German). The angle between the ventral sides of the dorsal walls of the stipes, one of the features used to describe the tubarium shape.

annulus (pl., annuli) (Kozłowski, 1949, p. 55); originally *bande annulaire* (French). Internal bands on the sicula and early thecae of some monograptids, comprised of fine, irregularly laminated cortical tissue forming thickened bands as secondary additions on the inside walls of siculae and thecae. Kraft (1926, p. 234) first misleadingly described this structure as Stillstandsgürtel (growth interruptions). Possible sicular annuli have also been described in dichograptids (Williams & Stevens, 1988).

Antisiculaseite (Wiman, 1895, p. 263; Holm, 1895, p. 436). Side of the graptoloid tubarium where the sicula is partly concealed by the crossing canal(s). See reverse.

antivirgellar spines Spines opposite to the virgella of diplograptacean graptolites, usually paired, rarely single or multiple.

apertural apparatus (Kozłowski, 1962, fig. 3; Urbanek, 1966, p. 305); originally l'appareil apertural (French) of Kozłowski (1949, p. 28). All derivatives of the apertural segment of metatheca, which may consist of an apertural lobe (or lobes), rostral processes, gorget, gular plate, and apertural lip.

apertural list (Lenz, 1994a, p. 1345). List around the thecal apertures, originally described for Retiolitidae, but also useful for other graptolites. The term selvage has been used for the same feature.

apertural spine. Projection in form of a spine originating on the ventral or lateral margin of the thecal aperture, single or paired.

Aperturalteil. See prosicula.

aperture. The opening of the thecal tubes. In the older literature (e.g., Barrande, 1850), the term orifice was used, but is now restricted to the secondary openings in the Retiolitidae; *ostium* (pl., *ostia*) is found in older literature for the apertures or openings of the housing of *Cephalodiscus.*

appendix (Bouček & Münch, 1952, p. 3). Reticulate tubular structure at distal end of the tubarium in the Retiolitinae, sometimes incorporating the nema and interpreted as a terminal theca by Bates, Kozłowska, and Lenz (2005, p. 709).

apron (Loydell & Maletz, 2004, p. 69). Hoodlike growth over the central portion of the thecal aperture, formed from normal fuselli, generally covering the proximal and lateral apertural margins of the thecal aperture; present in some streptograptids (Monograptidae).

arienigraptid suture (Maletz & Mitchell, 1996, p. 642). Visible line of contact between the ventral walls of $th1^2$ and $th2^1$ on the reverse side in certain Isograptidae (*Arienigraptus*, *Pseudisograptus*).

arms. Paired extensions of the collar in pterobranch zooids. Previously the term *lophophore* (see Lankester, 1884, p. 630) has been used for the arms of extant pterobranchs, but it is inappropriate as it suggests a homology to the Bryozoa.

aseptate. Biserial, dipleural tubarium lacking a median septum.

astogenetic patterns (Mitchell, 1987, p. 354). Sequence of budding at the initial dichotomy of the tubarium, giving rise to the first order stipes. See proximal development types.

astogeny. General biological term for the combined growth of individuals of a colonial organism; the growth of a graptolite colony describes the combined ontogenies of the zooids of a single colony (Urbanek, 1963, p. 148). See ontogeny.

auricula (pl., auriculae) (Kozłowski, 1962, p. 34). Expanded, earlike lateral lobes of highly modified thecae such as the cucullograptids (Monograptacea) and the Crustoide; also used for the lateral lobes in *Gothograptus auriculatus* Kozłowska & others (2019).

autocortex (Urbanek & Towe, 1974, p. 13; Urbanek & Mierzejewski, 1984, p. 76). The individual cortical envelope of a theca, especially an autotheca. See ectocortex.

autotheca (Kozłowski, 1949, p. 24). The larger type of regularly developed graptolite thecae. Name proposed by Kozłowski (1949) in lieu of the term hydrotheca of earlier workers, which related the graptolites to the hydrozoans. See theca.

axial cord (Sars, 1872, p. 11). See pectocaulus.

axil (Hopkinson, 1871, p. 20). Base of V-shaped bifurcation of dichotomously branched tubaria and especially the bifurcation of *Dicranograptus*, *Dicellograptus,* and *Oncograptus*.

axillary angle (Elles & Wood, 1904, p. 137). Angle between the dorsal sides of reclined stipes in uniserial and two-stiped reclined graptolites. See axil.

axonolipous (Frech, 1897, p. 556). Term used in multiramous to pauciramous uniserial graptoloids. Frech (1897) believed that the nema was lacking in these forms.

axonophorous (Frech, 1897, p. 555). Term used in scandent biserial and uniserial graptoloids in which the nema is enclosed in the tubarium or embedded in the dorsal wall of the stipes (see *Suborder Axonophora,* p. 329).

bande annulaire (French). See annulus.

bandages (Crowther & Rickards, 1977, p. 11). Parallel-sided deposits of aligned fibrils, usually covered by sheet fabric; mainly external; originally described as Chitinverdickungs-Bänder by Kraft (1926, p. 231, pl. 7). See cortical bandages, cortex. Kraft (1926, p. 231) described and illustrated the cortical bandages from isolated material, misinterpreting them as indications of the zooid anatomy (evidence of internal organs) due to his understanding of them being deposited on the inside of the sicula and thecae.

basal disk. Discoidal to irregular development originating from apex of the sicula for attachment of benthic graptolites; sometimes identified as a holdfast (see Bates & Urbanek, 2002).

basal membrane (Kozłowski, 1962, p. 10); originally *membrane interthécale* (French). Lower layer of the creeping tubes in encrusting graptolites and pterobranchs.

basal notch. (Urbanek, 1963, p. 147). Incision in the margin of the ventral wall of the basal part of the first theca of the sicular cladia in *Neodiversograptus beklemiskhevi* and *Linograptus posthumus*.

biform (Elles & Wood, 1911, p. 361). Graptoloid tubarium with proximal and distal thecae of different form showing gradual or abrupt change along the length of the stipes of the tubarium; originally proposed for monograptids with at least two different types of thecae, but it can also be used for other graptolites with a thecal gradient.

bilateral symmetry. General biological term; symmetrical disposition of the stipes of the graptolite tubarium around the sicula. See also isograptid symmetry and maeandrograptid symmetry.

bipolar (Urbanek, 1963, p. 137; Rickards, 1973a). Bilateral graptoloid tubarium formed as 1) a regeneration of a broken uniserial stipe through a pseudocladium or 2) a siculate monograptid with a sicular cladium; originally defined by Urbanek (1963, p. 137) exclusively for monograptids. Albani and others (2001, p. 390) identified janograptid proximal ends in dichograptids as regenerated uniserial stipes. The janograptid condition (genus *Janograptus*) in the Middle Ordovician is essentially an identical development to the bipolar regeneration with the formation of a pseudocladium in a monograptid.

biradiate (Bulman, 1950a, p. 68). Proximal development with two first-order stipes originating from the sicula through a single dicalycal theca; translated from bilateral; revised by Maletz (1992, p. 299). See triradiate, quadriradiate.

biserial. Scandent graptolitid tubarium with two series of thecae enclosing the nema; the thecal series can be arranged back to back (dipleural) or side by side (monopleural; also called duplex species by Lapworth (1873a, p. 501) and diprionid in older literature. See uniserial, triserial, quadriserial.

bitheca (pl., bithecae) (Holm, 1890, p. 10). Smaller type of regular graptolite theca, usually developed alternately on the right and left sides of the stipes; corresponds to the *gonangium* (pl., *gonangia*) of early workers (see Wiman, 1895, 1896c).

black stolon (Schepotieff, 1906, p. 465). The sclerotized, inflexible organic rod, usually embedded in the ventral wall of the mature tubes in the Pterobranchia. See pectocaulus.

blastocrypt (Urbanek, Mierzejewski, & Rickards, 1986, p. 101). Secondary dark inner layer of the graptoblast.

blastotheca (Urbanek, Mierzejewski, & Rickards, 1986, p. 99). Terminal portion of a stolotheca and housed by a zooid that never functioned as an autozooid, having been arrested in development at an early growth stage. See graptoblast, blastocrypt.

blastozooid (Kozłowski, 1971, p. 314). Term for the zooids of a graptolite colony formed through asexual budding.

branch. Single part of a branched graptolite tubarium, sometimes used for the entire colony; in its strict sense it refers to the segment between dichotomies in multiramous forms (Cooper & Fortey, 1982, p. 177). Earlier workers used the term *frond* (e.g., Hall, 1865). See stipe, which can be used interchangeably for branch.

branchial arms. See arm.

branchial plumes (M'Intosh, 1887, p. 10). Early term for the paired arms of pterobranch zooids; also *branchial arms*.

branching. Division of stipes. See dichotomous and cladial branching.

buccal disk (Lankester, 1884). See cephalic disk.

buccal shield (M'Intosh, 1887, p. 8). See cephalic disk.

budding. Development of daughter zooids from the mother zooids in the Pterobranchia; also used for the branching of stipes.

budding individual (see Bulman, 1932b, p. 26). Term used by earlier workers for the stolotheca or protheca.

calycle (Hall, 1865, p. 24). An early term for theca; see also *denticle, cellule, cell, cup,* and *denticle* (*Zahn* in German).

camara (pl., camarae) (Kozłowski, 1949, p. 170). Inflated proximal portion of autotheca in certain benthic, encrusting graptolites (camaroids, crustoids).

canaliculus (pl., **canaliculi**) (Urbanek, Mierzejewski, & Rickards, 1986, p. 103). System of parallel, fine canals perpendicular to the surface of the blastocrypt; first described but not named in Urbanek and Rickards (1974).

cauda (pl., caudae) (Hutt, 1974a, p. 80). Parallel-sided, tube-shaped part of the prosicula, closed at the apex and provided with a spiral thread; identical to the *nema prosiculae* of Kraft (1926, p. 222).

caulotheca (Lankester, 1884, p. 634). Thick, hard rim or cuticle formed on the gymnocaulus during transformation into the pectocaulus.

cell (pl., *cellule*). Term used by earlier workers for theca (see Barrande, 1850, p. 5; Hall, 1865).

central disk (Hall, 1865, p. 20). Web of sclerotized tissue uniting the proximal ends of stipes in some graptoloid tubaria, mostly Dichograptidae; interpreted to be formed by addition of cortical bandages or cortex, but not known from isolated material.

cephalic disk, **cephalic shield.** The frontal part of the pterobranch zooid with the glands secreting the tubarium; identical to the *buccal disk* or *buccal shield* of M'Intosh (1887, p. 8), the buccal shield and praeoral lobe of Lankester (1884), the proboscis of Harmer (1905, p. 26).

cephalic plumes (M'Intosh, 1887, p. 10; Ridewood, 1907, p. 221). Early term for the arms of the pterobranch zooids; also termed *branchial plumes, lophophore arms* or *branchial arms.*

Chitinverdickungs-Bänder (German) Kraft (1926, p. 231). See cortical bandages.

cladial branching (Elles & Wood, 1914, p. 505). Division of stipe where the branches originate from a thecal aperture or the sicular aperture. See dichotomous branching.

cladium (pl., cladia) (Elles & Wood, 1914, p. 505). Stipe developed from a mature thecal aperture through cladial branching. Urbanek (1963, p. 147) used the term cladium for any graptolite stipe, but it is suggested herein that the term be used in the restricted sense of Elles and Wood (1914), as it is generally used in the literature for a secondary branching from a thecal (or sicular) aperture. See *procladium, metacladium, pseudocladium*.

cladogeny (see Urbanek, 1963, p. 148). Describes 1) the growth of a colony or tubarium (Beklemishev, 1952); or 2) the branching of evolutionary lineages (Rensch, 1947).

clathrium (pl., clathria) (Elles & Wood, 1908, p. 306; Bates, Kozłowska, & Lenz, 2005, p. 709). Skeletal framework of lists forming the preservable part of the retiolitid tubarium; supporting the reticulum or an attenuated fusellum. Included in this definition are lists of both the thecal framework and the ancora sleeve (Retiolitidae). See reticulum.

clathriate. Possessing a clathrium.

*coenoecium (*pl., *coenoecia*) (Allman, 1856, p. 8). Describes the common dermal system of the Bryozoa [Polyzoa], consisting of ectocyst and endocyst; introduced for the tubarium of *Rhabdopleura* by Allman (in Norman, 1869a, p. 312) and commonly used for extant Pterobranchia; equivalent to the terms *rhabdosome* and tubarium in the description of the Graptolithina.

collar. 1) Part of the pterobranch zooid on which the arms are positioned behind the cephalic shield; term originates from the homologization of the tripartite body development with the Enteropneusta (*Balanoglossus*) (Harmer, 1905, p. 30). 2) Externally protruding part of fusellar rings in erect full rings of *Rhabdopleura* tubaria (Kulicki, 1969, p. 539). (3) Wide genicular rim or hood in *Lithuanograptus* (=*Metaclimacograptus*) described by Paškevičius (1976, p. 140); formed from microfusellar tissues (Maletz, 1997a, p. 21). See fusellar collar.

collum (pl., colla) (Kozłowski, 1949, p. 170). Erect distal tubular portion of the autotheca in some early benthic graptolites (camaroids); not homologous to erect tubes of *Rhabdopleura.*

colony. Biological term to describe close associations of individuals of one species living together in some degree of interdependence; In Graptolithina, describes the association of pterobranch individuals or zooids in constant organic contact with one other for mutual benefit and for secreting a common extracellular tubarium

columella (Cooper & Fortey, 1982, p. 282). Thickened column in the center of *Phyllograptus* colonies.

common canal (Barrande, 1850, p. 5; Hall, 1865, p. 23); originally *canal commun* (French). Continuous tubular cavity collectively formed by the prothecae of graptoloids connecting the individual thecae.

connecting canal (Törnquist, 1893, p. 5). Term used by earlier workers for the crossing canal.

connecting list (Bates, Kozłowska, & Lenz, 2005, p. 709). List linking transverse list and nema in Retiolitidae.

consecutive dichotomy (Cooper & Fortey, 1982, p. 176, fig. 6). Branching pattern in dichograptids in which only a single theca separates successive dichotomies, as in *Goniograptus.* See delayed dichotomy.

conotheca (pl., conothecae) (Bulman & Rickards, 1966, p. 50). Relatively large, conical theca with a small circular aperture; irregularly developed in tubaria of some Callograptidae.

contractile cord (Sars, 1872, p. 10). See gymnocaulus.

contractile stalk (Schepotieff, 1907b, p. 199). The unsclerotized, contractile stalk of the pterobranch zooid; identical to the contractile cord of Sars (1872, p. 10), the funiculus of Allman (1869b) and homologous to the pedicle or peduncle of *Cephalodiscus* (M'Intosh, 1887, p. 20). Originally *kontraktiver Stiel* (German). See gymnocaulus and zooidal stalk.

conus (pl., coni) (Hutt, 1974a, p. 80). Distal, cone-shaped part of the prosicula, separated from the cauda by an internal diaphragm.

corona (pl., coronae) (Eisenack, 1951, p. 134; Bouček & Münch, 1952, p. 5). Initial proximal part of the ancora sleeve in the Retiolitidae. As used by Bouček & Münch (1952), it comprises the ancora, ancora umbrella, and lists to the base of the first thecal pair.

corona stage. See ancora umbrella.

cortex, cortical tissue (Kozłowski, 1938, p. 190). The outer layer of the graptolite housing construction, formed by slender, parallel-sided bandages; the cortex produces the secondary thickening of the tubarium walls; the secondary lamellae of Harmer (1905, p. 10) in extant Pterobranchia. See fusellum.

cortical bandages (Crowther & Rickards, 1977, p. 11). Formation of cortical layers from thin bandages, crisscrossing the fusellar construction of the tubarium, first described in detail by Crowther (1978, 1981). Kraft (1926, p. 231) described cortical bandages as *Chitinverdickungs-Bänder* (German) and misinterpreted them as internal features. Bulman (1932a, pl. 3, fig. 7–8: *Climacograptus diplacanthus*) illustrated cortical bandages in *Diplacantograptus spiniferus.* See cortex.

crassal fabric (Urbanek & Towe, 1974, p. 4). Electron dense and homogeneous material, sometimes with indistinct layering but usually lacking a pattern,

producing a compact wall of considerable thickness forming the stolons.

crossing canal (Elles & Wood, 1901, p. 6). Proximal (prothecal or initial) portion of the primordial graptoloid thecae growing across the axis of the sicula on the reverse side of the sicula to develop fully on the opposite side. Earlier workers used the term *connecting canal* (see Törnquist, 1893, p. 5).

cryptopyle (Kozłowski, 1962, p. 19). Single or paired opening at the distal end of a graptoblast, opposite to the filum.

cryptoseptate (Urbanek, 1959, p. 290). Biserial tubaria in which the median septum is comprised of cortical listrs arranged as in septate forms but lacking a fusellar septal membrane.

cupula (pl., cupulae) (Loydell & Maletz, 2004, p. 68). Paired bulbous protuberances on the dorsal side of some monograptoid graptolites, flanking the nema. Cupulae are believed to represent prothecal folds at the base of the thecae. Cupulae occur in *Streptograptus* and related taxa (Monograptidae).

cyrtograptid budding (Urbanek, 1963, p. 148). Budding of a theca directly from the aperture of the mother theca. See cladial branching.

cyrtograptid stage (Urbanek, 1963, p. 148). Stage of phylogenetic modifications in the development of a colony, during which the process of astogeny produces a procladium and at least one thecal cladium that is generated by *cyrtograptid budding*. See cladial branching.

cyst. Common biological term. 1) Vesicles of varying size and shape occurring in autothecal cavities of crustoids. 2) Surface features in graptolites that may represent parasitic organisms.

declined (Elles & Wood, 1901, p. 5, fig. 3). Describes graptoloid tubaria with branches hanging below the sicula, subtending an angle of less than 180° but not parallel to each other (pendent).

deflexed (Elles & Wood, 1901, p. 5, fig. 3). Similar to declined but with distal extremities of stipes tending to become horizontal.

delayed dichotomy (Cooper & Fortey, 1982, p. 176, fig. 6). Branching pattern in dichograptids in which two or more thecae separate successive dichotomies after the first dichotomy, as, for example, in *Laxograptus*. See consecutive dichotomy.

dendroid, dendroidal. 1) Belonging to the order Dendroidea. 2) Descriptive term for tubarium growth showing irregular, bushy colony shapes in benthic graptolites.

denticle. Term used by earlier workers to describe the thecae of graptolites and later by English workers for the ventral extension of the prosicula of dendroids along the zigzagging line of suture; considered imprecise by Kozłowski (1949, p. 20), who replaced it by the term *languette*. See rutellum.

denticulate. Pointed sicular and thecal apertures provided with a short spine or rutellum.

development type. See proximal development type.

dextral (Cooper & Fortey, 1982, p. 174). Clockwise direction of growth of tubarium. See sinistral.

diad budding (Kozłowski, 1949, p. 141). Mode of budding in pterobranchs resulting in two zooids at each nodal division, lacking regularity of thecal succession. See also triad budding.

diaphragm (Hutt, 1974a, p. 80). Membrane stretching across the initial part of the prosicula and separating the conus from the cauda; identified first by Kraft (1926) as a membrane. See also stolonal diaphragm (Urbanek & Dilly, 2000).

diaphragm complex (Urbanek & Dilly, 2000, p. 214). Complex structure developed at the apex of the initial stolon of *Rhabdopleura* inside the mother theca.

dicalycal theca (Jaanusson, 1960, p. 303). Graptoloid theca giving rise to two daughter thecae, resulting in branching of multiramous graptolites. See monocalycal theca.

dichotomous branching. Stipe division where two branches diverge symmetrically from the parent stipe; see lateral branching, cladial branching. In a more restricted sense, also used for branching at the distal end of the graptolite.

dichotomy. Branching division with two stipes originating at the same point. The direction of growth of the parent stipe is abandoned, with the two stipes growing at identical angles away from it. See lateral branching.

dipleural (Jaanusson, 1960, p. 303). Biserial graptoloid tubaria in which two stipes are in back-to-back contact, resulting in two external lateral walls. See monopleural.

diprionid. Early term for biserial (Barrande, 1850; Tullberg, 1883, p. 13).

discophorous (Kozłowski, 1971, p. 314). Possessing a sicula with an attachment disk, but lacking a free nema; taken as indication of a benthic life style. See nematophorous.

discoidal preservation. Disklike view of the (multiramous) tubarium with the sicula roughly perpendicular to the stratification. See lateral preservation.

dissepiment. Strand of cortical tissue connecting adjacent branches or stipes in graptolite tubaria. Harmer (1905, p. 16) discusses numerous bridges connecting adjacent branches in *Cephalodiscus dodecalophus*. These may be constructionally homologous to the dissepiments in the Graptolithina. In botany, the term is used differently to denote a partition dividing an organ into chambers. See thecal bridge.

distal. Last-formed part of tubarium, stipe, or theca; farthest from the point of origin.

distal lobe (Loydell & Maletz, 2004, p. 69). Rounded or elongated, broadly triangular processes on the lateral apertural margins of streptograptids (Monograptidae).

diversograptid budding (Urbanek, 1963, p. 148). The budding of a theca directly from the aperture of sicula, producing only one sicular cladium and not capable of producing more cladia. See cladial branching.

diversograptid stage (Urbanek, 1963, p. 148). Stage of phylogenetic modifications in the development of a colony, in which astogeny results in the formation of a bipolar tubarium consisting of a *procladium* and sicular cladium and also of the thecal cladia budding from them.

dormant buds (Stebbing, 1970, p. 210). Large, closed, vesicular bodies; interpreted as enclosing hibernat-

ing zooids and also identified as sterile buds by Schepotieff (1907b, p. 198; sterile Knospen). See hybernacula, *statoblast*.

dorsal. Term denoting the side of the stipe opposite to the thecal apertures or a comparable side of the thecal aperture; not necessarily related to direction of growth but, presumably, to the dorsal side of the zooids.

dorsal apertural tongue Jaeger (1959, fig. 14); originally dorsales Zünglein (German). Term for the extension of the dorsal rim of the sicula into a rutellum-like construction in many Monograptidae. The dorsal tongue may be adorned with spines or other elaborations and should be differentiated from the ventral position of the rutellum in the Dichograptina and Sinograptina (Maletz, 1997d, p. 248).

duplex species (Lapworth, 1873a, p. 501). See biserial.

ectocortex (Crowther, 1981, p. 13; Urbanek & Mierzejewski, 1984, p. 76). The cortical material deposited on the outer surface of the thecal walls or, generally, on the outer surface of the tubarium. Urbanek and Towe (1974) differentiated the ectocortex into autocortex and rhabdocortex. See endocortex.

end bulbs (M'Intosh, 1887, p. 11). Bulbous structures at the tips of the arms of *Cephalodiscus* zooids. M'Intosh (1887, p. 11) described the end bulbs as glandular, but Harmer (1905, p. 39) stated that there is no evidence for a function of the end bulbs.

endocortex (Urbanek & Mierzejewski, 1984, p. 76). The cortical material deposited on the inner surface of the thecal walls or, generally, within the cavities of the tubarium. See ectocortex.

eucortex (Urbanek & Mierzejewski, 1984, p. 76). The secondary component made of the typical cortical tissue, including sheets, well-defined straight, parallel, fibrils and some ground substance.

everted. Outward-facing thecal aperture.

exoskeleton. Term often used for the coenecium or tubarium (rhabdosome) of graptolites. The graptolite tubarium is not an exoskeleton but a housing structure or domicile, secreted by the organism. See tubarium.

extensiform (Elles & Wood, 1901, p. 5, fig. 3). Term denoting stipes growing more or less horizontally away from the vertical sicula.

external common canal (Bates & Kirk, 1992, p. 127). See outer common canal.

external orifice (Barrande, 1850, p. 6). Term used by Barrande for the thecal aperture.

extroverted. Thecae turned back on themselves by the exaggerated growth of the dorsal margin of the aperture.

fibrils, fibrillar structure (Dilly, 1971, p. 502). Ultrastructural features of the graptolite fusellum; the fine elements forming the collageneous material of the graptolite and pterobranch fusellum. The term fibrils was also used for the surface patterns of cortical bandages in the Retiolitinae by Bates and Kirk (1978, pl. 4), now described as longitudinal striations (Lenz & Melchin, 1987, p. 162).

filum (pl., *fila*) (Kozłowski, 1949, p. 207). Remains of the stolon in graptoblasts.

finite. Graptolite tubarium with limited growth, forming terminal thecae of reduced size or special shape; present in some Retiolitidae, but also in the Axonophora, such as the genera *Brevigraptus* and *Corynoides.*

flabellate. Fan-shaped tubarium form with stipes spreading out in a single plane; used for benthic graptolites.

float. A membrane at the proximal or distal end of a tubarium that is interpreted as supporting a stable orientation of the tubarium in the water column or as a float or flotation device. See nematularium.

foramen (pl., foramina). Opening in the sicula for the development of the bud of th1[1]. See primary porus, resorption foramen.

fornical foramen (Cooper & Fortey, 1982, p. 180). The wide openings between thecal series in *Phyllograptus,* representing the remains of the median septum between the four scandent thecal series.

fornix (Cooper & Fortey, 1982, p. 180). The arched strut standing in place of the median septum in the axial region of the quadriserial *Phyllograptus.*

free ventral wall. The portion of the ventral thecal margin that extends beyond the aperture of the preceeding theca.

frond. Term used by earlier workers (e.g., Hall, 1865) for the stipes of graptolites.

funicle (from the Latin funiculus, funiculi) (Hall, 1865, p. 19; Lindholm & Maletz, 1989, p. 713). The combined first-order stipes in the multiramous graptoloids. Originally proposed by Hall (1865) for non-thecate intial parts of dichograptids connecting thecate stipes. It is now known that thecae are present throughout the proximal area in graptolite colonies, but that they may be obscured by secondary overgrowth.

funiculus (Allman, 1869b, p. 58). See gymnocaulus.

fusellar collar. Externally protruding part of fusellar ring in erect full rings of *Rhabdopleura* tubaria (Kulicki, 1969, p. 539); called ribs, Rippen, or Kragen in Andres (1977, p. 57). See collar.

fusellar tissue (Kozłowski, 1938, p. 190). Inner organic layer of the tubarium, generally comprised of alternating L and R bands of fuselli. See fusellum.

fusellum (pl., fusella) (Kühne, 1955, p. 363; Urbanek & Towe, 1974, p. 4; Urbanek & Mierzejewski, 1984, p. 74). Primary skeletal material of graptolites and pterobranchs, formed from fuselli. See cortex.

fusellus (pl., fuselli) (Kozłowski, 1949, p. 20). Individual half rings or full rings of scleroproteic material secreted by the cephalic disk of the graptolite and pterobranch zooids, forming the tubarium laid down sequentially. Fuselli were first described as *Querrunzeln* by Richter (1871, p. 233), who stated that they form a zigzag suture on the dorsal and ventral sides of the cells; recognized as growth lines by Lapworth (1873a). Harmer (1905, p. 10) identified fuselli as the primary lamellae in extant Pterobranchia. See growth lines.

geniculum (Jaanusson, 1960, p. 304). Angular bend in the upward ventral direction of growth of the graptoloid theca. It may be adorned with a thickened rim, spines, or other genicular processes.

genicular process (Jaanusson, 1960; Bates, Kozłowska, & Lenz, 2005, p. 709). Processes formed at the geniculum of a graptolite theca.

glossograptid bulge (Maletz & Mitchell, 1996, p. 643). Conspicuous proximal bulge formed by a variable number of proximal thecae growing in a spiral pattern and covering the sicula and th1[1] on both the obverse and reverse sides of the Glossograptidae; first illustrated from isolated material by Whittington and Rickards (1969).

gonangium (pl., *gonangia*). Term used by earlier workers for the bithecae (e.g., Wiman, 1895, 1896c). Ruedemann (1895) also used the term to describe the oval disk to which synrhabdosomes are attached.

graptoblast (Kozłowski, 1949, p. 206). Ovoid-shaped chambers present in crustoids; interpreted as rejuvenated zooidal chambers by Urbanek and Mierzejewski (1984) and Mierzejewski (2000a).

graptolite. General term for the tubaria of the Graptolithina; derived from the genus *Graptolithus* Linnaeus, 1735; originally interpreted as inorganic markings by Linnaeus (1735).

grapto-gonophore (Nicholson, 1866, p. 489). Fossils identified as ovarian vesicles or grapto-gonophores, but representing various non-graptolitic taxa (Page & others, 2009).

growth lines. Expression of the fusellar structure (see fuselli) on the surface of the graptolite tubarium; first described by Barrande (1850, p. 8; striae), but not recognized as such. Lapworth (1873a) was the first to describe the striae on the surface of many graptolites as growth lines. Richter (1871, p. 233) described growth lines of graptolites with the term Querrunzeln and remarked that they form a zigzag suture (Zickzacknaht) on the upper and lower side of the thecae (Zellen, cells).

gymnocaulus (Lankester, 1884, p. 629). Unsclerotized stolon situated behind the permanent terminal zooid in *Rhabdopleura* from which the zooids proliferate. Lankester (1884) used the term in a wider sense, including the zooidal stalks; identical to the contractile cord of Sars (1872, p. 10), the funiculus of Allman in Norman (1869a, p. 312) and homologous to the pedicle or peduncle of *Cephalodiscus* (M'Intosh 1887, p. 20). The term is also used for the homologous unsclerotized stolon in graptolites (Hutt, 1974*a*, p. 81).

heart-shaped axial cavity (Xiao & Chen, 1990, 1994). Cavity enclosed by the two reclined and subsequently scandent stipes in *Proncograptus, Procardiograptus,* and *Diceratograptus.*

helical line (Kozłowski, 1949, p. 56); originally ligne hélicoïdale (French). See also spiral thread or spiral line. Identical to the Schraubenlinie of Kraft (1926).

helicotheca (Kozłowski, 1949, p. 163); originally *hélicothèque* (French). Type of autotheca in Cyclograptidae with coiled initial part.

Höckerchen (Eisenack, 1951, fig. 11). See pustules.

horizontal. Graptoloid tubarium with stipes growing at a right angle to the axis of the sicula. See extensiform.

hybernacula (Lankester, 1884, p. 639). Large, closed, vesicular bodies; interpreted as enclosing hibernating zooids, also identified as statoblasts (Lankester, 1884, p. 639) and sterile buds by Schepotieff (1907b, p. 198: sterile Knospen). See dormant buds.

hydrorhabd (Frech, 1897, p. 549). See tubarium.

hydrosome. Term used by earlier workers for the graptolite tubarium, suggesting a relationship to the Hydrozoa. Ruedemann (1895, p. 224) used the term for synrhabdosomes.

hydrotheca (e.g.,Nicholson & Marr, 1895, p. 529). Term used by earlier workers for the autothecae of the Dendroidea and other benthic graptolite groups and for the thecae of the Graptoloidea, suggesting a relationship to the Hydrozoa.

hypoblastic (Legrand, 1987, p. 61). Term for a certain proximal development type.

infragenicular wall (Jaanusson, 1960, p. 304). Thecal wall between the geniculum and the preceeding theca in geniculate graptolites.

initial bud. Outgrowth formed by the first post-sicular zooid through a foramen in the sicular wall, producing the first theca of the tubarium.

initial foramen. Opening for the first post-sicular zooid of a graptolite colony.

Initialteil (Wiman, 1895, p. 263). See prosicula.

internal orifice (Barrande, 1850, p. 7). Primary opening in the mother theca from which the daughter theca originates.

interpleural list (Lenz, 1993a, p. 12). Medially placed ventral list connecting the upper apertural list of one theca with the lower apertural list of the succeeding thecal aperture of a retiolitid tubarium. See mid-ventral list.

interthecal septum (Törnquist, 1893). Membrane separating the overlapping thecal cavities in graptoloids. It comprises the dorsal wall of a theca and part of the ventral wall of the succeeding theca.

introverted. Inward-facing thecal aperture resulting from the exaggerated growth of the ventral wall of the thecae; usually accompanied by the sigmoidal curvature of the thecal axis.

introtorted. Refers to the change in direction of growth of the metatheca toward, rather than away from, the dorsal stipe margin, as in *Dicranograptus.*

isograptid arch (Cooper & Fortey, 1982, p. 180). The arch formed by the ventral walls of the dicalycal theca and its first daughter theca. The structure helps distinguish development types in dichograptids; in species with artus-type proximal development, there is a single thecal aperture showing beneath the arch (that of the sicula), whereas in isograptid-type proximal development, there are two apertures showing beneath the arch (those of the sicula and th1[1]).

isograptid suture (Maletz, 1994b, p. 28). Line of contact between the sicula and th1[1], which is visible in reverse view below the isograptid arch in many dichograptids. It gives a measure of the position of the crossing canals on the sicula.

isograptid symmetry (Cooper, 1973, p. 56; Cooper & Fortey, 1982, p. 180). Sicula and th1[1] forming a symmetrical pair. See maeandrograptid symmetry.

keroblastic (Legrand, 1987, p. 61). Term for a certain proximal development type in Llandovery axonophorans.

Kuppel (Eisenack, 1951, p. 156). See corona.

labia (pl., labiae) (Lenz & Kozłowska-Dawidziuk, 2004, p. 17). Thickened apertural lip with distinctive paired structures in Retiolitidae (*Neogothograptus*).

lacinia (Elles & Wood, 1908, p. 319; revised by Bates, 1990, p. 717). A three-dimensional network of unseamed lists, thickened by concentric growth of bandages. The lists are attached to ventral apertural spines, to paired obverse and reverse spines branching from the nema, and also to the virgella and paired dorsal sicular apertural spines. A lacinia is present in the Archiretiolitidae and in *Paraglossograptus* (Glossograptidae). Originally termed *marginal meshes* by Lapworth (in Hopkinson & Lapworth, 1875, p. 641).

lacuna stage (Eisenack, 1942, p. 31); originally Lacuna-Stadium (German). Second stage in the development of the initial foramen of the growth of the first theca in the Monograptacea. The primary foramen is surrounded by fusellar growth bands. See sinus stage, porus stage.

Längsverstärkungsleisten (Kraft, 1926, p. 224). See longitudinal strengthening rods.

languette (Kozłowski, 1949, p. 20, 22, and 33). The apertural ventral and dorsal terminal extensions of the thecae in dendroid graptolites along the zigzag suture line of the fuselli. It replaced the less-precise denticle of English workers, which had been originally used for the thecae of graptolites. Kozłowski (1949, p. 22) differentiates a dorsal languette and a ventral languette. The ventral languette is homologous to the rutellum of Williams and Stevens (1988).

lappet. Rounded lateral apertural processes of thecae or the sicula; mistakenly also used for ventral apertural lappets, now called rutelli.

lateral apertural list (Bates, Kozłowska, & Lenz, 2005, p. 709). The part of the apertural list in Retiolitidae that connects with the lists of the ancora sleeve.

lateral branching. A special case of dichotomous branching in which one of the stipes diverges at an angle to the parent stipe, which continues its original direction of growth (e.g., *Holograptus*).

lateral preservation. 1) Tubarium showing only one side (see discoidal preservation). 2) Lateral preservation in stipes indicated by the typical sawtooth appearance, showing thecal rutelli.

lateral proximal orifices (Bates, Kozłowska, & Lenz, 2005, p. 720). Openings on the lateral wall between the rim of the ancora umbrella and base of ancora sleeve.

left-handed (origin of thecae) (Stubblefield, 1929, p. 274; revised by Cooper & Fortey, 1982, p. 173). Refers to thecae originating on the (biologically) left side of the theca viewed from the dorsal side.

lenticular porus (Dawson & Melchin, 2007, p. 91). An opening for the emergence of the first post-sicular istal direction onto the virgellar spine. One or two truncated or incompletely formed fuselli may be present. The post-porus fuselli are deflected in the opposite direction but resume their original direction close to the virgellar spine, forming a lenticular primary opening for the th1 bud. See primary porus, resorption foramen.

line of symmetry. The line of symmetry passes through the sicula (see maeandrograptid symmetry) or between the sicula and the first theca (see isograptid symmetry).

linea (Lapworth, 1897, p. 251). See nema.

linograptid budding (Urbanek, 1963, p. 148). Term used to denote multiple sicular cladia.

linograptid stage (Urbanek, 1963, p. 148). A stage of phylogenetic modification in the development of a colony, in which a procladium and numerous sicular cladia are produced in astogeny; restricted to the genus *Linograptus.*

list (pl., lists) (revised by Bates, Kozłowska, & Lenz, 2005, p. 709). Skeletal list in Retiolitidae that strengthens the fusellar walls with localized cortical bandages.

longitudinal strengthening rods (Kraft, 1926, p. 224); originally Längsverstärkungsleisten (German). Cortical ridges on the outside of the prosicula, formed before the growth of the metasicula.

lophophore (Lankester, 1884, p. 630). Paired arms or groups of arms in the zooids of pterobranchs, provided with ciliated tentacles and situated adjacent to the mouth of the zooid; originally lophophore arms or branchial arms (Lankester, 1884, p. 630), but also branchial or cephalic plumes (M'Intosh, 1887, p. 10; Ridewood, 1907, p. 221). A lophophore is typically present in Brachiopoda, Bryozoa, and Phoronida; thus, the term should not be used for the Pterobranchia. See arms.

maeandrograptid symmetry (Cooper, 1973, p. 56; Cooper & Ni, 1986, p. 316). Used to describe $th1^1$ and $th1^2$ forming a symmetrical pair on both sides of the sicula. See isograptid symmetry.

manubrium (Cooper, 1973, p. 54; Maletz & Mitchell, 1996, p. 642). A complex and prominently shouldered structure on the reverse side of arienigraptid graptolites (Isograptidae), which is formed by the strong downward growth of the initial part of $th1^2$ and $th2^1$ and their descendant thecae. It always involves the formation of an arienigraptid suture. The sicula and the early thecae extend downward at least as far as their descendant thecae.

manubrium shoulders (Cooper & Ni, 1986, p. 315). Dorsal margin of the manubrium, from the origin of the stipes at the sicula to the sharp dorsal flexure in the dorsal stipe margin.

manubriate (Cooper, 1973, p. 56). Tubaria having a manubrium.

marginal meshes (Lapworth in Hopkinson & Lapworth, 1875, p. 641). See lacinia.

median plane (Cooper & Fortey, 1982, p. 178, fig. 8). The plane of symmetry of branching tubaria, containing the tubarium midline and the two first-order stipes.

median septum. Membrane in quadriserial, triserial, and biserial dipleural graptoloids, separating the thecal series, originating at various levels in the tubarium. In some biserial dipleural forms, a partial median septum occurs on the obverse side only.

membrane interthécale. See basal membrane.

mesial. 1) The middle part of the tubarium. 2) The middle part of the free ventral wall (supragenicular wall) of a theca.

metacladium (Urbanek, 1963, p. 147). Thecal or sicular cladium as opposed to *procladium* or main stipe. See cladium.

metasicula (Kraft, 1926, p. 225). Distal part of sicula comprised of fusellar growth bands or fuselli; named the *Aperturalteil* by Wiman (1895). See prosicula.

metatheca. The growth of the metatheca commences at the base/origin of the interthecal septum of the succeeding theca. In taxa lacking an interthecal septum, the metatheca can be defined as commencing its growth at the origin of the ventral wall of the succeeding theca. See protheca.

microfusellar tissue (Urbanek, 1966, p. 306). Fusellar substance comprised of extremely fine and somewhat irregular growth bands.

microtheca (Kozłowski, 1949, p. 163); originally microthèque (French). Type of autotheca occurring in Cyclograptidae, characterized by a narrow terminal portion and differently oriented apertures.

mid-ventral list (Bates, Kozłowska, & Lenz, 2005, p. 709). Centrally placed longitudinal list running from the transverse list or from the genicular list to the thecal lip (Retiolitidae). Identical to *interpleural list* of Lenz (1993a, p.12).

monocalycal theca (Jaanusson, 1960, p. 303). Graptoloid thecae giving rise to only one subsequent thecae. See dicalycal theca.

monofusellar tissue (Urbanek, 1958, p. 19). Fusellar substance deposited in single and not alternating series of growth bands, forming full fusellar rings (e.g., the erect tubes of *Rhabdopleura*) or in lateral lobes of thecal apertures.

monograptid budding (Urbanek, 1963, p. 148). Subapertural, nonperforational budding of theca from an initial, primary opening, subaperturally placed in relation to the definite aperture of the respective mother theca. See cladial branching.

monograptid stage (Urbanek, 1963, p. 148). Stage of phylogenetic modification in the development of a colony, in which the process of astogeny produces only a procladium by monograptid budding.

monopleural (Jaanusson, 1960, p. 303). Biserial graptoloid tubarium in which two stipes are in contact laterally, each stipe having only one lateral external wall (Glossograptidae). See dipleural.

monopodial growth. Type of colonial growth with permanent terminal zooid behind which new zooids arise as the stem elongates; known exclusively in *Rhabdopleura*. See sympodial growth.

monoprogressive branching (Cooper & Fortey, 1982, p. 177, fig. 6). Branching pattern in which only one of the two daughter stipes formed at a dichotomy divides again, with the other daughter stipe remaining unbranched, as in *Goniograptus,* after the first dichotomy. See progressive branching.

mouth-spine (Wiman, 1896c, p. 188). See virgella.

multiramous. Having numerous branches or many branches.

nema (pl., nemata or nemas) (Lapworth, 1897, p. 251). Filiform process or extension at the apex of the prosicula; originally defined by Lapworth (1897) as the flexuous primordial filiform process from which the sicula is suspended. The secretion of the nema starts at the tip of the cauda. The nema may be free (Dichograptina), incorporated in the tubarium (Diplograptina, Glossograptina), or fully visible on the dorsal side of the stipe (Monograptidae). The nema in the Diplograptina and Monograptidae is commonly called the virgula. Richter (1850, p. 201) mistook the nema as a siphon, based on the belief that graptolites are related to nautiloids. See pseudovirgula.

nema prosiculae (Kraft, 1926, p. 225). See cauda.

nemacaulus (Ruedemann, 1904, p. 487). Term proposed by Ruedemann (1904) in lieu of nema.

nematophorous (Kozłowski, 1971, p. 314). The possession of a free nema in the graptolite sicula, which is taken as indication of a planktic life style. See discophorous.

nematularium (Müller, 1975, p. 330; Bates, Kozłowska, & Lenz, 2005, p. 709: for retiolitids). Distal development of a vane or spiral structure of the nema.

nozzle (Loydell & Maletz, 2004, p. 69). The elongated arch on the dorsal side of the thecal aperture in streptograptids (*Streptograptus, Pseudostreptograptus, Mediograptus*).

obverse (Törnquist, 1893, p. 3). Refers to the side of the graptoloid tubarium on which the sicula is most completely visible and the crossing canals are covered; similar to Siculaseite of Wiman (1895) and others. See reverse.

occlusion. Sealing of the thecal aperture by sclerotized film, possibly made up of cortical material.

ontogeny. General biological term for the growth of organisms, used herein for the growth of an individual, a zooid; previously used by Kozłowski (1971, p. 314) only to describe the ontogeny of the sicular zooid, but it is applicable to all derived zooids. The combined ontogenies of all zooids of a colony represent the astogeny of the colony. See astogeny.

oozooid (Kozłowski, 1971, p. 314). Term for the sicular zooid.

order (of branching) or **order of stipes**. Successive divisions of dichotomous branches or successive generations of cladia. Maletz (1992, p. 298) preferred to use the term 1st to nth order of stipes in the Dichograptina instead of the terms primary and secondary stipes.

orifice (Loydell, Storch, & Bates, 1997, p. 748). An opening of the tubarium that is partially or entirely rimmed by lists of the ancora sleeve in Retiolitidae. Includes thecal orifices, proximal ventral orifices, proximal lateral orifices, and stomata. The term was used by earlier workers for thecal apertures (e.g., Barrande, 1850: internal and external orifices).

ostium (pl., *ostiae*). Term used in earlier graptolite literature for thecal apertures.

outer ancora (Bates, Kozłowska, & Lenz, 2005, p. 710). Structure formed by lists on the outside of the ancora umbrella in some Retiolitidae.

outer common canal (Bates & Kirk, 1992, p. 127). Initially identified as as external common canal. Development of a common canal between the lateral

thecal sides and the ancora sleeve on both sides of the retiolitine tubarium, often with regular or irregularly developed stomata. See common canal.

outer lamella (Urbanek & Towe, 1974, p. 5). Fabric of parallel fibrils in a fusellus immediately beneath the bounding pellicle of sheet fabric.

pachythecae (Kozłowski, 1970, p. 405). Large thecae in *Acanthograptus* with amorphous wall structure and no fuselli; interpreted as possibly parasitic in origin, like the tubothecae.

paracortex (Urbanek & Mierzejewski, 1984, p. 76). Secondary component of cortex made by multiple deposition of sheets separated by an intersheet material, lacking well-defined, individualized cortical fibrils; produced by a tightly packed, condensed meshwork of fibrous material.

parasicula (VandenBerg, 1990, p. 40). Tubular downgrowth of the sicular aperture in biserial graptolites. The term parasicula was first introduced by Eisenack (1938a, p. 156) for the misinterpreted metasicula of a dendroid graptolite, later identified as *Epigraptus bidens* (Eisenack, 1941a).

paratheca (pl., parathecae) (Mitchell, Chen, & Finney, 2007, p. 1123). Tubular outgrowths from the thecal apertures in the proximal part of some biserial graptolites (*Appendispinograptus*).

parietal list (Kozłowska-Dawidziuk, 1990, p. 194). Major oblique to horizontal lists on the obverse and reverse ancora sleeve panels, linking the vertical pleural lists. The parietal lists also form the obverse and reverse zigzag struture of many derived retiolitines (e.g., *Plectograptus, Holoretiolites*).

patagium (Kozłowska & Urbanek, 2013, p. 19). Fan-shaped membrane originating from a repeatedly branching rod on the sides of the tubarium in *Bohemograptus*.

pauciramous. Planktic pterobranch colony consisting of few branches.

pectocaulus (Lankester, 1884, p. 634). The sclerotized, inflexible black stolon, usually embedded in the ventral wall of mature tubes in the Pterobranchia; identical to the axial cord of Sars (1872, p. 11) and the chitinous rod of Allman (1869b). The stolon is presumably free in the tubarium of planktic graptolites but is rarely present in the fossil record. The terms pectocaulus and stolon can be used interchangeably, but the latter is more widely distributed.

pedicle (M'Intosh, 1887, p. 20). Thin, flexible, cylindrical stalk at the rear end of the *Cephalodiscus* zooids, provided with a sucker for attachment; new buds originate from the base of the pedicle; term borrowed from the terminology of the Brachiopoda. See gymnocaulus.

peduncle (M'Intosh, 1887, p. 6). Thin, flexible, cylindrical stalk at the rear end of the *Cephalodiscus* zooids, provided with a sucker for attachment; new buds originate from the base of the pedicle; M'Intosh (1887) used both pedicle and peduncle for the gymnocaulus of *Cephalodiscus*. The term is homologous to the gymnocaulus of *Rhabdopleura* and should not be used. See gymnocaulus. Term also used for pelecypods.

pendent (Elles & Wood, 1901, p. 5, fig. 3; Cooper, 1973, p. 52, text-fig. 5). Denotes a downward direction of growth of stipes or of thecae when the tubarium is oriented so that the apex of the sicula points vertically upward.

pericalycal (Bulman, 1968, p. 214; Maletz & Mitchell, 1996, p. 643). Taxa with an isograpid- or artus-type development, with the enclosure of the obverse side of the sicula by $th2^2$ (or $th1^2$ in some derived species), with resulting initial monopleural growth of the two thecal series such that the tubarium acquires a secondary rotational symmetry normal to the plane of isograptid symmetry. See platycalycal.

periderm (Törnquist, 1894, p. 377). Scleroproteic substance forming the tubarium of the Pterobranchia, comprised of an inner layer of alternating fusellar bands (fuselli) with growth lines and an outer (cortical) layer of finely laminated tissue from thin bandages. The term should not be used any more, as the name suggests a dermal origin, which is incorrect (Mitchell & others, 2013, p. 51). As there is no definite replacement term, the "material can simply be referred to as tubarium or wall material depending on the specific context" (Mitchell & others, 2013, p. 51).

plaited overlap, plaited arrangement (Cooper & Ni, 1986, p. 314; Lindholm, 1991, p. 289; Maletz & Mitchell, 1996, p. 642). 1) Parallel growth and overlap of several thecae, as in the manubrium of pseudisograptids. 2) The overlapping of thecae in bithecate and nonbithecate tubaria with lateral thecal origins (Lindholm, 1991). Both constructional features are developed independently but have similar results in their typical development of multiple parallel-oriented thecae.

platform (Loydell & Maletz, 2004, p. 69). Smooth concavity, usually with a distinct genicular rim, in which the coiled metatheca with its aperture sits. Common to streptograptids but occurring also in other monograptids.

platycalycal (Bulman, 1968, p. 214; Maletz & Mitchell, 1996, p. 643). Descriptive term used in biserial graptolites (Axonophora) to denote a concentration of budding on the reverse side of the tubarium with a largely free sicula on the obverse side. It largely describes a dipleural development. See pericalycal.

pleural disk (Finney, 1985b, p. 361). Paired disk structures growing from the pleural list of the thecae in a non-retiolitid axonophoran in a horizontal to subhorizontal fashion. Known only in *Dicaulograptus cumdiscus.*

pleural list (Bates, Kozłowska, & Lenz, 2005, p. 710). Side lists; lateral longitudinal lists of the ancora sleeve, connected to successive lateral apertural lists (septal bars). The pleural lists in *Dicaulograptus cumdiscus* (Finney, 1985b) are thecal lists and not homologous to the pleural lists of the Retiolitidae.

plumes. See arms.

polymorphic. Pterobranch colony comprising more than one kind of zooid or tubarium with more than one type of theca (autothecae, bithecae) or gradational thecal developments along the stipes, as in many monograptids.

polypary (Scharenberg, 1851, p. 5); originally polypenartige Geschöpfe (German for polyp-like organisms).

Term used by earlier workers for the tubarium (see Elles & Wood, 1902, p. xxvi).

polypide (Sars, 1872, p. 8). Early term for pterobranch zooid, suggesting a bryozoan relationship.

polypidum (Harkness, 1851, p. 60). Old term for tubarium.

polyzoarium (Sars, 1874, p. 24). Old term for the tubarium of *Rhabdopleura.*

porus stage (Eisenack, 1942, p. 29); originally *Porus-Stadium* (German). First stage in the development of the initial foramen for the growth of the first theca in many graptolites, except for derived monograptids. A hole is formed in the ventral side of the sicula for the emergence of the first post-sicular zooid. See sinus stage, lacuna stage.

post-coronal orifices (Lenz, 1993a, p. 12). Openings in the ancora sleeve above the ancora umbrella in the Retiolitida; they can be described as ventral orifices.

preoral lobe (Lankester, 1884, p. 625). Anterior glandular lobe or disk in the zooids of the pterobranchs secreting the tubarium. See also cephalic shield.

primary lamellae (Harmer, 1905, p. 10). Term introduced for the fuselli of extant Pterobranchia.

primary porus (Eisenack 1942, p. 31). Pores left as an initial opening during the growth of the sicula through the sinus and lacuna stages. See resorption foramen.

primary stipe. Monsen (1925, p. 160) already differentiated between primary and secondary stipes (Hauptzweige and Nebenzweige). The term was to describe the stipes originating from the sicula. See order of stipes.

primordial astogeny (Mitchell, 1987, p. 354). The initial part of a graptolite colony exhibiting specialized ontogenies with thecae determining the proximal development type. See proximal development type.

primordial series (of thecae) (Elles, 1897, p. 189). The thecal series starting with $th1^1$ in a biserial dipleural colony. See *second series*.

primordial thecae (Holm, 1895, p. 437; Mitchell, 1987, p. 354). The initial thecae of a graptolite colony exhibiting specialized ontogenies. See primordial astogeny.

proboscis. Term for the head part of enteropneusts, homologous to the cephalic shield of the pterobranchs. Generally used as a biological term for the tubular feeding and sucking organs of invertebrates, but also for the trunk of elephants.

procladium (Urbanek, 1963, p. 147; Bulman, 1970). Term proposed for main stipe of cladia-bearing tubarium, with normal cladia being distinguished as metacladia. The term procladium could in theory be used for any graptoloid stipe, but the name would imply a cladial origin which is misleading. See cladium.

progressive branching (Cooper & Fortey, 1982, p. 177, fig. 6). Branching pattern in which each of the two new branches formed at a dichotomy divide again, as in *Clonograptus, Etagraptus*, forming a multiramous colony. See monoprogressive branching.

prosicula (Kraft, 1926, p. 222). The initial part of sicula, secreted as a cone with faintly marked spiral thread to which longitudinal fibers are added; called the *Initialteil* by Wiman (1895).

prosicular ring (Bates & Kirk, 1992, p. 57). The sclerotized remains of the prosicula, preserved as a ring defining the prosicular aperture in many Retiolitidae.

prosoblastic (Bulman, 1963b, p. 671; Mitchell, 1987, p. 354). Type of diplograptid proximal development in which $th2^1$, and ultimately $th1^2$, grew upward and forward from their origin; $th1^2$ is roughly J-shaped with a downward-growing initial part. See streptoblastic.

protheca. Initial part of graptoloid theca before differentiation of succeeding theca (insertion of the median septum). In taxa without an interthecal septum, the point at which the theca becomes a complete tube, e.g., when the foramen of the daughter theca is closed, can be defined as the start of the metatheca. See metatheca.

prothecal fold (Mu, 1957, p. 412 [English text]). Inverted U-shaped curvature of part of protheca (usually initial portion) giving a nodded appearance to the dorsal margin of the stipe.

proximal. First-formed part of the tubarium, nearest to the point of origin of the colony, the sicula.

proximal development type (Elles, 1922, p. 170; Cooper & Fortey, 1982, p. 171; Mitchell, 1987, p. 354). Initial budding sequence of the tubarium. Proximal development types are commonly used to identify evolutionary relationships within the graptolites. Individual types are variably named and are not listed here. See astogenetic patterns.

proximal structure (Cooper & Fortey, 1982, p. 173). The proximal structure refers to the orientation, attitude, and arrangement of proximal thecae.

pseudanastomosis (Rickards & Lane, 1997, p. 173). Temporary fusion of adjacent branches to form an ovoid mesh including the transfer of thecae between stipes. See anastomosis.

pseudocladium (Urbanek, 1963, p. 147). The regenerated stipe of a bipolar tubarium lacking a sicula. A pseudocladium is a regenerated stipe and not formed through cladial branching; thus, the term is inappropriate. See cladium.

pseudocortex (Urbanek & Mierzejewski, 1984, p. 76). Secondary component of cortical tissue produced by accumulation of sheets with an extremely scarce and poorly defined intersheet material devoid of any fibrous elements.

pseudopericalycal (Cooper & Ni, 1986, p. 317). Term used to describe the proximal development in glossograptids. See pericalycal.

pseudovirgula (Urbanek, 1963, p. 147). Dorsal rod in the cladia of some Monograptidae, originating as a thecal or sicular apertural spines. Term used by Loydell and Cave (1994) for a secondary nema in *Cochlograptus veles*. See virgula.

pustule (Bates, Kozłowska, & Lenz, 2005, p. 710). Regular protuberances on the sheet fabric bounding bandages of lists in Plectograptinae (Retiolitidae); first recognized by Eisenack (1951, fig. 11; Höckerchen [German]).

quadriradiate (Bulman, 1950a, p. 68). Proximal development with four first-order stipes originating from the sicula through three successive dicalycal thecae; originally quadri-radiate in Bulman (1950a, p. 68) and revised by Maletz (1992, p. 303). See biradiate, triradiate.

quadriserial. Scandent graptoloid tubarium comprised of four rows of thecae in back-to-back contact as in *Phyllograptus*. See biserial, monoserial.

Querrunzeln (Richter, 1871, p. 233). Richter (1871) erroneously described growth lines of graptolites with this term and remarked that they form a zigzag suture (*Zickzacknaht*) on the upper and lower side of the thecae (Zellen). See growth lines, fuselli.

radicle (Hall, 1865, p. 19). Term used by earlier workers to identify the point of origin of the stipes or the "initial point" in graptolite tubaria; vague reference to the unrecognized sicula in dichograptids.

reclined (Elles & Wood, 1901, p. 5, fig. 3). Graptoloid tubarium with branches growing upward, subtending an angle of less than 180° between their dorsal sides.

reflexed (Elles & Wood, 1901, p. 5, fig. 3). Graptoloid tubarium with branches growing upward, similar to reclined, but with distal extremities of the stipes tending to be horizontal.

regenerative virgula (Urbanek, 1963, p. 147). Thickened cortical fiber, secondarily formed as an axis of the pseudocladium (regenerated stipe), as the result of regeneration in the Monograptidae. This feature is a secondarily grown nema.

resorption foramen (Kozłowski, 1949, p. 22); originally bourgonnement perforant (French). Opening in the sicula, formed by resorption by the initial bud of the first theca (th1[1] zooid). Kozłowski (1949, p. 23) called the primary opening for later thecae the bourgonnement apertural. See porus.

reticulum (pl., reticula) (Elles & Wood, 1908, p. 333; Bates, Kozłowska, & Lenz, 2005, p. 710). Delicate irregular network of secondary lists on the ancora sleeve and the thecal walls of the Retiolitidae.

retroverted. Thecal apertures facing proximally as the result of the hooked or reflexed shape of the metatheca, following excessive growth of the dorsal wall of the theca.

reverse (Törnquist, 1893, p. 3). Side of the graptoloid tubarium in which the sicula is partly concealed by the crossing canal(s); Antisiculaseite of Wiman (1895, p. 263), Holm (1895, p. 436), and others. See obverse.

rhabdocortex (Urbanek & Towe, 1974, p. 13; Urbanek & Mierzejewski, 1984, p. 76). The common cortical envelope of a tubarium or of a group of thecae. See ectocortex.

rhabdosome (Törnquist, 1890, p. 6). Housing or domicile of graptolites; hydrosome, polypary, polypier, polypariet, and stock (listed in Ruedemann, 1904, p. 483) are comparable terms used in earlier literature (e.g., Tullberg, 1883: *hydrosoma*). See tubarium.

rhabdosome midline (Cooper & Fortey, 1982, p. 178, fig. 8). The primary axis of symmetry of the tubarium, which passes medially through the tubarium, from top to bottom. See tubarium midline.

right-handed (origin of thecae) (Stubblefield, 1929, p. 274; revised by Cooper & Fortey, 1982, p. 173). Origin on the (biologically) right side of the sicula or later theca when viewed from dorsal side of the stipe.

root. Irregular branching structure made from cortical tissue, developed from apex of the sicula and serving for the attachment of benthic graptolites. The term is not recommended as the anchoring construction is not a root system (as in modern plants), but a development for firm attachment on a surface only.

rutellum (pl., rutella) (Williams & Stevens, 1988, p. 20; Maletz & Mitchell, 1996, p. 644). Rounded, ventral, outward apertural elaboration on graptolite thecae. Initially intended for the sicula only. Homologous with the languette of the Dendroidea.

saccoid (Elles & Wood, 1914, p. 505). "Sac-like expansion" forming the initial part of the cladial thecae in *Cyrtograptus*.

scalariform. Preservational view presenting ventral (thecal) aspect of the graptoloid tubarium, mostly used for biserial taxa, but applicable also for other graptolites.

scandent (Elles & Wood, 1901, p. 5, fig. 3). Graptoloid tubarium with stipes growing erect distally and enclosing or including the nema.

Schraubenlinie (Kraft, 1926, p. 222). German term translated as helical line, spiral thread or spiral line; identical to ligne hélicoïdale of Kozłowski (1949, p. 56).

sclerotized. Hardening of the tubarium walls after the secretion of scleroproteic substances by zooid(s).

scopulae (Elles & Wood, 1908, p. 319; referred to Hopkinson & Lapworth, 1875). Peculiar ramifying fibrous development from edges of median septum (in lasiograptids); identified as reproductive processes in Hall (1865).

seam (Bates & Kirk, 1978, p. 429). Feature in retiolitid graptolites indicating the presence of unpreserved fusellar walls.

secondary lamella (Harmer, 1905, p. 10). Early term for the cortical tissue in extant Pterobranchia.

secondary lists (Lenz, 1994a, p. 1345). See reticulum.

secondary stipes. See order of stipes, primary stipes.

second series (of thecae) (Elles, 1897, p. 189). The thecal series starting with th1[2] in a biserial, dipleural colony. See primordial series.

selvage. Thickened margin or rim, especially of the aperture of thecae with cortical bandages. See apertural list.

septal bar (Bates & Kirk, 1978, p. 437). See lateral apertural list.

septum. Membrane separating thecal series or thecae. See interthecal septum; median septum.

sheet fabric (Urbanek & Towe, 1974, p. 4). Electron-dense, homogeneous, or very densely reticulated pellicle delimiting particular fuselli or layers.

sicula (Lapworth, 1873a, p. 501). Housing of the initial zooid of a graptolite colony, formed by the prosicula and metasicula. Richter (1871, p. 236) first recognized the role of the sicula and described it as the foot (Fuß in German) or attachment

(Haftorgan) in *Monograptus priodon;* radicle and initial part are similar terms used in earlier literature.

sicular bitheca (Bulman, 1927b, p. 18; Stubblefield, 1929, p. 272). First bitheca of graptolite colony, associated with the sicula and visible on the obverse side of the proximal end.

sicula side (*Siculaseite*) (Holm, 1895, p. 436; Wiman, 1895, p. 263). Side of the graptoloid tubarium in which the sicula is usually partly visible and the crossing canals are covered. See obverse.

sicular zooid. The first zooid of a colony, secreting the sicula. It is the only zooid of a colony produced by sexual reproduction.

sigmoidal structure (Lenz, 1993a, p. 12, pl. 18,5). Solidly sclerotized, sigmoidally curved, bladelike mid-ventral structure in some Retiolitinae, running from the transverse list to the genicular list.

sinistral (Cooper & Fortey 1982, p. 174). Anticlockwise growth direction of proximal thecae. See dextral.

sinus stage (Eisenack, 1942, p. 31); originally Sinus-Stadium (German). First stage in the development of the initial foramen for the growth of the first theca in monograptids. A deep notch is formed at the ventral side of the temporal aperture of the sicula. See lacuna stage, porus stage.

solid axis (Barrande, 1850, p. 4; Hall, 1865, p. 21); originally *axe solide* (French). Term used by earlier workers for the virgella and nema of the graptolite tubarium.

spinoreticuli (Lenz, 1993a, p. 15). Reticular lappets of fusellar material attached to the genicular lists at the upper apertural lists of some Retiolitidae, common in *Spinograptus, Agastograptus;* can be branched or replaced by simple spines.

spiral thread or **spiral line** (Kraft, 1926, p. 222); originally Schraubenlinie (German). Spiral line of single fusellus forming the prosicula; also ligne hélicoïdale of Kozłowski (1949, p. 56). See helical line.

stalk. See zooidal stalk.

statoblast. Large, closed vesicular bodies, interpreted as enclosing hibernating zooids; also identified as sterile buds by Schepotieff (1907b, p. 198). Allman (1869b, p. 61) described what appear to be arrested buds that have not burst through the wall of the axial tubarian chamber as statoblasts. Statoblasts were originally described for bryozoans (Polyzoa) by Allman (1856, p. 37). See dormant buds.

sterile buds (Schepotieff, 1907b, p. 198); originally *sterile Knospen* (German). Large, closed vesicular bodies, interpreted as enclosing hibernating zooids; see dormant buds, hybernacula (Schepotieff, 1907b, p. 200).

Stillstandsgürtel (Kraft, 1926, p. 234). See annulus.

stipe (Jaanusson, 1960, p. 303; Bulman, 1970, p. 11). Single branch of a branched graptolite tubarium, sometimes used for the entire colony (in monograptids); in its strict sense it refers to the segment between successive dichotomies in multiramous forms (Cooper & Fortey, 1982, p. 177). Earlier workers used the term frond (e.g., Hall, 1865). See branch, which is used interchangeably for stipe.

stoloblast (Urbanek & Dilly, 2000, p. 218). The soft tissues of the stolon and its organic sheath, including the buds in Rhabdopleuridae.

stolon (Schepotieff, 1906, p. 514); originally black stolon (schwarzer Stolo in German). Thin, sclerotized sheath surrounding the unsclerotized thread of soft tissue, from which pterobranch buds originate; identical to the pectocaulus of Lankester (1884, p. 634).

stolotheca (Kozłowski, 1949, p. 24; Cooper & Fortey, 1983, p. 212). Originally one of the three principal types of thecae in dendroid graptolites (autotheca, bitheca, stolotheca); according to Cooper and Fortey (1983, p. 212), stolotheca and autotheca form a single continuous unit, the autotheca.

stoma (pl., stomata) (Bates, Kozłowska, & Lenz, 2005, p. 710). Lateral (obverse and reverse) orifices in the ancora sleeve, sometimes bounded by a chimney-like reticular wall in Retiolitidae.

striae (Barrande, 1850, p. 8). See growth lines.

strengthening rods (Kraft, 1926, p. 224). See longitudinal strengthening rods.

streptoblastic (Bulman, 1963b, p. 671; Mitchell, 1987, p. 354). Type of diplograptid development in which $th1^2$, $th2^1$, and even $th2^2$ grow essentially downward, with $th1^2$ being S-shaped and growing initially upward from its origin. See prosoblastic.

supradorsal (Cooper, 1973, p. 52, fig. 5) In horizontal and reclined dichograptids, that portion of the sicula and theca 1^1 that projects above the line of the dorsal margin of the diverging stipes.

supragenicular wall (Jaanusson, 1960, p. 304). Thecal wall above the geniculum.

suture. Boundary between fuselli (zigzag suture) or in cases between thecae (arienigraptid suture).

sympodial growth. Type of colonial growth in which each zooid is in turn a terminal zooid of its branch. See monopodial growth.

synrhabdosome (Ruedemann, 1904, p. 483; Gutierrez-Marco & Lenz, 1998). Originally defined as a colony of colonies, but now interpreted as an association of graptoloid tubaria, normally of one species (with rare exceptions), attached distally by their long, thin nemata to a particle or enmeshed in a tangle of thin nemata; rarely are tubaria of a synrhabdosome attached by the virgellae. Ruedemann (1895, p. 224) used the term hydrosome for the synrhabdosomes and the term rhabdosome for single tubaria.

taeniocortex (Urbanek & Mierzejewska, 1978, p. 639). A secondary component produced by the accumulation of well-defined, ribbonlike units, bundles of cortical fibrils, or made of a different material and sealed by a sheet or free of it.

terminal theca. Last theca developed in a finite tubarium, often reduced in size. See appendix.

test (Barrande, 1850). Term used by earlier workers for the tubarium of graptolites.

theca (pl., thecae) (Lapworth, 1873a, p. 502). Sclerotized tube or housing of the individual zooids of a graptolite colony. Lapworth (1873a) identified the theca as a chamber in which the organism sits. The term cell or cellule was often used in the earlier literature (see Elles & Wood, 1902, p. XVII).

thecal aperture. Distal opening of the thecae; earlier workers used the term orifice (and *ostia*), which is now restricted to the openings in the ancora sleeve

of the Retiolitidae (Bates, Kozłowska, & Lenz, 2005, p. 709).

thecal bridge (Maletz, 2019c, p. 152). Development of lateral connections between adjacent stipes through thecal tubes, while stipes retain their consistent lateral distance. Thecal bridges can be formed from a single thecal tube or be complex and include more than one tube. (see dissepiments).

thecal framework (Bates, 1990, p. 717; Bates, Kozłowska, & Lenz, 2005, p. 710). Regular network of lists, of thecal origin (i.e., excluding the lists of the ancora sleeve) in retiolitids. It comprises the nema, virga, virgella, transverse lists, lateral apertural lists, lips, and connecting lists. It is part of the clathrium of the Retiolitidae.

thecal gradient. Change in thecal style along a stipe. see biform.

thecal notation (Elles, 1897, p. 189–190). Scheme used in the naming of thecae, which was introduced by Elles (1897) and revised most recently by Cooper and Fortey (1982, p. 175–175).

thecorhiza (Kozłowski, 1949, p. 141); originally thécorhize (French). Encrusting basal disk in Cyclograptidae, comprised principally of prothecae, from which metathecae and bithecae arise singly, in clusters, or as branches.

transverse list (Bates, Kozłowska, & Lenz, 2005, p. 710). List at the base of a thecal wall. Homologous with the aboral list of non-retiolitid graptoloids, but because the retiolitids have no interthecal septum, the tranverse list forms the distal part of the thecal aperture. Originally identified as transverse rod.

triad (budding) (Kozłowski, 1949, p. 23). Process of budding resulting in regularly alternating triads of autothecae and bithecae; one autotheca and one bitheca originate on alternate sides from a mother-autotheca. See Wiman rule (Kozłowski, 1949, p. 17: règle de Wiman).

triradiate (Bulman, 1950a, p. 68). Proximal development with three first-order stipes originating from the sicula through two successive dicalycal thecae; originally triradiate (Bulman, 1950a, p. 68); revised by Maletz (1992, p. 303). See biradiate, quadriradiate.

triserial. Stipes or tubaria bearing three rows of serially arranged thecae, arranged back to back. See uniserial, biserial, quadriserial.

tubarium (Lankester, 1884, p. 624). Dwelling or housing of the Pterobranchia, secreted from a glandular region on the cephalic shield of the pterobranch zooid; originally proposed for *Rhabdopleura* as a replacement for the inappropriate term coenoecium. Sars (1874) introduced the term polyzoarium for the genus *Rhabdopleura.* The term rhabdosome has long been used for the tubarium of extinct graptolite taxa (see Bulman, 1955, 1970). Mitchell and others (2013) reintroduced the term tubarum for extinct and extant Pterobranchia.

tubarium midline (Cooper & Fortey, 1982, p. 178, fig. 8; rhabdosome midline). The primary axis of symmetry of the tubarium, which passes medially through the tubarium from top to bottom. The tubarium is normally oriented, for descriptive purposes, with the sicula vertical, apex uppermost, and the tubarium midline vertical. In biserial graptolites, the midline lies along the median septum and the nema.

tubotheca (Kozłowski, 1970a, p. 394). Tubular structures without fuselli, on the tubaria of some Cyclograptidea and Dendroidea; interpreted as the tubes of other animals living in association with graptolite colonies.

twig (Wiman, 1895, p. 301); originally Zweig (German). Compound branches in some dendroid graptolites (callograptids). Wiman (1895) differentiated between Ast (branch or stipe) and Zweig (twig).

two thecae repeat distance (2TRD) (Howe, 1983, p. 635). Measuring unit for the thecal spacing, used most commonly for Monograptidae, but more recently introduced to diplograptid and dichograptid graptolites.

umbellate theca (Bulman, 1970, p. 12). Type of autotheca in some Cyclograptidae, characterized by enlarged, reflexed, umbrella-shaped hood extending back over the aperture of preceeding autotheca; initially called umbrella-like thecae (Bulman & Rickards, 1966, p. 62).

uniserial. Stipes or tubaria bearing a single row of serially arranged thecae. See biserial, triserial, quadriserial.

ventral (Kozłowski, 1949, p. 22). 1) The side of the metasicula giving rise to the rutellum and on which th1[1] originates (see Maletz, 1992). 2) Side of the stipe on which the thecal apertures are located; not necessarily related to position of growth of tubarium but assumed to be related to ventral side of the zooid.

vesicular diaphragm (Urbanek & Dilly, 2000, p. 222). Globular swelling on main stolon coinciding with the nodes or points of origin of daughter stolons in *Rhabdopleura.*

virga (Bates & Kirk, 1992, p. 57; Bates, Kozłowska, & Lenz, 2005, p. 710). List formed of cortical bandages laid down on the outer surface of the prosicula, which connects the nema and the virgella in Retiolitidae.

virgella (pl., virgellae) (Törnquist, 1897, p. 4; Kozłowski, 1949, p. 54, fig. 7F and footnote 2). Structure formed by the growth of the fuselli on the metasicula extending distally from the sicular aperture to form a spine; first described correctly by Kozłowski (1949); called the mouth-spine by Wiman (1896, p. 188). Maletz (2010a) described the evolutionary development and differentiated dorsal and ventral virgellae.

virgellarium (Urbanek, 1963, 175). Umbrella-shaped structure developed at the tip of the virgella in linograptids (Monograptidae); also used to describe other secondary secretions related to the virgella.

virgellar tape (Chen, 1986, p. 127 [English text]). Structure on the virgella, poorly defined, unclear.

virgula (Wiman, 1896c, p. 188). Term originally proposed for a hollow rod extending from the prosicula. Wiman (1896c, fig. 2 and 5) used the term even for the part of the virgella incorporated into the sicula in his illustrations of monograptids and diplograptids (including retiolitids). The virgula is the older term and is often used for the nema in monograptids but not for dichograptids (see Rickards, 1996). See nema, pseudovirgula.

web structure. See membrane.

Wiman rule (KOZŁOWSKI, 1949, p. 17); originally règle de Wiman (French). Process of budding resulting in regularly alternating triads of autotheca, bitheca, and stolotheca. See triad budding.

zigzag list (BATES, KOZŁOWSKA, & LENZ, 2005, p. 710). The zigzag list is made of clathrial lists or ancora sleeve lists.

zigzag suture (RICHTER, 1871, p. 233; KRAFT, 1926, p. 227); originally Zickzacknaht, Zick-Zacknaht, Wechselzeilennaht (German). Regular connection of the fusellar half rings on the dorsal and ventral sides of the thecae.

zooecium (pl., *zooecia*) (HARMER, 1905, p. 10). The individual housing tubes of *Cephalodiscus* zooids; term adopted from Bryozoa terminology. See tubarium.

zooid. Soft-bodied individual inhabiting the theca or the tubarium (thecal zooid, sicular zooid).

zooidal stalk (FOWLER, 1904, p. 25). Flexible connection of trunk of pterobranch zooid to stolon system; initially including the gymnocaulus.

THE HISTORY OF GRAPTOLITE CLASSIFICATION

Jörg Maletz

Graptolite classification has experienced highs and lows during more than 250 years of research, beginning with a lot of misunderstanding and a trial-and-error method of searching to find a useful taxonomy for the graptolites. Its path has included many wrong directions along the way. From our modern perspective and understanding of fossils, this haphazard search for improvement may seem puzzling, but we need to bear in mind that scientific improvement is a natural development that comes only with the increase of data. Elles and Wood (1902, p. i–xxviii) discussed in detail the history of graptolite research up to the early twentieth century, providing important insight into the early beginnings of classification.

THE EARLY YEARS

From the first notice of a possible graptolite published in the 1700s (von Bromell, 1727, as discussed in Tullberg, 1882b) until the 1850s, when early monographic works on graptolites began appearing, very little was written on these fossils. Linnaeus (1735) coined the term *Graptolithus* in his first edition of *Systema Naturae*. However, he did not regard *Graptolithus* as a fossil, later stating, "a fossil, properly speaking is not a graptolite" (Linnaeus, 1768, p. 173), but he intended its use for possible inorganic markings on shales. He provided an illustration of a "*Graptolitus*" in *Skånska resa* (Linnaeus, 1751), that can easily be recognized as the depiction of a graptolite (Fig. 111.1). It later became the term for all graptolites and still survives today in some form in the name for the subclass Graptolithina Bronn, 1849, even though the genus names *Graptolithus* Linnaeus, 1758 and *Graptolites* M'Coy, 1850 are now unfamiliar to us. Tullberg (1882b, p. 5) discussed the identity of the Linnaeus (1751) material and named the locality as a gravel hill near Östra Herrestad in Scania, Sweden. He identified the graptolite specimens as *Climacograptus scalaris* L. and *Monograptus triangulatus* Harkn., based on later records of graptolites from this locality, but the current whereabouts of this material is unknown. *Climacograptus scalaris* L. is recognized as *Normalograptus scalaris* (Hisinger, 1837) today (e.g., Loydell & Maletz, 2009) and provides the term for the scalariform view (ventral or apertural view) of biserial graptolites (Maletz, Bates, & others, 2014). *Demirastrites triangulatus* (Harkness, 1851) is an important index fossil for the *Demirastrites triangulatus* Biozone of the basal Aeronian, Llandovery age (Loydell, 2012).

Very little was written on graptolites during the early years of the 1800s, perhaps not surprisingly, until Wahlenberg (1821) realized that some of the Linnaeus material actually represented fossils. However, Wahlenberg accepted the Walch (1771, suppl. IVc) opinion referring the graptolites to the orthoceratites. In the following years, this was a common practice (e.g., Bronn, 1835; Geinitz, 1842). Other authors preferred to identify graptolites as polyps in a general sense (Murchison, 1839; Hisinger, 1837; Portlock, 1843). Quenstedt (1840, p. 274–276) discussed what he called 'Graptolithi Linn' under the heading Nautileen, but he suggested including these graptolites with the foraminiferans.

Brongniart (1828) described *Fucoides dentatus,* now *Levisograptus dentatus,* (see Maletz, 2011c) and *Fucoides serra*, now *Tetragraptus serra* (see Cooper & Fortey, 1982) as plants. In general, the research of graptolites was in its infancy, and paleontologists voiced quite diverse opinions on the taxonomical relationship due to the lack of sufficient data. Graptolites were related to hydroids, corals, even foraminiferans, and, not surprisingly, to plants. One can still expect that fossils described as early

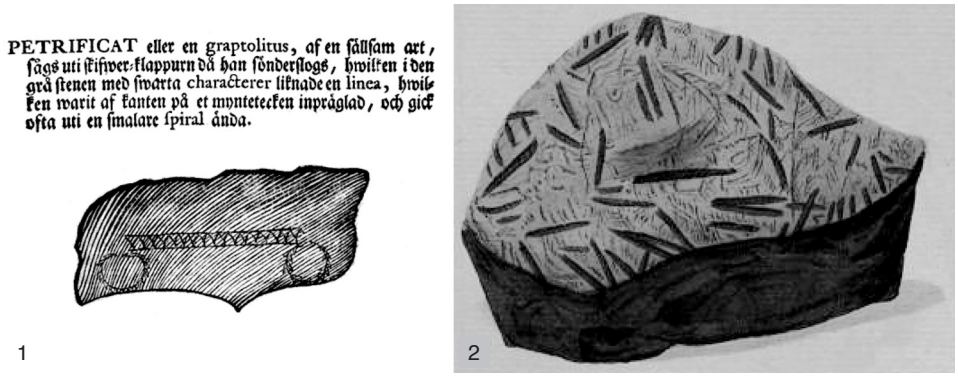


Fig. 111. Early graptolite illustrations. *1,* First illustration of *Graptolitus* (Linnaeus, 1751, p. 147); *2,* possible glacial boulder with graptolites, Stargard, Mecklenburg (Walch, 1771, pl. suppl. 4c,5).

land plants may turn out to represent pterobranchs, as demonstrated by the example of the Middle Ordovician *Boiophyton* from the Prague Basin (Kenrick, Kvacek, & Bengtson, 1999).

Some confusion arose over the naming of graptolites with the introduction of the genus name *Priodon,* apparently suggested but not published by S. Nilsson (see Tullberg, 1882b, p. 7; cited also in Elles & Wood, 1902, p. vii). The name was first used by Bronn (1835, p. 56), who indicated the homonymy with the genus *Priodon* Cuvier in Quoy & Gaimard, 1825 and introduced the genus name *Lomatoceras* instead. Hisinger (1837) replaced the name *Priodon* with *Prionotus* Hisinger, 1837, which, unfortunately, is a homonym of *Prionotus* Lacépède, 1801 (Osteichtyes, Triglidae). The classification confusion finally ended with the suppression of *Lomatoceras* through ICZN Opinion 198 (1954b). In the following years, a number of additional genus name taxa were erected, but the need for an upper-level taxonomy was not evident.

1850–1865

Joachim Barrande (1850) and James Hall (1847, 1865) laid the scientific foundation of graptolite research by describing their faunas with astonishing detail and insight and developed a first taxonomic system (Ruedemann, 1904, p. 469). The mid-nineteenth century was the time during which geologists in many regions of the world began to describe graptolite faunas (e.g., Harkness, 1851; Suess, 1851; Geinitz, 1852; Salter, 1852; Roemer, 1855). Thus, knowledge increased immensely and rapidly, and the graptolites settled into their place within the Anthozoa.

M'Coy (1850, p. 270) established the family Graptolitidae of the Silurian Radiata (Zoophyta) as the first family group taxon of the Graptolithina. He differentiated the uniserial taxa under the genus name *Graptolites* from the biserial ones for which he proposed the new name *Diplograpsis,* now *Diplograptus* (see Mitchell, Maletz, & Goldman, 2009). This may be viewed as the first step in the differentiation of genus-level taxa and the starting point of graptolite taxonomy. It also demonstrated that the differentiation of uni- and biserial taxa and later, the differentiation based on the number of stipes was becoming the basic concept of graptolite classification.

Barrande (1850) provided a terminology for the structural features he observed and recognized two subgenera, *Monoprion* and *Diprion*, based on the number of thecal rows. Additional genera were based on the characteristic isolation of the long thecae (*Rastrites* Barrande, 1850) and the ancora sleeve meshes of the retiolitids (*Gladiolites* Barrande, 1850; *Retiolites* Barrande, 1850).

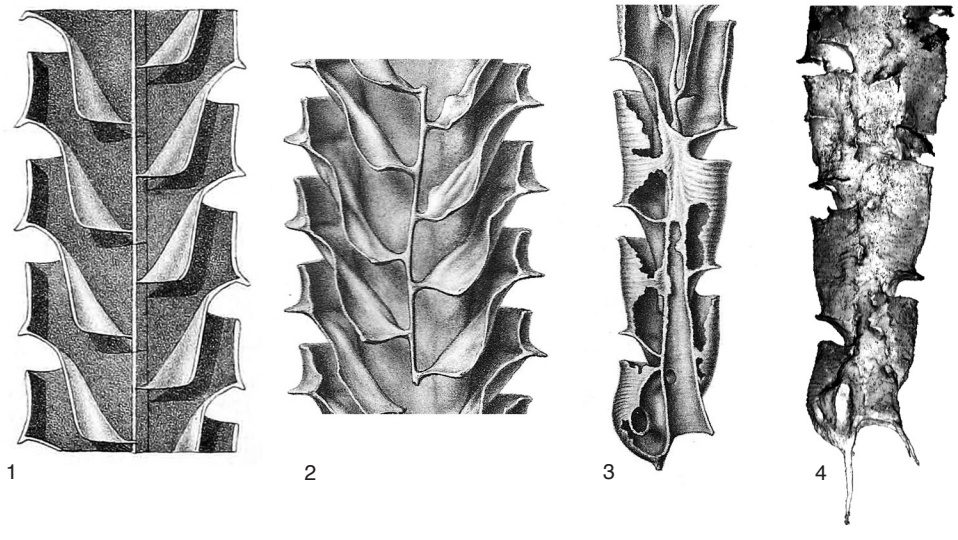


FIG. 112. Comparison of illustrations of *Geniculograptus typicalis* (HALL, 1865). *1,* Reconstruction of internal development (Hall, 1865, pl. A*9*); *2,* internal development, illustration by G. Liljevall for HOLM (Bulman, 1932c, pl. 5,*40a*); *3,* proximal end in obverse view, showing internal structure (Bulman, 1932c, pl. 5,*43*); *4,* proximal end in obverse view, SEM photo, reversed (new). Illustrations not to scale.

By the 1850s, GEINITZ (1852, p. 19) had already recognized five different genera of graptolites (*Diplograpsus, Nereograpsus, Cladograpsus, Monograpsus,* and *Retiolites*). He suggested abandoning the name *Graptolithus* because it was being used for all graptolites (in the same way that the term trilobite or ammonite was used) as an informal label for a group of organisms, an idea also advocated by GURLEY (1896). The genus *Graptolithus* was finally suppressed through ICZN Opinion 197 (1954a).

James HALL (e.g., 1847, 1865) was the second of the great observers of graptolite details. His illustrations (largely done by R. P. Whitfield) are highly accurate (Fig. 112.1), as can be confirmed from the preserved specimens in various museum collections. The illustrations, in part, are comparable to the illustrations of G. Liljevall for HOLM (Fig. 112.2–112.3) and even surpass modern SEM illustrations in clarity (Fig. 112.4). However, not even James HALL was immune to the inclusion of trace fossils as graptolites. For instance, he included *Oldhamia* FORBES, 1848 as a possible graptolite genus (HALL, 1865, p. 51), demonstrating that the scientific understanding of graptolites was not yet settled.

1866–1880

ELLES and WOOD (1902) described the years between 1866 and 1880 as a period in which British workers dominated graptolite research. The interval also saw the beginning of a more comprehensive biostratigraphic use of graptolite faunas. The increasing number of described genera and a better understanding of them led to the addition of higher-level taxa by NICHOLSON (1872a, 1872b) and LAPWORTH (1873a, 1873b), but the general structure of the taxonomic tree of the graptolites remained fairly simple (Fig. 113). The construction of the stipes from one, two, or more rows of thecae became the main character used for differentiation of groups within the graptolites. NICHOLSON (1872b, p. 101) used the Graptolitidae at the level of a subclass of the Hydrozoa and differentiated the sections Monoprionidae, Diprionidae, and Tetraprionidae based on the number of back-to-back attached stipes (uniserial, biserial, and quadriserial in modern terms). LAPWORTH (1873a, 1873b)

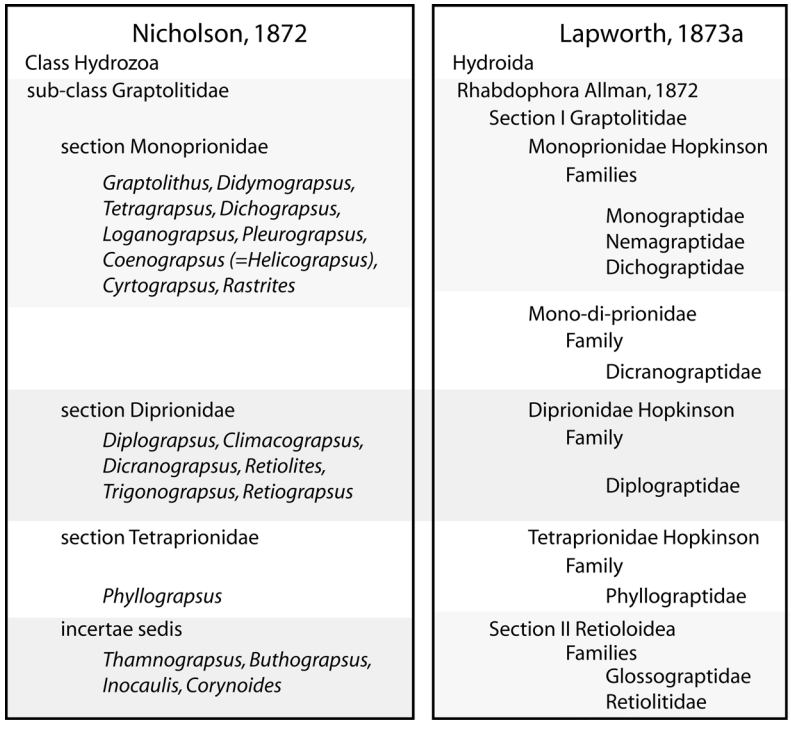


Fig. 113. Comparison of the graptolite taxonomy of Lapworth (1873a, 1873b) and Nicholson (1872b) (new).

assembled the graptolites under the term Rhabdophora Allman, 1872 and differentiated the Graptolitidae M'Coy, 1850 and the Retioloidea Lapworth, 1873b as two sections, each with a number of families (Fig. 113). The main difference between the two was Lapworth's addition of the Monodiprionidae (family Dicranograptidae) and the section II Retioloidea (which included Glossograptidae and Retiolitidae), taxa not considered by Nicholson (1872b). Nicholson (1872a) and Allman (1872) discussed the relationships of the graptolites and the extant pterobranchs (known only from *Rhabdopleura* at the time) and came to the conclusion that the graptolites were highly aberrant hydrozoans.

The classifications of Lapworth and Nicholson are not too different from Tullberg's (1883) classification, but Tullberg (1883, p. 12) introduced a number of new taxa with the Monophyontes, Monoamphiphyontes, and Amphiphyontes, which were not accepted by the community and quickly fell into disuse.

The most important aspect of graptolite research in this era became the demonstration of the biostratigraphical use of the graptolite faunas (Lapworth, 1878, 1879b, 1879c, 1879d, 1879e, 1880b, 1880c, 1880d, 1880e, 1880f), even though graptolites had been used for biostratigraphic purposes earlier (Hall, 1850; Nicholson, 1868b). A decade later, Lapworth's (1878) demonstration of the use of graptolite faunas in the thick greywacke succession of the Moffat Series was a milestone in stratigraphic and paleontological research (see Fortey, 1993, fig. 1). During the nearly 150 years since, our biostratigraphic resolution has increased considerably (Loydell, 2012), yet the basic succession of Lapworth is still recognizable and has changed very little. Today, graptolite biostratigraphy is a standard for working

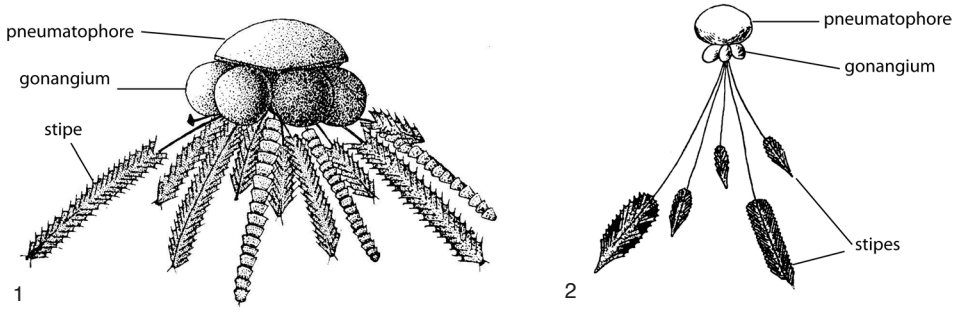


FIG. 114. Historical graptolite reconstructions. *1, Diplograptus pristis* HALL, 1865 (non HISINGER, 1837) (now *Orthograptus quadrimucronatus* (HALL, 1865) (adapted from Ruedemann, 1895, pl. 2); *2, Petalolithus folium* (HISINGER, 1837) (adapted from Frech, 1897, fig. 193). It should be noted that the gonangia and the pneumatophore have never been verified from fossil material and may not exist (Maletz, 2015).

with Paleozoic sedimentary successions and has become an important tool for geological exploration (e.g., PODHALAŃSKA, 2013).

1880–1918

In the years from 1880 to 1918, graptolite research was so dominated by the Scandinavian authors HOLM, MOBERG, TÖRNQUIST, and TULLBERG, that the period may be termed the Scandinavian Period. It is characterized by the detailed taxonomic and biostratigraphic description of very well preserved Ordovician and Silurian graptolite faunas of Scandinavia. The work of HOLM (1895) on chemically isolated, three-dimensionally preserved graptolites is a milestone in graptolite research, even though GÜMBEL (1878) was the first to observe graptolites chemically isolated from the surrounding rocks. This method provided much better information on the tubarium construction than the usual flattened shale material or the strongly tectonized specimens available to most researchers.

Much of HOLM's material of chemically isolated Ordovician graptolites from Scandinavian limestones was published posthumously by BULMAN (e.g., 1932c, 1933a, 1936a). The specimens possess fine details up to the presence of cortical bandages on the tubarium surface and provide, for the first time, detailed information on the proximal development of the graptolites. HOLM also worked with serial sections to understand the development of material trapped in the sediments.

FRECH (1897) introduced the differentiation into the Axonophora and the Axonolipa, based on whether the graptolite had development of the nema as a leading rod of the colony or lacked an extended nema. He identified the nema as an axis to which the thecae were attached in the Axonophora. According to FRECH (1897, p. 568), this axis was lacking in the Axonolipa. Even though he misinterpreted part of the graptolite colonies and their development (see Fig. 114.2), following the interpretation of the synrhabdosomes of RUEDEMANN (1895), the Axonophora were reintroduced into the graptolite classification by MALETZ, CARLUCCI, and MITCHELL (2009).

RUEDEMANN (1895) probably wrote the most influential paper of the period. His reconstruction of *Orthograptus quadrimucronatus* (HALL, 1865) under the name *Diplograptus pristis* presented a so-called supercolony with basal cyst or pneumatophore, gonangia, and numerous stipes. He also provided a dorsal and lateral view of a similarly reconstructed supercolony of *Diplograptus ruedemanni* (GURLEY, 1896). This interpretation (Fig. 114.1) may be regarded as the most discussed and most copied graptolite illustration ever. It still appears in modern paleontology textbooks

(e.g., Prothero, 2013), even though the gonangia and pneumatophore have not been verified from fossil material (Maletz, 2015).

THE TWENTIETH CENTURY

The twentieth century was dominated by detailed research on graptolite taxonomy and biostratigraphy and the recognition of the worldwide distribution of graptolite faunas. Graptolites are now known from all continents except Antarctica. The use of graptolite biostratigraphy in economical geology often led to increased research. The Bendigo and Castlemain goldfields of Victoria, Australia (see Hall, 1895; Phillips & Hughes, 1996) are the reason for the detailed Ordovician graptolite biostratigraphy established for the region (Harris & Thomas, 1938a; VandenBerg & Cooper, 1992). Research centers developed with a high number of scientists concentrating on graptolite research in Australia (T. S. Hall, Harris, Thomas); China (Hsü, Mu); Europe (Bouček, Bulman, Eisel, Jaeger, Kozłowski, Rickards); North America (Clark, Decker, Ruedemann); Russia (Obut, Sobolevskaya, Tzaj); and many other regions. The increasingly detailed work and mounting data led to two editions on graptolites published by the *Treatise on Invertebrate Paleontology* (Bulman, 1955, 1970), but taxonomic understanding diverged due to language barriers, lack of communication, and incompatible taxonomic concepts (see Rigby, 1986; Maletz, 2014b).

The constructional morphology of graptolites became important after the recognition of proximal-end development as a key to classification. This was possible with the availability of increasing amounts of chemically isolated graptolites and relief material. Kozłowski (1938, 1949) became one of the leading-edge scientists, describing numerous benthic graptolite taxa from material chemically isolated from cherts. Graptolites were now routinely identified based on their proximal-end construction, and numerous proximal-end development types were established (e.g., Fortey & Cooper, 1986; Mitchell, 1987; Melchin, 1998). Understanding of the distribution patterns of graptolite faunas along with the recognition that not all faunal elements are distributed worldwide, led to the development of the concept of graptolite biogeography (e.g. Skevington, 1969; Goldman & others, 2013).

CLADISTICS

In recent years, graptolite taxonomy and evolution have received a much-needed boost as cladistic methods became increasingly popular (e.g., Fortey & Cooper, 1986; Mitchell, 1987; Lenz & Melchin, 1997; Maletz, Carlucci, & Mitchell, 2009; Melchin & others, 2011; Štorch & others, 2011; Melchin, Lenz, & Kozłowska, 2017). This new method of analyzing graptolite construction and attaining information for a phylogenetic interpretation has dramatically changed our understanding of graptolite taxonomy and evolution. The concept centers around homologous characters and the monophyly of clades (Hennig, 1950, 1965). In the end, it is not really a new concept (see, for instance, Gegenbaur, 1870, p. 78–81), but the idea has never before been promoted so vehemently. Any taxonomic approach searches for homologous characters for classification but does not necessarily state this explicitly. Certainly, even Linnaeus (1758) thought about meaningful characters. Thus, early graptolite taxonomies used easily recognizable characters such as the number of stipes as sorting features. The Monoprionidae and Diprionidae were established as early as the nineteenth century (Hopkinson, 1869), and even now we use these in a modified sense as the Monograptidae and Diplograptidae. In general, they were correct and precise at the time and were based on useful characters, but "the devil is in the details," as the saying goes.

Apart from the latest compilations of the *Treatise* (Bulman, 1970), a comprehensive modern analysis of all graptolites does not exist. Mu and others (2002) provided the latest overview on current graptolite taxonomy in their compilation of all grap-

tolite faunas from China. They modified the taxonomic system slightly by adding and rejecting a number of family-level taxa. The latest classification (MALETZ, 2014b) provides a combination of cladistic and conservative phenetic taxonomy, keeping up with the established taxonomic groups but placing them on firmer ground through cladistic analyses when possible, while also accepting analyses from constructional morphology on the graptolite tubaria. See *Classification of the Hemichordata,* which follows on page 188.

CLASSIFICATION OF THE HEMICHORDATA

- Phylum Hemichordata Bateson, 1885a, p. 111
  - ?Class Planctosphaeroidea, van der Horst, 1936, p. 612
  - Class Enteropneusta Gegenbaur, 1870, p. 158
    - Stem group taxa (no family assignment)
    - Crown group taxa
      - Family Harrimaniidae Spengel, 1901, p. 215
      - Family Spengelidae Willey, 1899, p. 239
      - Family Ptychoderidae Spengel, 1893, p. 359
      - Family Torquaratoridae Holland & others, 2005, p. 374
  - Class Pterobranchia Lankester, 1877, p. 448
    - Subclass Cephalodiscida Fowler, 1892b, p. 297
      - Family Cephalodiscidae Harmer, 1905, p. 5
    - Subclass Graptolithina Bronn, 1849, p. 149
      - Family Rhabdopleuridae Harmer, 1905, p. 5
      - Family Cysticamaridae Bulman, 1955, p. 42
      - Family Wimanicrustidae Bulman, 1970, p. 52
      - Family Dithecodendridae Obut, 1964, p. 306
      - Family Cyclograptidae Bulman, 1938, p. 22
      - Order Dendroidea Nicholson, 1872b, p. 101
        - Family Dendrograptidae Roemer in Frech, 1897, p. 568
        - Family Callograptidae Hopkinson, in Hopkinson & Lapworth, 1875, p. 663
        - Family Mastigograptidae Obut & Sobolevskaya, 1967, p. 58
      - Order Graptoloidea Lapworth in Hopkinson & Lapworth, 1875, p. 633
        - Suborder Graptodendroidina Mu & Lin in Lin, 1981, p. 244
          - Family Anisograptidae Bulman, 1950, p. 79
        - Suborder Sinograptina Mu, 1957, p. 387
          - Family Sigmagraptidae Cooper & Fortey, 1982, p. 259
          - Family Sinograptidae Mu, 1957, p. 387
          - Family Abrograptidae Mu, 1958, p. 261
        - Suborder Dichograptina Lapworth, 1873b, table 1 facing p. 555
          - Family Dichograptidae Lapworth, 1873b, table 1 facing p. 555
          - Family Didymograptidae Mu, 1950, p. 180
          - Family Pterograptidae Mu, 1950, p. 180
          - Family Phyllograptidae Lapworth, 1873b, table 1 facing p. 555
        - Suborder Glossograptina Jaanusson, 1960, p. 319
          - Family Isograptidae Harris, 1933, p. 85
          - Family Glossograptidae Lapworth, 1873b, table 1 facing p. 555
        - Suborder Axonophora Frech, 1897, p. 607
          - Infraorder Diplograptina Lapworth, 1880e, p. 191
            - Family Diplograptidae Lapworth, 1873b, table 1 facing p. 555
            - Family Lasiograptidae Lapworth, 1879c, p. 454
            - Family Dicranograptidae Lapworth, 1873b, table 1 facing p. 555
            - Family Climacograptidae Frech, 1897, p. 607
          - Infraorder Neograptina Štorch & others, 2011, p. 368
            - Family Normalograptidae Štorch & Serpagli, 1993, p. 14
            - Superfamily Retioloidea Lapworth, 1873b, table 1 facing p. 555
              - Family Neodiplograptidae Melchin & others, 2011, p. 296
              - Family Retiolitidae Lapworth, 1873b, table 1 facing p. 555
            - Superfamily Monograptoidea Lapworth, 1873b, table 1 facing p. 555
              - Family Dimorphograptidae Elles & Wood, 1908, p. 347
              - Family Monograptidae Lapworth, 1873b, table 1 facing p. 555

PHYLUM HEMICHORDATA

Jörg Maletz and Christopher B. Cameron

Phylum HEMICHORDATA Bateson, 1885

[Hemichordata Bateson, 1885a, p. 111; *nom. transl. ex* class Hemichordata Bateson, 1885a, p. 111, Hyman, 1959, p. 74] [=Klasse Helminthomorpha Grobben, 1908, p. 505, *non* Helminthomorpha Pocock, 1887 (Diplopoda, millipedes); =subphylum Stomochordata Dawydoff, 1948, p. 367]

Hemichordate synapomorphies include a tripartite body; a muscular-secretory-locomotory preoral organ (enteropneust proboscis or pterobranch cephalic shield) that encloses a heart-kidney coelomic complex, including a stomochord; a collar with paired valved mesocoel ducts and pores; and a trunk that includes a ventral postanal extension of the metacoels (enteropneust juvenile tail or pterobranch stalk). *Cambrian, Terreneuvian* (*Fortunian*)*–Holocene* (extant): worldwide.

?Class PLANCTOSPHAEROIDEA van der Horst, 1936

[Planctosphaeroidea van der Horst, 1936, p. 612]

The species *Planctosphaera pelagica* Spengel, 1932 is based on a large, spherical larva that may exceed 25 mm in diameter and is the sole member of the monotypic class Planktospharoidea. The surface is laced with paired and ramified food grooves lined by two continuous ciliated bands used in filter feeding (Hart, Miller, & Madin, 1994). The viscera are clearly visible through the jelly interior and include a mouth that is located internal to paired stomodeal canals, followed by an esophagus, stomach, and intestine with a terminal anus. It has a triangular-shaped protocoel with a posterior extending duct and pore. A muscle strand connects the protocoel with an apical nerve plate, and from the other two corners paired horns extend anteriorly along the stomach. Paired mesocoels and metacoels are located on either side of the intestine. Except for the paired stomodeal canals to the mouth and the horns of the protocoel, all of these features are present in enteropneust tornaria. Other apomorphies include a ventral depression that extends into the larva as paired boot-shaped diverticula positioned on either side of the intestine and posterior stomach.

Planctosphaera Spengel, 1932, p. 4 [**P. pelagica;* OD]. Hypertrophied, spherical tornaria-type larva with bilateral symmetry; gut system U-shaped; mouth and anus close together on ventral side; surface covered by a complex ciliated band; internal organs occupy only a small part of the whole sphere. *Holocene* (extant): Atlantic Ocean, Pacific Ocean (no known fossil record).——Fig. 115. **P. pelagica* Spengel, Bermuda, western Atlantic Ocean, scale bar, 5 mm (Hart, Miller, & Madin, 1994, fig. 1B).

The taxonomic and phylogenetic affinities of *Planctosphaera pelagica* are not clear but its morphology is similar to that of enteropneust tornaria (Spengel, 1932; van der Horst, 1936) and its deep-water collection localities suggest that it may be a hypertrophied tornaria that has not undergone metamorphosis due to absence of a settlement cue (Hadfield & Young, 1983). Hadfield (1975) and Halanych, Tassia, and Cannon (2019) regarded the taxon as the giant larva of a deep-water enteropneust, thus, probably of the Torquaratoridae.

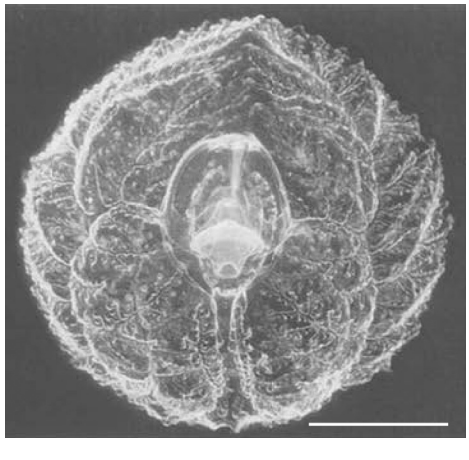


Fig. 115. Class Planctosphaeroidea (p. 189).

A few specimens of *Planctosphaera pelagica* were collected from deep-water trawls in the Bay of Biscay (Spengel, 1932; Damas & Stiasny, 1961) and other regions of the Atlantic Ocean (see Scheltema, 1970, fig. 1), but it is also known from shallow water adjacent to Bermuda (Hart, Miller, & Madin, 1994). Specimens from the Pacific Ocean are from a depth of 75–500 m near O'ahu in the Hawaian islands (Hadfield & Young, 1983). Scheltema (1970) suggested this was a warm-water species due to the biogeographic distribution of the few known specimens. Hadfield and Young (1983) suggested a worldwide distribution of this organism probably originating from abyssal depths. Hart, Miller, and Madin (1994) described suspension feeding of a single living larva from surface waters near Bermuda in the western Atlantic Ocean.

CLASS ENTEROPNEUSTA

Christopher B. Cameron

Class ENTEROPNEUSTA Gegenbaur, 1870

[*nom. correct*. Haeckel, 1879, p. 469 *pro* Enteropneusti Gegenbaur, 1870, p. 158]

Free living, solitary worms ranging from lengths of less than a millimeter to 1.5 meters; entirely marine; body tripartite, with proboscis, collar, and trunk; proboscis coelom contains heart-kidney-stomochord complex; preoral ciliary organ posterior-ventral; collagenous Y-shaped nuchal skeleton extends from proboscis through neck before bifurcating into paired horns in collar; paired dorsal perihaemal coeloms associated with collar dorsal blood vessel; anterior trunk pharynx perforated with paired gill slits that connect via atria to external gill pores; mesocoel ducts connect collar coeloms to first pair of gill pores atria; larvae possess locomotory ciliated band (telotroch), and when tornaria present, apical plate retractor muscle. *Cambrian* (*Miaolingian, Wuliuan*)*–Holocene* (extant): worldwide.

The class Enteropneusta is differentiated among four living families: the Harrimaniidae, Spengelidae, Ptychoderidae, and Torquaratoridae, based in large part on the structure of the heart-kidney coelomic complex, gills, gonads, liver sacs, and diverticula of the coelomic compartments. The modern families are a crown group clade with respect to the Cambrian fossil stem group, which includes *Oesia disjuncta* Walcott, 1911 and *Spartobranchus tenuis* (Walcott, 1911).

The following systematic descriptions are limited to eight genera with fossil evidence—three from the stem group, and five from the crown group. Excluded genera are only known from extant species. What we understand at this point, based on the pattern of appearance of these seven fossil acorn worm species, is: 1) the evolution of acorn worms is characterized by an evolutionary stasis—the harrimaniid body plan of *Spartobranchus tenuis* appears in the Cambrian and persists to this day in the Harrimaniidae, including *Saccoglossus* (Fig. 117); 2) this body plan was followed by that of a spengelid in *Mazoglossus ramsdelli* from the Pennsylvanian (Bardack, 1997) and then by a torquaratorid, characterized by collar lips, in a Lower Triassic trace fossil (Twitchett, 1996); and 3) the complex ptychoderid body plan appeared last in *Ptychodera callovianum* from the Upper Jurassic (Alessandrello, Bracchi, & Riou, 2004; Cameron, 2016) (Fig. 117).

STEM GROUP TAXA

The stem group enteropneusts include tube-dwelling taxa with a vermiform body that consists of a proboscis, a collar, and a

trunk with a pharynx framed by multiple, paired, circumferential gill bars and slits.

Gyaltsenglossus Nanglu, Caron, & Cameron, 2020, p. 4238 [**G. senis;* OD]. Vermiform with a maximum length of ~2 cm; body consists of an elongate, ovoid proboscis, a crown of six feeding arms, a cylindrical trunk, and a round posterior structure; feeding arms possess roughly 15 pairs of symmetrical tentacles; gut is straight; anus terminates immediately before the posterior structure. *Cambrian* (*Miaolingian, Wuliuan, Bathyuriscus* Biozone–*Elrathia* Biozone): Canada.——Fig. 116,*3. *G. senis,* holotype, ROMIP 65606, scale bar, 2 mm (Nanglu, Caron & Cameron, 2020, fig. 1).

Oesia Walcott, 1911, p. 132 [**O. disjuncta;* OD [=*Margaretia* Walcott, 1931, p. 2 (type, *M. dorus,* OD), Nanglu & others, 2016, p. 2] Tripartite body with proboscis, collar, and trunk; trunk unusual, possessing extensive pharynx and lacking esophagus and intestine; posterior grasping appendage; tubes, fibrous with spirally arranged openings. *Cambrian* (*Miaolingian, Wuliuan, Bathyuriscus* Biozone–*Elrathia* Biozone): Canada.——Fig. 116,*2. *O. disjunta,* USNM 57630, lectotype (selected by Szaniawski, 2005, p. 2), one of three specimens illustrated by Walcott (1911), Burgess Shale, Walcott Quarry, British Columbia, Canada, scale bar, 10 mm (new, photo by J.-B. Caron).

Spartobranchus Caron, Conway Morris, & Cameron, 2013, p. 503 [**Ottoia tenuis* Walcott, 1911, p. 130; OD]. Vermiform, maximum length 10 cm; body comprised of short proboscis, collar, pharyngeal area with as many as 40 pairs of gill and tongue bars; elongate posterior trunk ending in bulbous unit; gut straight, anus terminal; approximately one-quarter of specimens associated with tube of organic walls; tube varies from straight, completely circular, to helicoidal, and sometimes branching; no more than one individual per tube has been observed. *Cambrian* (*Miaolingian, Wuliuan, Bathyuriscus* Biozone–*Elrathia* Biozone): Canada.——Fig. 116,*1a–b. *S. tenuis* (Walcott); *1a,* USNM 108494, lectotype (selected by Caron, Conway Morris, & Cameron, 2013, supplement 1, from a small number of specimens supposedly collected by Walcott [1911], who described but never illustrated *Ottoia tenuis,* and the whereabouts of his material is unknown), specimen missing proboscis and terminal portion of trunk, polarized light; *1b,* complete specimen, ROM 62123; scale bars, 3 mm in 1*a,* 2 mm in *1b* (Caron, Conway Morris, & Cameron, 2013, fig. 1).

CROWN GROUP TAXA

Family HARRIMANIIDAE Spengel, 1901

[Harrimaniidae Spengel, 1901, p. 215]

Simple morphology, largely characterized by features it lacks; no dorsal collar nerve roots arising from the collar nerve cord; gills lack synaptaculae that bridge primary and secondary gill bars; trunk lacks hepatic sacs, circular muscle fibers, and lateral septa, only dorsal and ventral septa present; intestinal pores only rarely present; posterior projecting horns of Y-shaped proboscis skeleton extend at least to middle of collar; longitudinal proboscis musculature may be arranged diffusely, in radial plates, or in

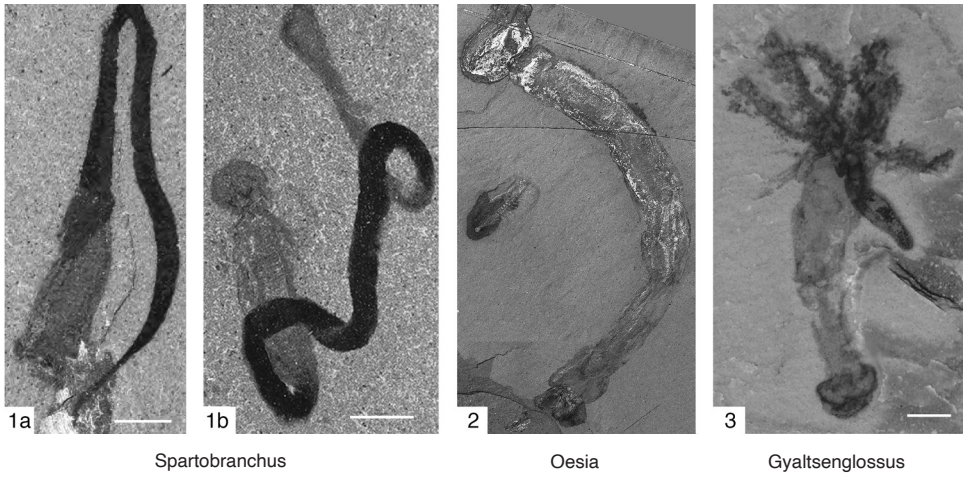


Fig. 116. Stem group Enteropneusta (p. 191).

concentric rings; development via short-lived, non-feeding larvae that become juveniles with adhesive post-anal tail. *Carboniferous* (*Pennsylvanian, Moscovian*)–*Holocene* (extant): worldwide.

The Harrimanidae comprises ten living genera, including one (*Saxipendium* Woodwick & Sensenbaugh, 1985) that was previously assigned to its own family (Deland & others, 2010; Worsaae & others, 2012). *Saccoglossus* is the most speciose and familiar genus (Cameron, Deland, & Bullock, 2010). Its longitudinal proboscis musculature is arranged in concentric rings, whereas other genera may be arranged diffusely (e.g., *Mesoglossus*) or in radial plates (e.g., *Protoglossus* van der Horst, 1939).

Saccoglossus Schimkewitsch, 1892, p. 2 [**Balanoglossus mereschkowskii* Wagner, 1885, p. 46; OD] [=*Balanoglossus* (*Dolichoglossus*) Spengel, 1893, p. 360 (type, *D. kowalewskii* Agassiz, 1873, SD Spengel, 1901, p. 215)]. Proboscis long; longitudinal muscle fibers of proboscis arranged in several concentric rings; middorsal longitudinal groove may be present; collar usually very short compared to proboscis; dorsal interbranchial genital ridges and dorsal gonads absent but lateral extrabranchial genital ridges may be present; intestinal pores typically present; perihaemal cavities always present; peribuccal cavities usually present. [Many species favor quiet muddy-sandy flats not far from the mouth of a bay, living in semi-permanent and helical-shaped burrows and throwing up low conical mounds of quasi-spiral fecal castings. See Cameron, Deland, and Bullock, 2010; also see Fig 4.2.] *Carboniferous* (*Pennsylvanian, Moscovian*)–*Holocene* (extant): worldwide.——Fig. 117,*1. S. testa* Cameron, 2016, holotype, FMNH PE 45216, one of two counterparts, scale bar, 1 cm (new).

Megaderaion Arduini, Pinna, & Teruzzi, 1981, p. 105 [**M. sinemuriense;* OD]. Elongate worm divided into elongate, rounded, and ogival proboscis; collar wider than long, tapering trunk; single specimen small (2 cm) lacking gonadal wings, hepatic sacs, and enlarged branchial region, characteristic of family Harrimaniidae; resembles *Mesoglossus,* with medium-long proboscis. [See Deland & others, 2010.] *Lower Jurassic* (*Sinemurian, Coroniceras bucklandi* Biozone): Italy.——Fig. 117,*2. *M. sinemuriense,* holotype, i751, Museo Civico di Storia Naturale di Milano, scale bar, 2 mm (Arduini, Pinna, & Teruzzi, 1981, fig. 1).

Family SPENGELIDAE Willey, 1899

[Spengelidae Willey, 1899, p. 239] [=Glandicipitidae Spengel, 1901, p. 215]

Anterior vermiform process of stomochord present in all members; skeletal horns usually extend over whole length of collar; dorsal nerve roots arising from collar nerve cord rare; lateral septum absent; hepatic caeca and synapticula may or may not be present; circular muscle fiber layer positioned inside longitudinal muscle layer in trunk. *Carboniferous* (*Pennsylvanian, Moscovian*)–*Holocene* (extant): worldwide.

In the cases where development has been documented, Spengelidae species have a tornaria larva (Cameron & Perez, 2012). The family includes four living genera (see **van der** Horst, 1939; Cameron & Perez, 2012). Cameron (2016) referred *Mazoglossus ramsdelli* to the family Spengelidae, thus, extending an extant enteropneust family to include a Carboniferous fossil species.

Mazoglossus Bardack, 1997, p. 89 [**M. ramsdelli;* OD]. Small (specimens less than 10 cm total length); recognizable as an enteropneust by outline shape of proboscis, collar, and trunk. *Carboniferous* (*Pennsylvanian, Moscovian*): USA (Illinois).——Fig. 117,*3. *M. ramsdelli,* FMNH PE 23053, one of two counterparts, complete specimen, scale bar, 1 cm (adapted from Cameron, 2016, fig. 2C).

Family PTYCHODERIDAE Spengel, 1893

[Ptychoderidae Spengel, 1893, p. 359] [=Balanoglossidae Willey, 1899, p. 239]

Lateral septa in trunk; invariable absence of abdominal pores; lack of vermiform process of stomochord; dorsal nerve roots in collar present; skeletal horns rarely reach beyond anterior half of collar; synapticulae form bridges between primary and secondary gill bars in pharynx, hepatic caeca usually present; dorsolateral ciliated grooves in abdominal part of alimentary canal; circular muscle fibers in trunk, usually outside the longitudinal fibers; development occurs through typical tornaria larva. [Cameron & Ostiguy, 2013, p. 144.] *Middle Jurassic* (*Callovian*)–*Holocene* (extant): worldwide.

Ptychoderidae includes four extant genera, including the familiar *Balanoglossus*. *Mesobalanoglossus* is herein included in the Ptychoderidae. Cameron (2016) referred the Middle Jurassic *Megaderaion callovianum*

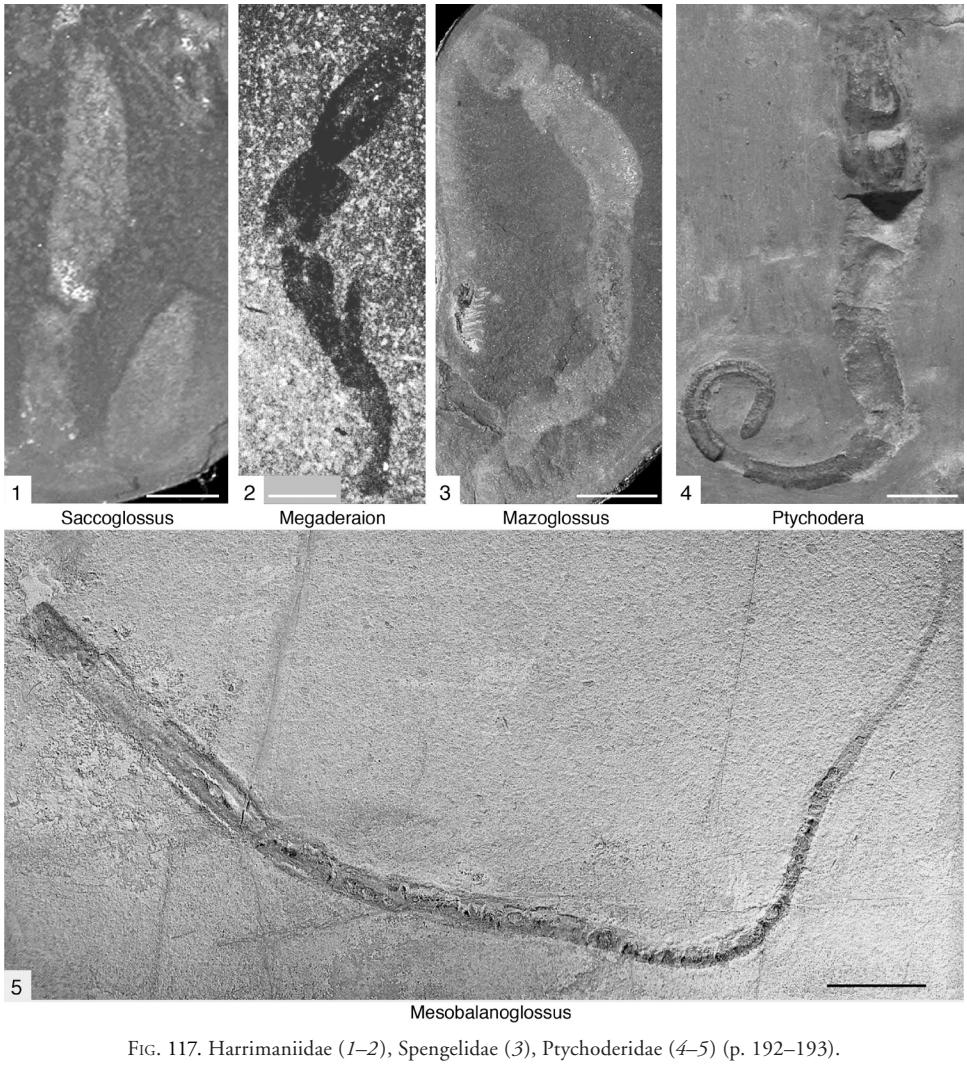


FIG. 117. Harrimaniidae (*1–2*), Spengelidae (*3*), Ptychoderidae (*4–5*) (p. 192–193).

ALESSANDERELLO, BRACCHI, & RIOU, 2004 to the Ptychoderidae. The species is herein included in the genus *Ptychodera*.

Ptychodera ESCHSCHOLTZ, 1825, p. 740 [**P. flava;* M]. As for family, except gill pores open by long slits, whereas those of *Balanoglossus* open by small pores. Middle Jurassic (Callovian)–Holocene (extant). ——FIG. 117,*4. P. callovianum,* (ALESSANDRELLO, BRACCHI & RIOU, 2004), holotype, MNHN L.P.M.-B. 48352, scale bar, 5 mm.

Mesobalanoglossus BECHLY & FRICKHINGER in FRICKHINGER, 1999, p. 77 [**M. buergeri;* OD] Single specimen, 68.8 cm long, with diminutive proboscis, collar, and long trunk with bristles interpreted as gill bars; trunk tapers posteriorly, anterior wide part interpreted as gonadal wings. *Upper Jurassic* (*lower Tithonian, Hybonoticeras hybonotum* Biozone): Germany.——FIG. 117,*5. *M. buergeri,* holotype, scale bar, 5 cm (Bechly & Frickhinger in Frickhinger, 1999, fig. 144).

Family TORQUARATORIDAE Holland & others, 2005

[Torquaratoridae HOLLAND & others, 2005, p. 374]

Proboscis broad, short, dome shaped; collar wide, usually embellished with lateral lips; body semi-transparent, frequently brightly colored; muscular system poorly developed; collagenous proboscis skeleton



and gill bars greatly reduced; proboscis skeletal horns absent from all species but *Torquarator bullocki* (Holland & others, 2005). *Lower Triassic* (*upper Olenekian*)–*Holocene* (extant): worldwide.

The family Torquaratoridae is exclusive to the deep sea (Holland & others, 2005, 2009; Holland, Kuhnz, & Osborn, 2012). There are seven genera (Jabr, Archambault, & Cameron, 2018; Ezhova, 2021).

Fossil specimens of the Torquaratoridae are unknown, but a single resting trace from the Lower Triassic (Olenekian) Werfen Formation of northern Italy (Twitchett, 1996) suggests, through its characteristic shape, the presence of the family in the Mesozoic (Fig. 118).

Fig. 118. Resting trace of torquaratorid enteropneust, scale bar, 1 mm (Twitchett, 1996, fig. 2.1).

PTEROBRANCHIA

Jörg Maletz and Christopher B. Cameron

Class PTEROBRANCHIA Lankester, 1877

[Pterobranchia Lankester, 1877, p. 448]

Fixed, sedentary to planktic organisms with communal or colonial zooids divided into three regions: preoral lobe (cephalic shield), collar, and trunk; collar extends to form one or more pairs of arms, each bearing double row of ciliated tentacles; trunk elongated posteriorly to form a zooidal stalk that extends to pectocaulus as interconnection between zooids in colonial forms; soft gymnocaulus connects developing buds and permanent terminal zooid in *Rhabdopleura* Allman, 1869; external organic (?collagen, keratin, or chitin) housing or domicile (tubarium) comprised of a series of tubes built from sequential addition of rings or half rings of organic material (fusellum) in most taxa. Cambrian (Series 2, Stage 3–4, *Olenellus* Zone)–*Holocene* (extant): worldwide in marine environments.

PTEROBRANCHIA *incertae sedis*

Maletz and Steiner (2015) included the genus *Yuknessia* Walcott, 1919 as *incertae sedis* in the Pterobranchia, as they were not able to recognize details supporting an inclusion in the Cephalodiscida or Graptolithina,

even though they provided definite evidence of fusellar construction (see also LoDuca & others, 2015).

Yuknessia Walcott, 1919, p. 235 [**Y. simplex;* M]. Organisms with long, slender thecal tubes formed from organic material and bearing evidence of fusellar construction; thecal tubes may widen toward the aperture; circular attachment structures at base of tubes; no interconnection between individual tubes recognizable. *Cambrian* (*Miaolingian, Wuliuan, Bathyuriscus/Elrathina–Ptychagnostus punctuosus* Zones): Canada, USA.——Fig. 119. **Y. simplex* Walcott, 1919, USNM 35406, holotype, scale bar, 5 mm (Maletz & Steiner, 2015, fig. 15).

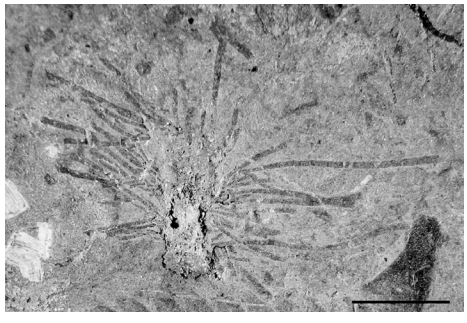


Fig. 119. Pterobranchia *incertae sedis* (p. 195).

SUBCLASS CEPHALODISCIDA

Jörg Maletz and Paul Gonzalez

Subclass CEPHALODISCIDA Fowler, 1892

[Cephalodiscida Fowler, 1892b, p. 297] [=Cephalodiscoidea Beklemishev, 1951]

Fixed, sedentary marine organisms with communal zooids divided into three regions, preoral lobe (cephalic shield), collar, and trunk; collar extends to form several pairs of arms, each bearing double row of ciliated tentacles; trunk elongated posteriorly to form stalk with sucker at base from which new zooids are generated asexually; external proteinaceous housing or domicile (the tubarium) comprised of series of tubes built from sequential addition of full rings or half rings of organic material in most taxa; tubaria with separate zooidal tubes to communal dwellings; housing construction unknown in one genus. *Cambrian* (*Miaolingian,* ?*Wuliuan*)–*Holocene* (extant): worldwide in marine environments.

INTRODUCTION

The Cephalodiscida is a group of pseudocolonial, benthic organisms, typically living in large communities and known largely from extant members. The 18 described extant species belong to a single genus, *Cephalodiscus,* which is divided into four subgenera: *C.* (*Orthoecus*), *C.* (*Idiothecia*), *C.* (*Cephalodiscus*), and *C.* (*Acoelothecia*). These species are present in waters from the Antarctic to the tropics. See Table 1 for the geographical ranges.

Most species were described from fixed specimens acquired at great depths during expeditions of the late nineteenth and early twentieth centuries and have not been studied since. Most recent observations of living colonies were of a shallow water population of *C.* (*C.*) *gracilis* from Bermuda.

Zooid morphology is fairly homogenous across species (see p. 5–7). Individual zooids are small (1–10 mm) and exhibit the tripartite body plan characteristic of the phylum Hemichordata. The anterior body region (prosome) consists of a ciliated cephalic shield used for locomotion and secretion of the tubarium. The mesosome, or collar region, extends into two to nine pairs of arms (depending on species and developmental stage) used in filter feeding. Ciliated tentacles on each arm capture food particles, and cilia on the arms transport it toward the mouth. The trunk contains the U-shaped digestive tract and extends into an extensible stalk. The stalk ends in an adhesive disk, from which asexually budded individuals originate. Unlike rhabdopleurid pterobranchs, cephalodiscids possess gill slits, a defining feature of Deuterostomia. In enteropneust hemichordates and filter-feeding chordates, the pharynx is perforated with tens to hundreds of gill slits used in pumping water. In cephalodiscids, only one pair of gill slits is present. This reduction may be associated with the evolution of external filter feeding with arms and tentacles in the pterobranch lineage.

Table 1. Geographical range of *Cephalodiscus*

Region	Species
Antarctic waters	*C.* (*C.*) *hodgsoni* Ridewood, 1907 [=*C.* (*C.*) *aequatus* Andersson, 1907] *C.* (*C.*) *inaequatus* Andersson, 1907 *C.* (*I.*) *nigrescens* Harmer, 1905 *C.* (*O.*) *densus* Anderson, 1907 *C.* (*O.*) *solidus* Andersson, 1907
Subantarctic waters	*C.* (*C.*) *dodecalophus* M'Intosh, 1887
Temperate regions	*C.* (*I.*) *levinseni* Harmer, 1905 *C.* (*I.*) *evansii* Ridewood, 1918 *C.* (*O.*) *australiensis* Johnston & Muirhead, 1951 *C.* (*I.*) *gilchristi* (Ridewood, 1906)
Tropical regions	*C.* (*C.*) *gracilis* Harmer, 1905 *C.* (*C.*) *sibogae* Harmer, 1905 *C.* (*C.*) *indicus* Schepotieff, 1909 *C.* (*C.*) *graptolitoides* Dilly, 1993

Cephalodiscid communities appear to originate from a single, sexually produced founder zooid, comparable to the sicular zooid of the Graptolithina (see 7–9). Subsequently formed members of the pseudocolony are produced asexually through budding from the base of the stalk. Mature zooids may separate from the stalk of the mother zooid and lead an independent life but stay in the community. Thus, in many tubaria, a number of interconnected zooids (as many as 20 in some species) at various stages of development are attached to the base of the stalk of the mother individual, and entirely separate individuals may be rare (see Lester, 1985; Dilly, 2014). Mature zooids formed through asexual budding appear to be able to reproduce asexually. This method of asexual reproduction differs from rhabdopleurid pterobranchs, in which asexually budded individuals remain connected by a stolon system. In this regard, cephalodiscids represent an intermediate strategy between solitary enteropneusts and fully colonial rhabdopleurid pterobranchs.

TUBARIUM CONSTRUCTION

The Cephalodiscida secrete a housing construction, the tubarium, from fuselli and cortical material (with the possible exception of *Atubaria* Sato, 1936, in which zooids appear to be living as naked individuals on corals). Contrasting with their highly conserved zooidal morphology, the tubaria of the Cephalodiscida are very diverse and form the basis of their taxonomy. Because the tubarium is the only feature that can be compared with graptolites, observations on tube building and behavior in extant cephalodiscids may provide insights into the morphology and behavior of extinct species.

The tubaria can be encrusting, compact, or even branched, dendroid in shape, and replicating many shapes, as seen in colonial Graptolithina. In many taxa, the individual dwelling tubes of the zooids are completely separate, forming pseudocolonies where large masses of tubes are connected by or enclosed in extrathecal (cortical?) material. However, in some taxa, a communal dwelling of interconnected tubes or other three-dimensional constructions is formed for the protection of the zooids. Apertural openings may be smooth and straight or bear a variety of elaborations, from robust rutelli to strong apertural spines.

There are three major types of tubarium organization in *Cephalodiscus:* 1) In *Cephalodiscus* (*Orthoecus*), the tubarium is comprised of discrete, nearly straight and parallel-sided tubes (Fig. 120.5). The individual tubes originate from a basal surface, a hardground or rock surface, and create a meadow. Tubes are built of somewhat annular growth increments resembling the fuselli of graptolites and are cemented together by secondary deposits that contain large amounts of embedded foreign material (sand, debris). 2) In *Cephalodiscus* (*Idiothecia*), the individual tubes are partly enclosed in a thick development of cortical tissue and form erect structures, commonly with branching stipes. These tubes are closed at the base and have straight to rutellate openings oriented in every direction (Fig. 120.1). Observations in *C.* (*Idiothecia*) *nigrescens* indicate that more than one adult and its buds may share a single tube (Dilly, 2014). 3) In the subgenus *C.* (*Cephalodiscus*), discrete cylindrical tubes are lacking, and the tubarium consists of an interconnected network of irregularly shaped cavities. The openings in the communal tubaria (generally termed ostia) are either simple or adorned with single or multiple spines (Fig. 120.2–120.3, Fig. 120.6) on which zooids perch to feed (Lester, 1985). Addition of material between preexisting spines is common, and spines are commonly embedded into the walls of the tubarium. Most species form erect branching tubaria, with lateral connections resembling the dissepiments and anastomosis of the Graptolithina. Encrusting forms also occur, for example, *Cephalodiscus* (*C.*) *graptolitoides*. Thecal apertures of the *Cephalodiscus* (*C.*) *calciformis* Emig, 1977 have a very unusual shape—a wide, funnel-shaped structure not found in any

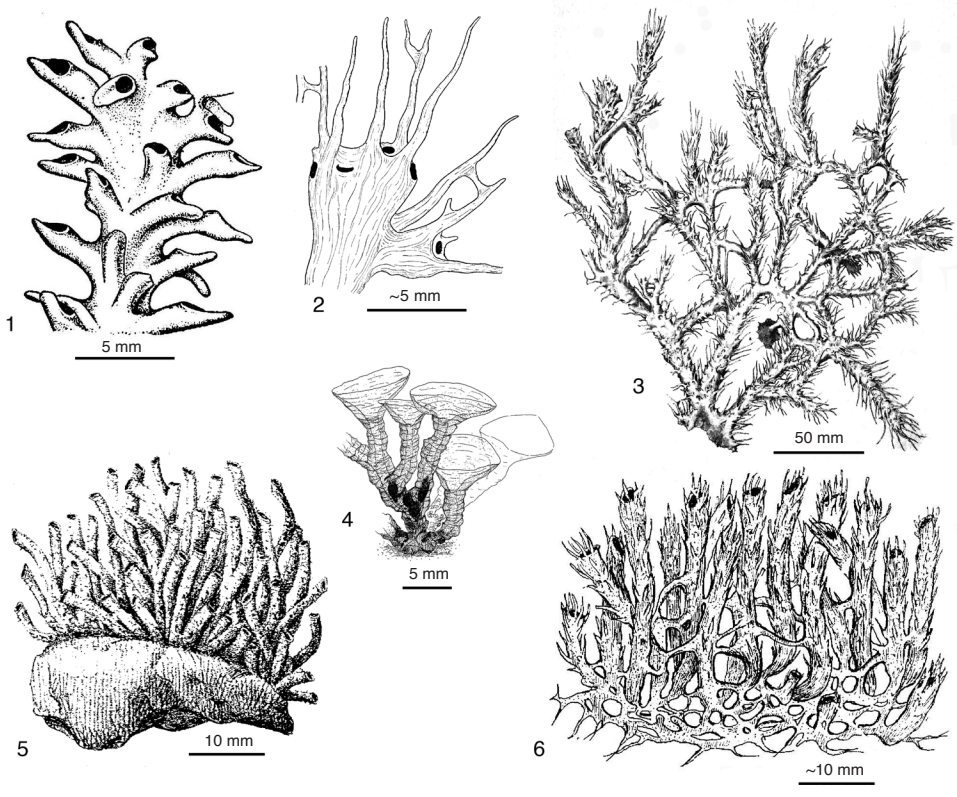


FIG. 120. Tubarium shape in the Cephalodiscidae. *1, Cephalodiscus* (*Idiothecia*) *levinseni* HARMER, 1905 (Kozłowski, 1949, fig. 9c); *2, Cephalodiscus* (*Cephalodiscus*) *hodgsoni* RIDEWOOD, 1907, fragment showing apertures with multiple spines (John, 1931, fig. 1); *3, Cephalodiscus* (*Cephalodiscus*) *dodecalophus* M'INTOSH, 1887 (M'Intosh, 1887, pl. 1); *4, Cephalodiscus* (*Cephalodiscus*) *calciformis* EMIG, 1977 (Emig, 1977, fig. 1); *5, Cephalodiscus* (*Orthoecus*) *rarus* ANDERSSON, 1907 (Andersson, 1907, pl. 2,*6*); *6, Cephalodiscus* (*Cephalodiscus*) sp. (Dawydoff, 1948, fig. 82).

other pterobranch (Fig. 120.4). The tubes of the tubarium are interconnected and inhabited by the zooids and their attached asexually developing buds. These zooids are comparable to those in other species of *Cephalodiscus* (*Cephalodiscus*), but little detail is known about their development and interconnection. In the monospecific subgenus *Acoelothecia,* the tubarium is dissolved into a complex mesh of spines and bars in which the zooids roam freely.

The phylogeny of the extant subgenera of *Cephalodiscus* is unresolved, and as a result, the relationships of the constructional features of their tubaria are unknown. The complete individual tubes of *Cephalodiscus* (*Idiothecia*) RIDEWOOD, 1906 and *Cephalodiscus* (*Orthoecus*) ANDERSSON, 1907 may represent the plesiomorphic mode of tubarium construction, as their features are shared with those of the closely related Graptolithina.

In many aspects, the tubarium construction of the Cephalodiscidae has features also apparent in the construction of the tubaria of the Graptolithina. Erect tubaria have branching and lateral connection of stipes, even though the zooids do not work in a colony but are separate as individuals. GONZALEZ and CAMERON (2012) investigated the ultrastructure of *Cephalodiscus* tubaria in the subgenera *Cephalodiscus, Idiothecia,* and *Orthoecus* and noted a continuum in thickness and development of fusellar-like and cortical-like layers but were unable to recognize clearly differentiated cortical bandages. The investigation indicated that

fibril type and arrangement may be evolving independently from larger scale features of the pterobranch tubaria. The interpretation of cortical material in *Cephalodiscus* (see Kozłowski, 1967; Dilly, 1993) may be misleading, as the material is not differentiated into the distinct bandages of the Graptolithina (see, for instance, Crowther & Rickards, 1977; Crowther, 1978, p. 474). Thus, the evolutionary origin of the cortical bandages might not be traced back to the cephalodiscids.

THE FOSSIL RECORD

The Cephalodiscida are mainly known from modern, extant taxa, but a few possible fossil cephalodiscid taxa have been described. These are preserved only in the form of their tubaria, and their zooids are absent from the fossil record. As a result, differentiating fossil cephalodiscids from closely related Graptolithina can be difficult because interconnected housing constructions are present in both taxa. The oldest possible cephalodiscid taxon may be a fragment found in the Kaili Formation of China (Harvey & others, 2012), but the poor preservation precludes the identification as a cephalodiscid or graptolitid (Maletz, 2014a).

Rickards and Durman (2006) referred the upper Cambrian genus *Aellograptus* Obut, 1964 and its type species *A. savitskyi* Obut, 1964 to *Cephalodiscus,* thus synonymyzing *Aellograptus* with *Cephalodiscus*. The genus is here kept as a separate cephalodiscid genus, as details of the tubarium construction are not available. The size difference from *Cephalodiscus* (*I.*) *levinseni* tubaria quoted by Rickards and Durman (2006) may be regarded as a species-specific character. Other potential cephalodiscid genera are the Ordovician taxa *Eocephalodiscus* Kozłowski, 1949, *Melanostrophus* Öpik, 1930, and *Pterobranchites* Kozłowski, 1967. Of these, only *Eocephalodiscus* has unanimously been referred to the cephalodiscids, and to its own family Eocephalodiscidae (see Kozłowski, 1949). The affinity of the genus *Melanostrophus* has been the focus of a long debate. The genus was known from very fragmentary and poor material, in which Eisenack (1937) first recognized fusellar construction. Zessin and Puttkamer (1994) discussed new material of *Melanostrophus* and erected the family Melanostrophidae for this taxon. Mierzejewski and Urbanek (2004) referred to *Melanostrophus* as a *Cephalodiscus*-like taxon based on their investigation of isolated fragments. *Pterobranchites* is known from small fragments, and its tubarium construction is unknown. Similarities to the encrusting *Cephalodiscus* (*C.*) *graptolitoides* may exist. Schweigert and Dietl (2013) described *Cephalodiscus*? *nusplingensis* as a possible cephalodiscid pterobranch from the Upper Jurassic Nusplingen lithographic limestone of Germany but were unable to verify the presence of fusellar construction.

Family CEPHALODISCIDAE Harmer, 1905

[Cephalodiscidae Harmer, 1905, p. 5] [incl. Eocephalodiscidae Kozłowski, 1949, p. 194; Melanostrophidae Zessin & Puttkamer, 1994 p. 564; Atubaridae, *nom. dub.,* herein]

Fixed, sedentary marine organisms with communal zooids divided into three regions, preoral lobe (cephalic shield), collar, and trunk; collar extends to form several pairs of arms, each bearing a double row of ciliated tentacles; trunk elongated posteriorly to form stalk with sucker at base, from which new zooids are generated asexually; external proteinaceous housing or domicile (the tubarium) comprised of a series of tubes built from sequential addition of full rings or half rings of organic material in most taxa; tubaria with separate zooidal tubes to communal dwellings, unknown in one genus. *Cambrian* (*Miaolingian,* ?*Wuliuan*)*–Holocene:* worldwide in marine environments.

The Cephalodiscida include a single family, the Cephalodiscidae Harmer, 1905. A differentiation of the Eocephalodiscidae Kozłowski, 1949 for fossil members appears unnecessary, as is the introduction of the Melanostrophidae Zessin and Puttkamer,

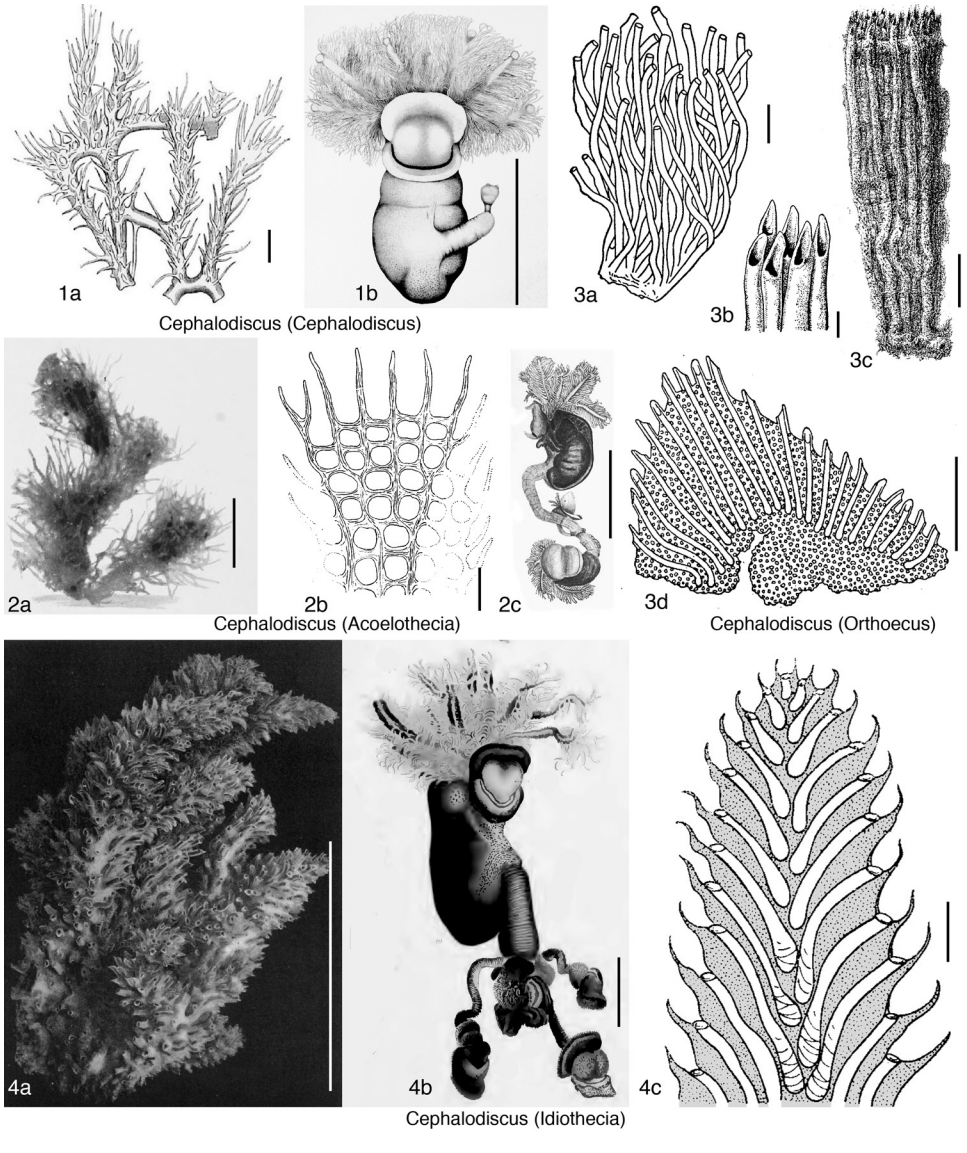


FIG. 121. Cephalodiscidae (extant) (p. 202–203).

1994, based on the taxon *Melanostrophus,* recently recognized as a possible cephalodiscid pterobranch (MIERZEJEWSKI & URBANEK, 2004). The latter authors rejected the genus *Stolonofolliculus* ZESSIN & PUTTKAMER, 1994 with its type *Melanostrophus signum* ÖPIK, 1930 and, thus, viewed the Stolonofolliculidae ZESSIN and PUTTKAMER, 1994 as a *nomen dubium* (MIERZEJEWSKI & URBANEK, 2004, p. 521–522). The name Atubaridae has been used in the Encyclopedia of Life and Catalogue of Life (online at eol.org), but appears to be a *nomen dubium,* as a published diagnosis and description is not available.

A number of subgenera have been erected in the genus *Cephalodiscus* based on the tubarium construction but not on the anatomy of the zooids. If known from the

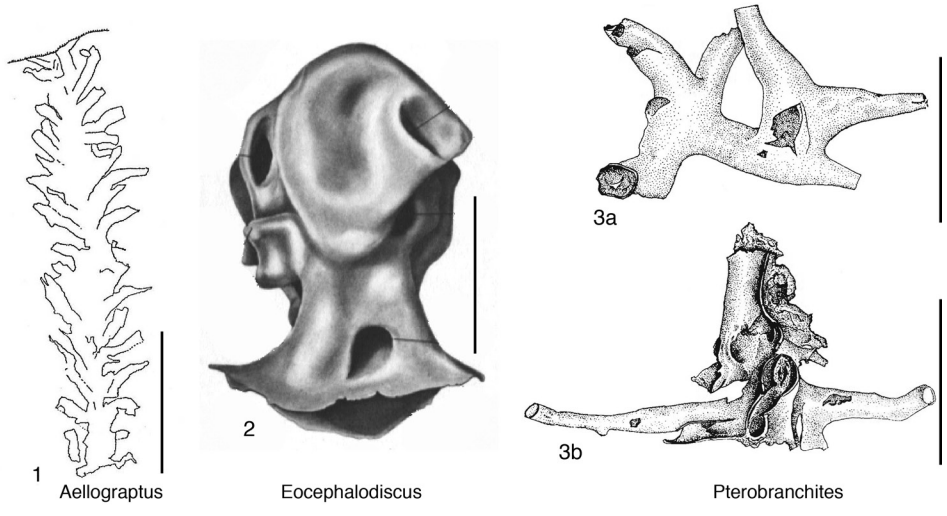


FIG. 122. Cephalodiscidae (fossil) (p. 203).

fossil record only, these subgenera would certainly have been treated as separate genera.

Cephalodiscus M'INTOSH, 1882, p. 348 [**C. dodecalophus;* OD]. Tubarium comprised of series of tubes secreted from the sequential addition of full rings or half rings of organic material in most taxa; tubarium with separate zooidal tubes to communal dwellings and may be reduced to a meshwork of bars; tubarium shape varies from encrusting to erect and branching; with or without spines at apertures. *Cambrian* (*Miaolingian,* ?*Wuliuan*)*–Holocene:* worldwide in marine environments.

C. (**Cephalodiscus**) M'INTOSH, 1882, p. 348, *non Cephalodiscus* BERLESE, 1918, p. 12, =*Capitodiscus* VITZTHUM, 1931, p. 144 (Arachnida) [**C. dodecalophus;* OD] [=*Demiothecia* RIDEWOOD, 1906, p. 191 (type species never selected)]. Encrusting to erect branched tubarium with communal cavity open to all zooids; apertures with single or multiple long spines. *Cenozoic* (*Eocene*)*–Holocene* (extant): worldwide.——FIG. 121,*1a–b*. **C.* (*C.*) *dodecalophus* (type specimen not designated by M'INTOSH, 1882); *1a,* fragment of tubarium showing branches and bridges, long apertural spines common; *1b,* zooid with attached bud (M'Intosh, 1887, pl. 2). Scale bars, 10 mm (*1a*); 1 mm (*1b*).

C. (**Acoelothecia**) JOHN, 1931, p. 241 [**C.* (*A.*) *kempi;* M]. Tubarium consists of meshwork of spines and bars; no true communal cavity present; spaces between meshwork irregular and occupied by zooids and their buds. *Holocene* (extant): Antarctic Ocean (Ross Sea, Victoria Land, McMurdo Sound, Ross Island, Cape Royds).——FIG. 121,*2a–c*. *C.* (*A.*) *kempi* (type specimen not designated by JOHN, 1931); *2a,* part of tubarium, scale bar, ~10 mm (John, 1931, pl. 34,*2*); *2b*, small piece showing spines and bars, scale bar, 1 mm (John, 1931, fig. 4); *2c,* zooid with buds, scale bar, 1 mm (John, 1931, pl. 35,*2*).

C. (**Idiothecia**) RIDEWOOD, 1906, p. 191 [**C. nigrescens* LANKESTER, 1905, p. 400; SD BULMAN, 1970, p. 17)]. Tubaria with individual tubes for each mature zooid; tubarium erect, with complex stipes or without branching; apertures with blunt lips or rutelli; individual tubes enclosed in masses of spongy material forming bulk of tubarium; in longer tubes lower part may be closed off; zooids lack end swellings or refractive beads on arms (JOHN, 1931, p. 233–235). *Holocene* (extant): worldwide.——FIG. 121,*4a–c*. *C.* (*I.*) *nigrescens; 4a,* holotype, tubarium, scale bar, ~10 cm (Lankester, 1905, pl. 8); *4b,* zooid with several buds, scale bar, ~1 mm (Ridewood, 1907, pl. 3,*8*); *4c,* section through tubarium, scale bar, ~5 mm (Dawydoff, 1948, fig. 83; Ridewood, 1907, pl. 4,*10*).

C. (**Orthoecus**) ANDERSSON, 1907, p. 11 [**C. solidus;* SD BULMAN, 1970, p. 17)]. Encrusting tubaria with individual tubes for each mature zooid; basal parts of tubes may be connected by extratubarial spongy material; individual tubes laterally connected to each other or distally free and isolated; apertures simple, straight, or with short rutellum. *Holocene* (extant): worldwide.——FIG. 121,*3a*. *C.* (*O.*) *densus* ANDERSSON, 1907, small tubarium; see RIDEWOOD, 1918, p. 40 for synonymy of *C. rarus,* scale bar, 10 mm (Kozłowski, 1949, fig. 9A).——FIG. 121,*3b–d*. **C.* (*O.*) *solidus;* thecal apertures (*3b*) and fragment (*3c*) of tubarium (Kozłowski, 1949, fig. 9); *3d*, specimen showing sand grains in the tissue

surrounding the zooidal tubes (Ridewood, 1918, fig. 2). Scale bars, 2 mm (*3b*); 10 mm (*3c–3d*).

Atubaria Sato, 1936, p. 105 [**A. heterolopha;* OD]. Cephalodiscid zooids without known tubarium. *Holocene* (extant): Asia (Japan, Dyogasima, Sagami-Bay, east side of Honshu).——Fig. 123, *a–c*. **A. heterolopha. a,* mature zooid (Komai, 1949, fig. 1); *b,* immature zooid (Hyman, 1959, fig. 66D); *c,* characteristic granule-covered antero-internal arm (Sato, 1936, fig. 5a). Scale bars, 0.5 mm.

Aellograptus Obut, 1964, p. 306 [**A. savitskyi;* M]. Elongate, unbranched, or sparsely divided tubarium with numerous short, projecting, cylindrical thecae. *Cambrian* (*Furongian, Paibian*): Russia (Siberia), Australia (Tasmania).——Fig. 122,*1*. **A. savitskyi,* paratype, SM A79058, Siberia, scale bar, 10 mm (Rickards & Durman, 2006, fig. 23B).

Eocephalodiscus Kozłowski, 1949, p. 195 [**E. polonicus;* OD]. Compact tubarium with isolated chambers for zooids; chambers with large circular openings; no apertural elaborations. *Lower Ordovician* (*Tremadocian*): Poland.——Fig. 122,*2*. **E. polonicus,* holotype, scale bar, 5 mm (Kozłowski, 1949, pl. 33,*1b*).

Melanostrophus Öpik, 1930, p. 10 [**M. fokini;* OD]. Tubarium comprised of long, slender, circular, subcircular, or subpolygonal erect zooidal tubes, rarely branched; zooidal tube wall made of thin fusellar layer and very thick outer and inner cortical deposits; tubes fused by their walls to form a cuplike colony. *Middle Ordovician* (*upper Darriwilian*)*–Upper Ordovician* (*Sandbian,* Kukruse Stage): Estonia, Germany (glacial boulder).——Fig. 124, *a–b*. **M. fokini, a,* holotype, TUG 11053-19, Ubja, Estonia, scale bar, 10 mm; *b,* northern Germany, scale unknown (Zessin & Puttkamer, 1994, fig. 2).

Pterobranchites Kozłowski, 1967, p. 123 [**P. antiquus;* OD]. Tubarium of irregularly aggregated tubes and elongated vesicles; no apertural elaborations. *Lower Ordovician* (*Tremadocian*): Poland (glacial boulder).——Fig. 122,*3a–b*. **P. antiquus,* syntypes, two fragments of a single colony, scale bars, 1 mm (Kozłowski, 1967, fig. 11).

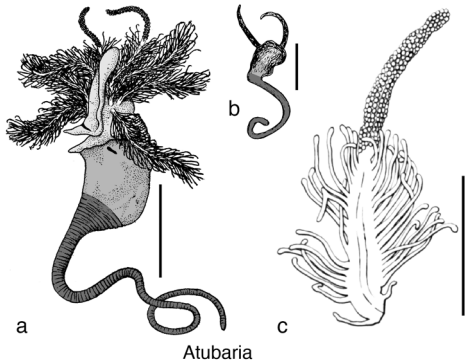


Fig. 123. Cephalodiscidae (extant) (p. 203).

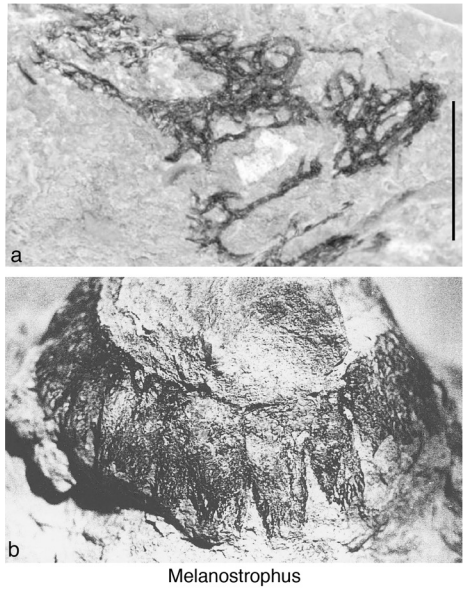


Fig. 124. Cephalodiscidae (fossil) (p. 203).

SUBCLASS GRAPTOLITHINA AND BENTHIC FAMILIES OF UNCERTAIN RELATIONSHIPS

Jörg Maletz and Elena Beli

Subclass GRAPTOLITHINA Bronn, 1849

[Graptolithina Bronn, 1849, p. 149] [=Rhabdophora Allman, 1872, p. 380] [incl. order Rhabdopleurida Fowler, 1892b, p. 297; order Rhabdopleuroidea Beklemishev, 1951, p. 414; order Graptovermida Kozłowski, 1949, p. 204, herein]

Pterobranchs with a colonial habit, building a tubarium from individual fusellar rings and half rings or, in some instances, featureless membranes; rigid stolon system (black stolon) connects the individual, clonally produced zooids attached to stolon by highly flexible and extendable zooidal stalk. *Cambrian* (*Terreneuvian, Fortunian*)*–Holocene* (extant): worldwide.

Mitchell and others (2013) defined the taxon based on a detailed cladistic analysis of Paleozoic benthic graptolites and extant pterobranchs and regarded serial budding from an interconnected stolon system as the defining synapomorphy. The Graptolithina can be characterized as pterobranchs with a clonal, colonial development, secreting a tubarium from individual fusellar rings and half rings, as was described by Mitchell and others (2013) and Maletz (2014b).

Fossil taxa can be recognized through the preservation of the tubarium. More rarely, the black stolon and the diaphragm complexes are preserved. These are not formed from fusellar tissue and generally have not been recognized as pterobranch remains. Several authors (e.g., Mierzejewski, 1986; Urbanek & Dilly, 2000; Maletz, 2014b) identified stolonal remains, initially identified as hydroids, as putative stolonal fragments of Graptolithina. Mierzejewski (1986) was able to convincingly combine the remains of *Kystrodendron longicarpus* (Eisenack, 1938b) (stolon with cysts) and *Eorhabdopleura urbaneki* Kozłowski, 1970b (tubes of fusellar construction) into a single rhabdopleurid taxon.

The precise status of the families of the benthic graptolites within the subclass Graptolithina has not yet been established. Thus, they are considered to represent preliminary taxonomic units of uncertain value. Their diagnoses are based on strongly limited features of fragmentary material.

Kozłowski was against the use of the family rank as a taxonomic unit (Mierzejewski, 1986, p. 174) and used the order level to differentiate his graptolite taxa. Thus, he erected the orders Camaroidea Kozłowski, 1938; Crustoidea Kozłowski, 1962; Graptovermida Kozłowski, 1949; Tuboidea Kozłowski, 1938; and Stolonoidea Kozłowski, 1938. These are not used by this author (see Maletz, 2014b) because the included taxa are impossible to relate precisely to other groups of the Graptolithina and are largely considered as taxa *incertae sedis,* based on a strongly limited number of fragmentary specimens of unknown relationships. Bengtson and Urbanek (1986) identified *Stolonodendrum* (Stolonoidea) as creeping tubes of Rhabdopleuridae. Maletz and Beli (2018) included the genus *Graptovermis* Kozłowski, 1949 (Graptovermida) in the Rhabdopleuridae. The remaining taxa are listed here as the family level taxa Wimanicrustidae Bulman, 1970; Cysticamaridae Bulman, 1955; and Cyclograptidae Bulman, 1938.

Obut (1960) erected the order Dithecoidea for erect growing dendroids with diad budding, dimorphism of the thecae, but lacking bithecae; and he included the families Dithecodendridae Obut, 1957; Siberiograptidae Obut, 1957; and Chaunograptidae Bulman, 1955. Obut (1974) added the order Archaeodendrida. All these taxa are based on highly fragmented material and herein included in the family

Dithecodendridae Obut, 1964 until better known.

Family RHABDOPLEURIDAE Harmer, 1905

[Rhabdopleuridae Harmer, 1905, p. 5] [incl. Chaunograptidae Bulman, 1955, p. 36, *partim;* Idiotubidae Kozłowski, 1949, p. 144, *partim;* Stolonodendridae Bulman, 1955, p. 43; Rhabdopleuroididae Mierzejewski, 1986, p. 176; Rhabdopleuritidae Mierzejewski, 1986, p. 177; ?Rhabdohydridae Mierzejewski, 1986, p. 151]

Colonial pterobranchs with encrusting tubarium, having irregular fusellar rings or regular zigzag sutures in creeping and erect tubes; resorption foramen for the origination of new tubes; erect thecal tubes parallel sided or gradually widening, with simple or ornamented apertures; zooids connected through robust stolon system having diad budding with diaphragm complexes and dormant bud capsules (cysts); featureless dome secreted by sicular zooid. *Cambrian* (*Terreneuvian, Fortunian*)–*Holocene* (extant): worldwide.

The Rhabdopleuridae represent a group of encrusting benthic organisms, restricted to the marine environment. They possess a complex life cycle with a planktic, swimming larval stage and a benthic stage, growing through asexual production of clonal zooids and forming encrusting colonies with various structures, known only from extant taxa. Rhabdopleurids occur from the shallow intertidal zone to the deep marine regions, from the tropical equatorial regions to Arctic and Antarctic regions. The fossil remains of their tubaria can easily be compared to the tubaria of a number of extant species. The modern taxa provide the only information of the soft body anatomy of the rhabdopleurids.

MORPHOLOGY

The complexities of the tubarium of the Rhabdopleuridae are known in some detail from the extant genus *Rhabdopleura* Allman in Norman, 1869a, but details of fossil taxa are difficult to interpret, as they are usually based on highly fragmented material. Two main features have to be differentiated: 1) the tubarium secreted from fusellar rings and half rings by the zooids; and 2) the stolon system (pectocaulus) formed as a dermal construction on the surface of the living tissues of the gymnocaulus with all its additional developments in the form of thecal cones, dormant bud capsules, cysts, and diaphragm complexes. Schepotieff (1907b) described early colony development in *Rhabdopleura normani* Allman in Norman, 1869a. His description includes the presence of the Embryonalblase (dome) and an Embryonalring (initial circular part of the stolon), formed from the stolon. The rhabdopleurid tubarium starts with the dome, sometimes homologized with the prosicula of the Graptoloidea (see Maletz, Steiner, & Fatka, 2005; Mitchell & others, 2013). The dome is secreted by the sicular zooid as a featureless membrane in which the larva morphs into the mature zooid. It generally has an ovoid shape and is attached to the substrate on one side. The zooid emerges from one side of the dome by resorbing a foramen into the membrane and starts to secrete the first fusellar rings. In most *Rhabdopleura,* even the earliest fuselli form half rings and a dorsal zigzag suture on the developing metasicular tube (Dilly, 1986). The sicular zooid produces a horizontal, encrusting thecal tube with a distinct dorsal zigzag suture and a flat basal surface, with which it is attached to the substrate. In other (fossil) taxa, the initial fuselli may be irregularly formed, but details are available from few specimens.

Sars (1872), Lankester (1884), and Schepotieff (1907b) described and illustrated the tubarium of the extant *Rhabdopleura normani* in some detail and provided the most complete understanding of any rhabdopleurid tubarium. The tubarium of *Rhabdopleura compacta* Hincks, 1880a is largely comparable in its construction (see Hincks, 1880a; Stebbing, 1970a, 1970b), but the presence of a permanent terminal zooid is not confirmed. All rhabdopleurids produce a tubarium in the shape of interconnected tubes for the individual zooids. These tubaria possess a number of characteristics not present in other pterobranchs. Early

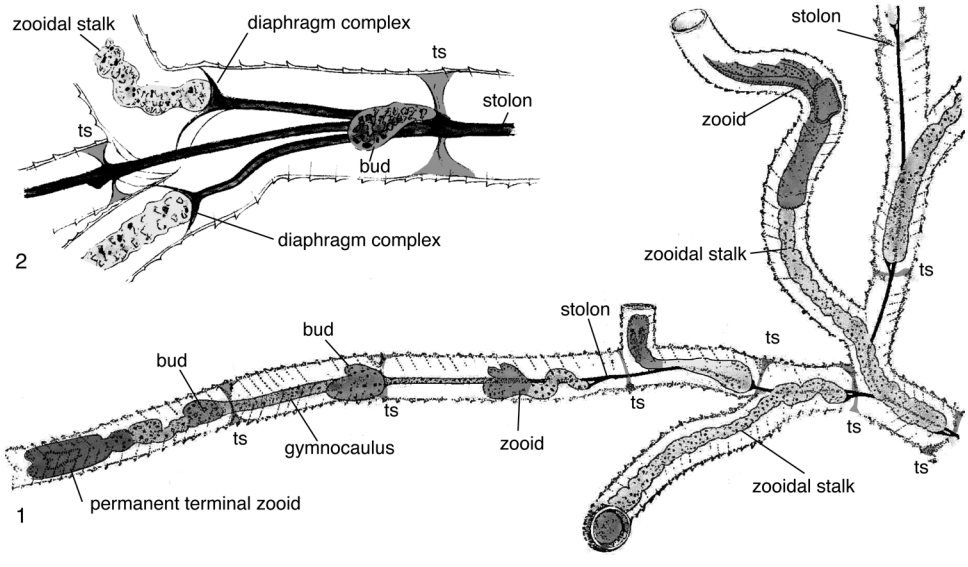


FIG. 125. *Rhabdopleura normani* ALLMAN in NORMAN, 1869a, monopodial growth and stolon system with diaphragm complexes. *1,* Growing end of colony showing monopodial growth with permanent terminal zooid (adapted from Ridewood, 1907, fig. 7); *2,* branching point; *ts*, transverse septum (adapted from Lankester, 1884, pl. 41,*7*). Color version available in *Treatise Online,* 101.

rhabdopleurids appear to possess irregularly placed fusellar sutures, for example, *Sphenoecium wheelerensis* MALETZ & STEINER, 2015 (see MALETZ & STEINER, 2015), but details are only available from a few specimens. *Sphenoecium obuti* (DURMAN & SENNIKOV, 1993) (see DURMAN & SENNIKOV, 1993; SENNIKOV, 2016a, 2016b) from the middle Cambrian of Siberia already has a relatively regular development of the sutures closely resembling the zigzag suture of extant *Rhabdopleura*.

The most remarkable character of the *Rhabdopleura normani* tubarium is the monopodial development of the main stem, the branching axis (LANKESTER, 1884, p. 625) or "Hauptröhre" of SCHEPOTIEFF (1907b, p. 213), but a comparable feature is not known in most other *Rhabdopleura* taxa. Colony growth is achieved through the increasing length of the main stem and the addition of new thecal tubes ("Wohnröhren" in SCHEPOTIEFF, 1907b, p. 213) at the sides of this stem. The permanent terminal zooid (Fig. 125.1) produces fusellar half rings and increases the length of the stipe. At regular or irregular distances, transverse septa are formed to separate individual segments of the stem into compartments for the developing zooids (LANKESTER, 1884; SCHEPOTIEFF, 1907b; URBANEK & DILLY, 2000). The development of the transverse septa starts from the inner wall of the tubes, as incompletely developed septa indicate (SCHEPOTIEFF, 1907b, p. 220).

The zooids resorb an opening into one side of the main stem, invariably at the distal end of the compartment (see SCHEPOTIEFF, 1907b, p. 220; KOZŁOWSKI, 1949, fig. 14E) and start to build erect thecal tubes from fusellar full rings. These tubes can reach considerable lengths and are inhabited by a single zooid attached to the stolon system with a highly flexible gymnocaulus. The main stem invariably bears a dorsal zigzag suture in *Rhabdopleura*, but the thecal tubes have full fusellar rings with a single oblique suture. A distinct collar is typically also present in the fuselli of the thecal tubes but in fossil material may be difficult to recognize.

The interconnection between the zooidal development and the tubarium construction

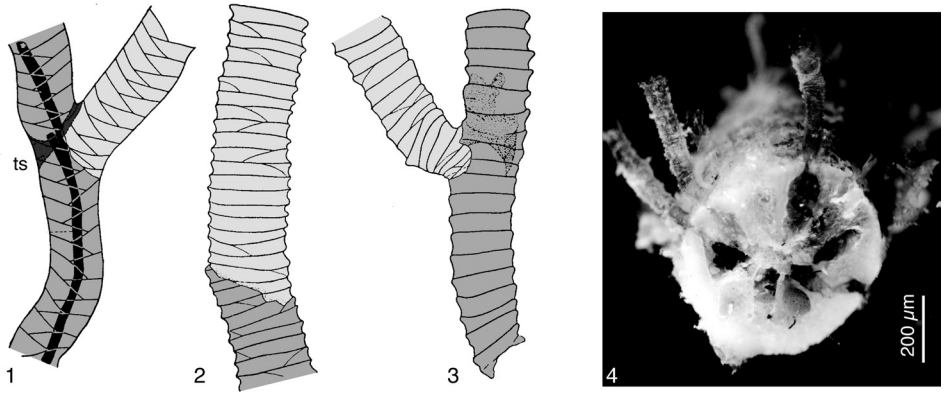


FIG. 126. Branching of tubarium. *1,* Main stem with branching, see stolon and transverse septum (*ts*); *2,* part of erect thecal tube with regeneration; *3,* erect tube with unusual lateral branching. (adapted from Kozłowski, 1949, fig. 14); *4, Rhabdopleura recondita* BELI & others, 2018 finds shelter inside the dead branches of bryozoan hosts, erect tubes project from the pores (new; photo courtesy of Stefano Piraino). Color images available in *Treatise Online,* 101.

in *Rhabdopleura normani* and possibly in other members of the genus is an important observation. LANKESTER (1884, p. 627) noted that the creeping (recumbent) tubes with their characteristic zigzag sutures are invariably secreted by immature zooids before arms have developed. The mature zooids with their two, fully formed arms secrete the full rings of the erect thecal tubes. Thus, the zooids morph in their initial compartments into fully grown organisms before they break through the tube wall and start secreting the thecal tubes. The permanent terminal zooid represents the model of an immature zooid before the maturation process is finished.

Branching of the main stem can be produced irregularly and appears to be through a resorption foramen and the immediate development of a dorsal zigzag suture of the new branch (Fig. 126.1). An illustration of KOZŁOWSKI (1949, fig. 14A) shows the original branch and the laterally originating secondary branch, at the base of which truncated fuselli of the previous branch can be seen. A transverse septum separates the continuing part of the main branch. Branching of the thecal tubes is generally not noted, but KOZŁOWSKI (1949, fig. 14C) illustrated a fragment that appears to show an unusual resorption foramen and the growth of a secondary thecal tube (Fig. 126.3). Regeneration of thecal tubes is more common (Fig. 126.2) and can be seen by the irregular break across a tube and the subsequent addition of fusellar full rings (RIGBY, 1994a). Typically, the new addition is also less strongly colored than the older part of the tubarium.

One of the most conspicuous features of the Rhabdopleuridae is the stolon system connecting the individual zooids. The fully developed stolon system is a black rod either lying free within the main tube or attached to the ventral tube wall, which develops as the gymnocaulus hardens to form the stolon system (black stolon) and is surrounded by denser, dark material (LANKESTER, 1884, p. 636). This dark stolonal material is formed from dense crassal fabric, as is the stolon system of other graptolites (URBANEK & TOWE, 1974; BATES & URBANEK, 2002; SAUNDERS & others, 2009). In extant rhabdopleurids, the stolon is often easily visible through the translucent tubarium (see URBANEK & DILLY, 2000).

Initially, the stolon (gymnocaulus) is naked and flexible and begins to lengthen behind the terminal zooid and its developing buds (Fig. 125.1). When a number of buds are formed and separated into their individual chambers, the gymnocaulus within these chambers subsequently and slowly thickens and hardens, attaining a dark coloration and losing its original flexibility (LANKESTER, 1884).

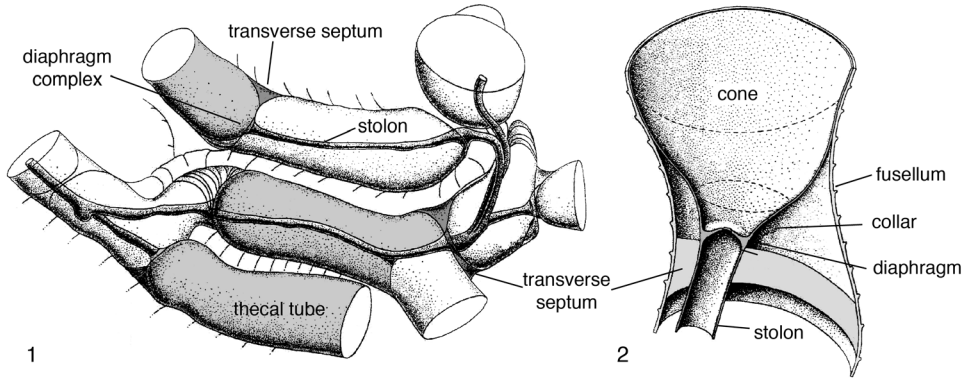


FIG. 127. The stolon system. *1,* stolon and inner lining (cone) of thecal tubes; *2,* diaphragm complex and connection to the fusellar tube (adapted from Urbanek & Dilly, 2000).

A short branch of the stolon connects to the zooidal stalk of the zooids (Fig. 125.1). At the tip of the zooidal stolon, a diaphragm complex (URBANEK & DILLY, 2000) develops (Fig. 127), representing the encysting shell of a dormant bud or a resting stage of the developing zooid, also called the pigmented peridermal capsule (URBANEK & DILLY, 2000, p. 210). These capsules were first recognized by LANKESTER (1884) who termed them hibernacula. Later, SCHEPOTIEFF (1907b) referred to them as sterile Knospen (sterile buds). STEBBING (1970a) concluded that these buds were able to develop into zooids and introduced the term dormant buds. In thecal tubes of active zooids, these capsules are open distally and appear to be an inner lining of the tube over considerable distances, adhering closely to the fusellar wall (URBANEK & DILLY, 2000, p. 214). The zooid is independent of this thecal lining, as indicated from retracted zooids with a coiled zooidal stalk in the terminal diaphragm complex (URBANEK & DILLY, 2000, fig. 9).

When KOZŁOWSKI (1949) introduced the order Graptovermida, he described them as tubes of unknown origin, possessing a flat basal surface indicating an encrusting habit. He documented the presence of fuselli in some specimens. The Graptovermida can be included in the Rhabdopleuridae as they are easily interpreted as remains of a sigmophyllic *Rhabdopleura*-like species. KOZŁOWSKI (1949, p. 206) indicated the presence of an ovoid initial part or dome in *Graptovermis spiralis* KOZŁOWSKI 1949, termed a cul-du-sac ovale. The vermiform tubes represent the creeping tubes of the tubarium, with zigzag suture lines on the upper surface of the tubes. The erect tubes with their collared full fusellar rings may not be preserved. MIERZEJEWSKI (1988) discussed the graptovermids in some detail based on chemically isolated material from Öland, Sweden. The material consisted of stolonal developments with strongly elongated cysts or buds, similar to the diaphragm complexes of extant rhabdopleurids. MIERZEJEWSKI (1988) interpreted them as resting stolothecae of encrusting graptolites. However, the ultrastructure of the graptovermids has not yet been investigated.

EVOLUTION

The evolutionary origin of the Rhabdopleuridae is uncertain, but a number of observations have led to some understanding. Earliest rhabdopleurid fossils originated during the middle Cambrian and may be referred to the genus *Sphenoecium* (MALETZ & STEINER, 2015). Specimens clearly show the clonal, colonial development through the presence of interconnected thecal tubes in encrusting colonies with erect, unbranched distal thecal tubes.

Sphenoecium wheelerensis and *Sphenoecium mesocambricus* (Öpik, 1933) belong to the oldest members of the group. However, *Sphenoecium obuti* appears to be the oldest well-preserved rhabdopleurid. Very little is known about the diversification of the Graptolithina in the upper Cambrian, and even the cladistic analysis (Mitchell & others, 2013) did not provide sufficient evidence for an evolutionary interpretation of the early origins of the group. Rhabdopleurids with numerous modern tubarium features are present during the Ordovician (Skevington, 1965; Mierzejewski, 1986) but may not be referred to the genus *Rhabdopleura*. Chemically isolated material of *Sokoloviina* Kirjanov, 1968 may represent the oldest rhabdopleurid record in the lower Cambrian (Fortunian), as it has fusellar construction and collars on the tubes.

The earliest taxon referable to the extant genus *Rhabdopleura* may be *Rhabdopleura hollandi* Rickards, Chapman, & Temple, 1984 from the Silurian *Spirograptus turriculatus* Biozone of Wales (Rickards, Chapman, & Temple, 1984), and older rhabdopleurids can be referred to the genus *Kystodendron* Kozłowski 1959a (see Mierzejewski & Kulicki, 2001, 2002, 2003a).

Chapman, Durman, and Rickards (1995) identified fragmentary material from the Ordovician (upper Darriwilian) of China as *Rhabdopleura sinica* Kozłowski, 1959a, fig. 10. *Rhabdopleura graysoni* Chapman, Durman, & Rickards, 1995 from the Visean (Carboniferous) resembles the extant *Rhabdopleura compacta*, but little detail of the tubarium development is available. Another record from the Carboniferous is *Rhabdopleura delmeri* Mortelmans, 1955 from Belgium. Fossil records of rhabdopleurids from the Mesozoic and Cenozoic are rare, and few specimens have been described. Kozłowski (1956a) described *Rhabdopleura vistulae* Kozłowski, 1956a from the Danian (Cretaceous) of Poland, and Kulicki (1969, 1971) recorded the species *Rhabdopleura kozlowskii* Kulicki, 1969 from the Callovian (Jurassic) of Poland. A single record of *Rhabdopleura* exists from the Eocene of England (Thomas & Davies, 1949a, 1949b, 1950).

Rhabdopleura Allman in Norman, 1869a, p. 311 [**R. normani;* M] [=*Halilophus* Sars, 1868, p. 255 (type, *H. mirabilis*), *nom. nud.,* herein]. Rhabdopleurids with thigmophyllic to thigmophobic tubarium; creeping tubes with fusellar half rings and dorsal zigzag sutures, sutures on ventral sides indistinct or lacking; sicular zooid forms dome from which the metasicula and first autotheca develop; creeping tubes with irregularly to regularly produced partitions; erect tubes with irregularly placed sutures and full fusellar rings; branching occurs only in creeping tubes; apertures simple, straight; fuselli on erect tubes with distinct collar; stolon system with diad budding and complex diaphragm complexes. ?*Silurian* (*Llandovery, Spirograptus turriculatus* Biozone)–*Holocene* (extant): worldwide.——Fig. 128,*1*. **R. normani,* part of tubarium, Shetland Sea, ~165 m depth, scale bar, ~1 mm (Allman, 1869b, pl. 8,*1*).

Archaeolafoea Chapman, 1919, p. 390 [** A. longicornis;* M] [=*Archaeocryptolaria* Chapman, 1919, p. 392 (type, *A. skeatsi,* SD Bulman, 1970, p. 55), syn. by Maletz & Steiner, 2015, p. 1097]. Tubarium construction of colonial pterobranch formed from organic tubes; creeping and branching, elongated central tube with erect and unbranched lateral tubes bearing simple, straight apertures; parallel-sided lateral tubes formed from fusellar half rings or full rings, possibly with irregularly developed oblique sutures; stolon and zooidal development unknown. *Cambrian* (*Miaolingian*)–*?Ordovician:* Australia (Victoria).——Fig. 128,*2a. *A. longicornis,* holotype, NMV P 13112, scale bar, 1 mm (new).——Fig. 128,*2b. Archaeocryptolaria skeatsi* Chapman, 1919, holotype, NMV P 13114, scale bar, 1 mm (new).

Chaunograptus Hall, 1882, p. 225 [**Dendrograptus* (*Chaunograptus*) *novellus;* M] [=*Desmohydra* Kozłowski, 1959a, p. 227 (type, *D. flexuosa;* OD), syn. by Mierzejewski, 1986, p. 163] [=*Epallohydra* Kozłowski, 1959a, p. 230 (type, *E. adhaerensis,* OD), syn. by Mierzejewski, 1986, p. 163]. Tubarium formed from organic tubes; creeping and branching, elongated central tube with unbranched lateral tubes bearing simple, straight apertures; fusellar construction; stolons and zooidal development unknown. *Cambrian* (*Miaolingian, Wuliuan, Ptychagnostus praecurrens* Biozone)–*Silurian* (*Wenlock*): Poland, USA.——Fig. 128,*4a–b. *C. novellus* (Hall); *4a,* syntype, NYSM 3170/1, specimens attached to *Eospirifer radiatus* (brachiopod), scale bar, 10 mm (Hall, 1882, pl. 1); *4b,* syntype, FMNH UC 11989, specimen attached to *Eucalyptocrinus* (echinoderm), scale bar, 1 mm (new).——Fig. 128,*4c. C. flexuosus* (Kozłowski, 1959a), holotype, ZPAL material, Poland, glacial boulder, scale bar, 1 mm (Kozłowski, 1959a, fig. 10).——Fig. 128,*4d. C. adhaerensis* (Kozłowski, 1959a), holotype, ZPAL material, Poland, glacial boulder, scale bar, 1 mm (Kozłowski, 1959a, fig. 10).

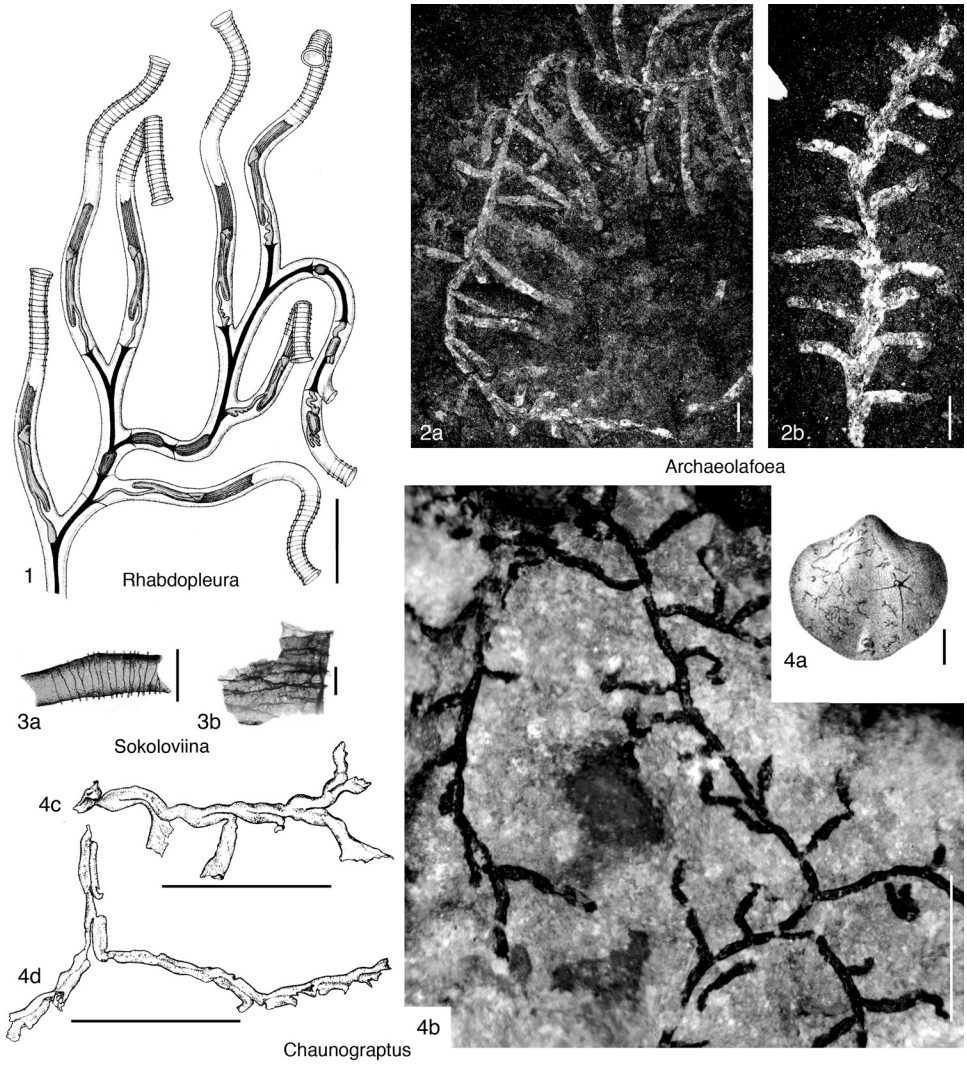


FIG. 128. Rhabdopleuridae (p. 210–213).

Epigraptus EISENACK, 1941a, p. 25 [**E. bidens;* M] [=*Idiotubus* KOZŁOWSKI, 1949, p. 144 (type, *I. typicalis,* OD), syn. by MIERZEJEWSKI, 1978, p. 566]. Encrusting thecorhiza of unknown form; erect portions of autothecae arising directly from surface of thecorhiza; autothecal apertural apparatuses in form of single or two lamelliform or bifurcate process; stolon system unknown. *Lower Ordovician* (*Tremadocian*)–*Silurian, Ludlow:* Estonia, Germany, Poland, Sweden (glacial boulder).——FIG. 129,*1a–b. *E. bidens; 1a,* neotype, GPIT S.G. 158, Nr. (Eisenack, 1974, p. 671); *1b,* holotype (not preserved), Sandbian, Wesenberg (Rakvere), Estonia (Eisenack, 1941a, fig. 1). Scale bars, 1 mm.——FIG. 129,*1c*. *Epigraptus* sp., small colony with part of dome, whereabouts unknown, scale bar, 1 mm (Andres, 1977, fig. 27).——FIG. 129,*1d*. *E. typicalis* (KOZŁOWSKI, 1949), holotype, ZPAL material, Poland, scale bar, 1 mm (Kozłowski, 1949, pl. 13,*1*).

Graptovermis KOZŁOWSKI, 1949, p. 206 [**G. spiralis;* OD]. Rhabdopleurids with thigmophyllic tubarium; creeping tubes with fusellar development; thecal apertures and erect tubes unknown; sicular zooid forms dome; details of tubarium unknown. *Lower Ordovician* (*Tremadocian*): Poland (glacial boulder).——FIG. 129,*2a–c. *G. spiralis; 2a–b,* holotype, ZPAL material, in dorsal (*a*) and ventral (*b*) views; *2c,* paratype, ZPAL material, showing spiral development from ventral side, scale bars, 1 mm (6,*2a–c,* Kozłowski, 1949, pl.

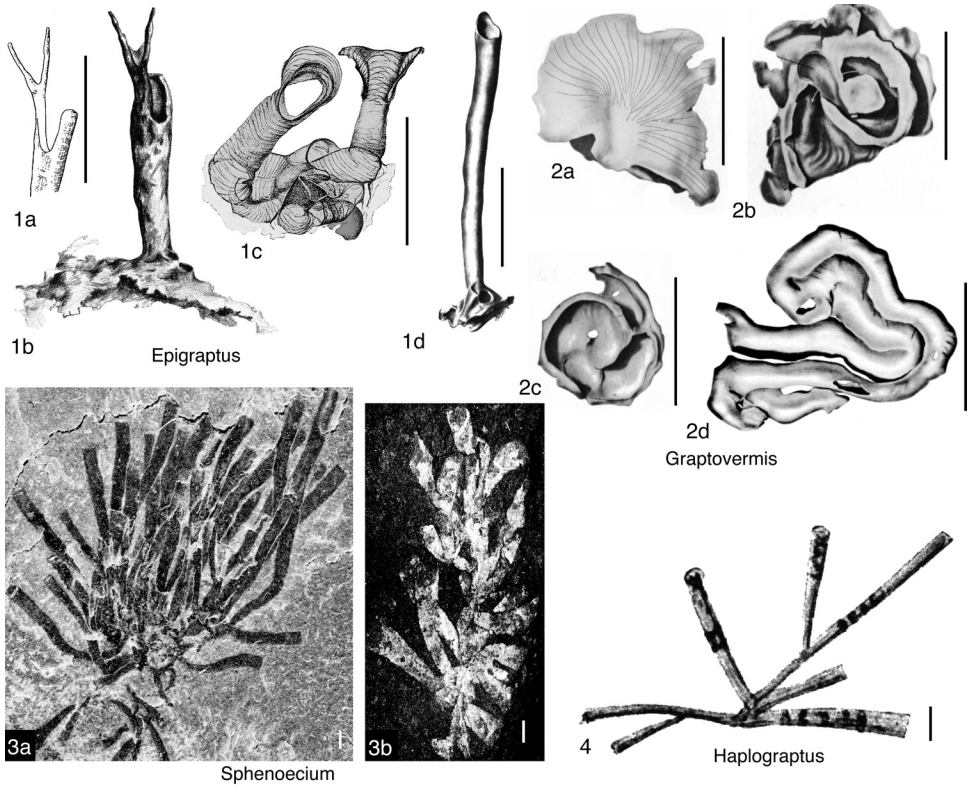


FIG. 129. Rhabdopleuridae (p. 211–213).

36).——FIG. 129,*2d. G. intestinalis* KOZŁOWSKI, 1949, holotype, ZPAL material, scale bar, 1 mm (Kozłowski, 1949, pl. 35,*6*).

Haplograptus RUEDEMANN, 1933, p. 323 [**H. wisconsinensis;* OD]. Branched, encrusting to erect tubes with elongate conical or vermiform, erect theca forming irregularly dendroid tubarium. *Cambrian* (*Furongian*)–*Middle Ordovician* (*Darriwilian*): China, Canada, USA.——FIG. 129,*4*. **H. wisconsinensis* RUEDEMANN, 1933, holotype. repository unknown. scale bar, 1 mm (Ruedemann, 1947, pl. 40,*6*).

Kystodendron KOZŁOWSKI, 1959a, p. 252 [**Chitinodendron longicarpus* EISENACK, 1938b, p. 237; OD] [=*Eorhabdopleura* KOZŁOWSKI, 1970, p. 4 (type, *E. urbaneki,* OD); *nom. dub.,* MIERZEJEWSKI, 1986, p. 184] [=?*Cylindrotheca* EISENACK, 1934, p. 66 (type, *C. profunda,* OD); *nom. dub.,* MIERZEJEWSKI, 1986, p. 183]. Zooidal and stolonal tubes similarly developed as in *Rhabdopleura;* major stolon and peduncular stolons of cysts of sterile buds without diaphragms; sterile bud cysts circular in cross section, simple or composite. *Ordovician:* Poland (glacial boulder).——FIG. 130,*2a*. **K. longicarpus* (EISENACK), holotype, ZPAL material, stolon with cysts, scale bar, 1 mm (Eisenack, 1938b, fig. 18).——FIG. 130,*2b–c. Kystodendron urbaneki (*KOZŁOWSKI, 1970), holotype, ZPAL material, thecal tube fragments, scale bar, 0.1 mm (Kozłowski, 1970, fig. 1).

Rhabdopleurites KOZŁOWSKI, 1967, p. 126. [**R. primaevus;* OD]. Colony encrusting, with dendroidal part underdeveloped, comprised of stolonal and zooidal tubes; fusellar tubes varying from 0.3 to 0.6 mm in width and fuselli 60 to 100 µm wide; fusellar collars varying in size, sometimes very large; some stolonal tubes nonfusellar; stolons without diaphragms; sterile bud cysts missing. *Ordovician* (*Darriwilian*): Germany, Poland, Sweden (glacial boulder).——Fig. 130,*1a–b. *R. primaevus;* syntypes, ZPAL material, thecal tubes; scale bars, 0.5 mm (Kozłowski, 1961, fig. 13).

Rhabdopleuroides KOZŁOWSKI, 1961, p. 4 [**R. expectatus;* M]. Tubarium exclusively comprised of creeping stolonal and zooidal tubes; stolons without cysts of sterile buds. *Middle Ordovician* (*Darriwilian*)–*Upper Ordovician* (*Sandbian*): Poland (glacial boulder).——FIG. 130,*3a–d. *R. expectatus; 3a–b,* holotype, not preserved (Mierzejewski, 1986, p. 177); *3c,* paratype, ZPAL material; *3d,* lectotype (designated by MIERZEJEWSKI, 1986, p. 177), ZPAL material (Kozłowski, 1961, 1970, fig. 2). Scale bars, 0.5 mm.

Sokoloviina KIRJANOV, 1968, p. 22 [**S. costata;* OD]. Small- to medium-sized tubes of black color with

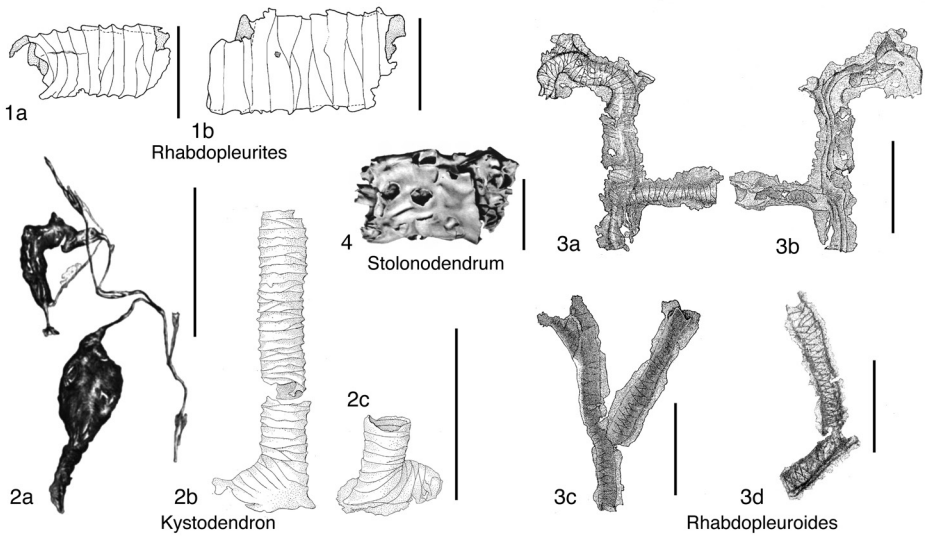


FIG. 130. Rhabdopleuridae (p. 212–213).

collars in the form of sharp-pointed or circular annular growths. *Cambrian* (*Terreneuvian, Fortunian*): Estonia, Ukraine (Podolia).——FIG. 128,*3a-b.* **S. costata; 3a,* syntype, tube fragment, scale bar, 1 mm (Kirjanov, 1968, pl. 3,*8*); *3b,* chemically isolated fragment, scale bar, 10 µm (Sokolov, 1997, pl. 9,*4*).

Sphenoecium CHAPMAN & THOMAS, 1936, p. 205 [**Sphenothallus filicoides* CHAPMAN, 1917, p. 92; SD BULMAN, 1970, p. 57, *pro Sphenothallus* CHAPMAN, 1917, *non* HALL, 1847, p. 261 [=phylum Cnidaria VAN ITEN, COX, & MAPES, (1992, p. 143); =*Rhabdotubus* BENGTSON & URBANEK, 1986 (type, *R. johannssoni,* OD), syn. by MALETZ & STEINER, 2015, p.1098; =*Fasciculitubus* OBUT & SOBOLEVSKAYA, 1967, p. 56 (type, *F. tubularis,* OD), syn. by MALETZ & STEINER, 2015, p. 1098]. Tubarium construction of colonial pterobranchs formed from organic tubes; short creeping and branching tubes with distally erect and unbranched, slowly widening tubes with simple, straight apertures; tubes formed from fusellar half rings or full rings with irregularly developed oblique sutures; colony shapes often dependent on the availability of suitable surface for attachment, from small and circular to elongate or with multiple branchings covering larger areas. *Cambrian* (*Miaolingian, Wuliuan*)–*Ordovician:* worldwide.——FIG. 129,*3a*. **S. wheelerensis* MALETZ & STEINER, 2015, Spence Shale, Wellsville Mountains, Utah, USA, scale bar, 1 mm (Maletz & Steiner, 2015, fig. 17C).——FIG. 129,*3b.* **S. filicoides* (CHAPMAN), NMV P 47737, well-preserved specimen, scale bar, 1 mm (Maletz & Steiner, 2015, fig. 12C).

Stolonodendrum KOZŁOWSKI, 1949, p. 194 [**S. uniramosum;* OD]. Branched stolonal tubes with cysts and elongated thecal tubes with fusellum showing irregular sutures. [These were interpreted as creeping tubes of Rhabdopleuridae by BENGTSON & URBANEK 1986, p. 294.] *Ordovician* (*Tremadocian*): Poland (glacial boulder).——FIG. 130,*4*. **S. uniramosum,* holotype, ZPAL material, scale bar, 1 mm (Kozłowski, 1949, pl. 32,*2*).

POSSIBLE RHABDOPLEURID STOLONS

Numerous fragments of strings or slender tubes of organic material—sometimes with attached rounded or elongated bodies and distinct branching patterns—have been found from the Paleozoic and have generally been identified as hydroid remains (e.g., KOZŁOWSKI, 1959a). MIERZEJEWSKI (1986) erected the family Rhabdohydridae for the genera *Rhabdohydra* KOZŁOWSKI, 1959a and *Palaeotuba* EISENACK, 1934 and regarded it as an extinct group related to the hydrozoan suborder Athecata HINCKS, 1868. A number of taxa originally described as possible hydroids have subsequently been referred to the Pterobranchia (see MIERZEJEWKSI, 1986; BATES & URBANEK, 2002; MALETZ, 2014b). MUSCENTE, ALLMON, and XIAO (2015, p. 79) especially questioned the hydroid fossil record in the Paleozoic and suggested a hemichordate origin for many remains. They recognized that lower Paleozoic putative hydroid fossils are either preserved as carbonaceous microfossils

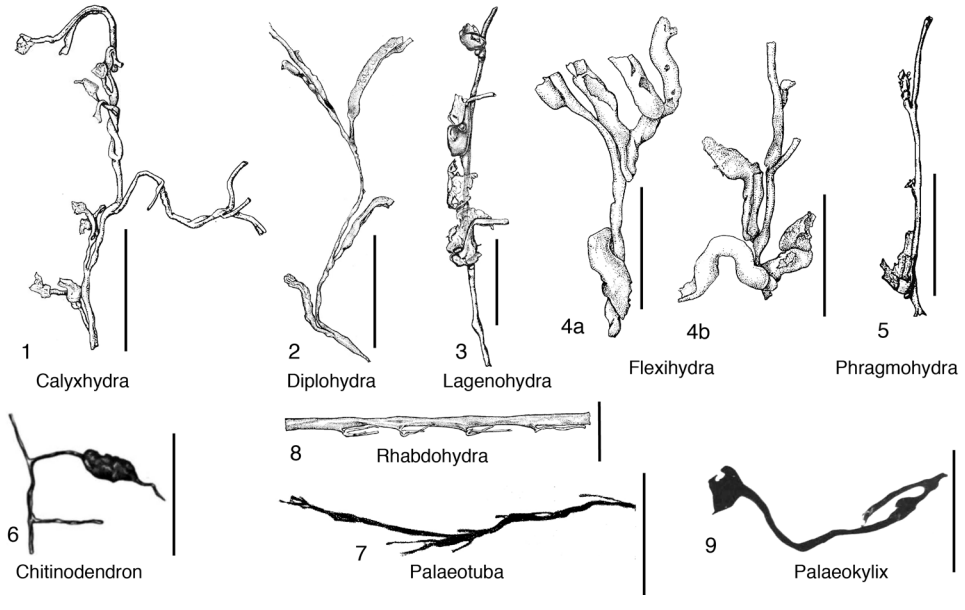


FIG. 131. Rhabdopleurid stolons (p. 214–215).

or as alumosilicate films (pressure shadow minerals, see UNDERWOOD, 1992; MALETZ & STEINER, 2015), but younger taxa are commonly preserved as bioimmured fossils. KEUPP, DOPPELSTEIN, and MALETZ (2016) described the rare occurrence of the stolon system of a rhabdopleurid preserved *in situ* on a Lower Jurassic hardground.

Calyxhydra KOZŁOWSKI, 1959a, p. 221 [**C. gemellithecata;* OD; =rhabdopleurid stolon, MIERZEJEWSKI, 1986, p. 168]. Branching system with more or less regular dichotomous divisions; terminal branches with conical tubes; no diaphragms. *Ordovician:* Poland (glacial boulder).——FIG. 131,*1. *C. gemellithecata,* holotype, ZPAL material, scale bar, 0.5 mm (Kozłowski, 1959a, fig. 3).

Chitinodendron EISENACK, 1938b, p. 236 [**C. bacciferum;* SD KOZŁOWSKI, 1959a, p. 251; =?rhabdopleurid stolon, herein]. Branched stolon system with irregularly placed oval cysts. *Ordovician–Silurian:* Estonia, Poland.——FIG. 131,*6. *C. bacciferum,* holotype, ZPAL material, scale bar, 0.5 mm (Eisenack, 1938b, fig. 13).

Diplohydra KOZŁOWSKI, 1959a, p. 240 [**D. longithecata;* OD] [=order Rhabdopleuroidea BEKLEMISHEV, 1951, p. 19, MIERZEJEWSKI & KULICKI, 2002, p. 171]. Stolon system devoid of diaphragms, peduncular stolons, and true capsules of the dormant buds; major stolon with irregularly arranged lateral offshoots; lateral offshoots form diads comprised of the two daughter stolons; as a rule, one of the daughter stolons is strongly inflated and sometimes forms an imperfect composite cyst. *Ordovician–Permian* (*Roadian*): Norway (Barents Shelf), Poland (glacial boulder).——FIG. 131,*2. *D. longithecata,* holotype, ZPAL material, scale bar, 1 mm (Kozłowski, 1959a, fig. 16).

Flexihydra KOZŁOWSKI, 1959a, p. 225 [**F. undulata;* OD; =?rhabdopleurid remains, herein]. Short stolons with elongated, flexible thecal cups; fusellum unknown. *Ordovician:* Poland (glacial boulder).——FIG. 131,*4a–b. *F. undulata,* syntype, ZPAL material, scale bars, 0.5 mm (Kozłowski, 1959a, fig. 7).

Lagenohydra KOZŁOWSKI, 1959a, p. 245 [**L. phragmata;* OD; =rhabdopleurid stolon, MIERZEJEWSKI, 1986, p. 193]. Stolon system with distinct thecal dimorphism; each node bears two differently shaped thecae; fusellum unknown. *Ordovician:* Poland (glacial boulder).——FIG. 131,*3. *L. phragmata,* holotype (specimen not preserved, see MIERZEJEWSKI, 1986, p. 194), scale bar, 0.5 mm (Kozłowski, 1959a, fig. 22A).

Palaeokylix EISENACK, 1932, p. 266 [**P. chitinosus;* OD; *nom. dub.,* herein]. Simple branched stolon with thecal cup; fusellum unknown. *Ordovician–?Silurian*: Russia (Oblast Kaliningrad, formerly Samland) (glacial boulder).——FIG. 131,*9. *P. chitinosus*, holotype, ZPAL material, scale bar, 0.1 mm (Eisenack, 1932, pl. 11,*22*).

Palaeotuba EISENACK, 1934, p. 54 [**P. polycephala;* OD; =?rhabdopleurid stolon, MIERZEJEWSKI, 1986, p. 179]. Stolon system with multiple branchings. *Upper Ordovician* (*lower Sandbian,* Kukruse Stage):

Estonia, Poland (glacial boulder).——Fig. 131,*7*. **P. polycephala,* holotype, repository unknown, scale bar, 1 mm (Eisenack, 1934, pl. 4,*5*).

Phragmohydra Kozłowski, 1959a, p. 238 [**P. articulata;* OD; =?rhabdopleurid remains, herein]. Stolon system with complex peduncular diaphragms; fusellum unknown. *Ordovician:* Poland (glacial boulder).——Fig. 131,*5*. **P. articulata,* holotype, ZPAL material, scale bar, 0.5 mm (Kozłowski, 1959a, fig. 15a).

Rhabdohydra Kozłowski, 1959a, p. 235 [**R. tridens;* OD; =?rhabdopleurid remains, herein]. Stolon system with multiple peduncular diaphragms; fusellum unknown. *Ordovician:* Poland (glacial boulder), Sweden.——Fig. 131,*8*. **R. tridens,* ZPAL material, holotype, scale bar, 0.5 mm (Kozłowski, 1959a, fig. 14A).

Family WIMANICRUSTIDAE Bulman, 1970

[Wimanicrustidae Bulman, 1970, p. 52] [incl. Hormograptidae Bulman, 1970, p. 52]

Encrusting Graptolithina with irregularly branching colonies made of creeping stipes; segments of stipes comprised of autothecae and bithecae produced in triads; autothecae usually with inflated proximal portion and erect distal neck, typically provided with elaborated apertural lobes; bithecae cylindrical, adnate throughout their length; stolon system usually having distinct annulation; graptoblasts routinely produced as resting bodies, which morphologically form normal part of colony (synapomorphic feature of the Wimanicrustidae); cortical deposits spurious, cortical bandages not observed. *Ordovician* (*Tremadocian, Drepanoistodus deltifer* Conodont Biozone)–*Silurian* (*Ludlow,* ?*Ludfordian, Saetograptus leinwardinensis/ Cucullograptus aversus* Biozone): worldwide.

Kozłowski (1962) based the systematic classification of his order Crustoidea almost exclusively on the evidence of chemically isolated distal parts of autothecae, especially on the morphology of their apertural apparatuses (Fig. 132), because most other details of the colonies were unknown. The genus *Hormograptus* may be considered to represent a wimanicrustid preserved in sediment and is not chemically isolated from the sediment, thus, providing a better idea on the tubarium shape and construction. However, Mierzejewski (2000a) regarded

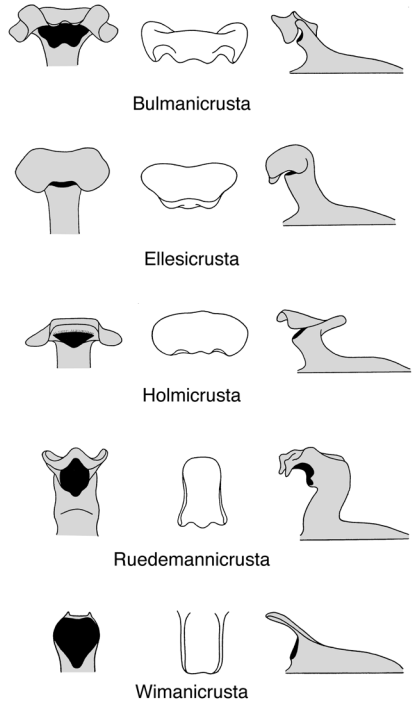


Fig. 132. The apertural modifications of thecae in the Wimanicrustidae in apertural, dorsal, and lateral views (from left to right). The apertural openings are shown in black (Kozłowski, 1962, fig. 13).

the material of *Hormograptus* as completely useless for generic and specific identification of crustoid genera and species. All crustoids have beaded stolons, i.e., stolons provided with fine transverse annulations (Kozłowski, 1962; see also Urbanek & Mierzejewski 1984; Mierzejewski, Kulicki, & Urbanek, 2005) and an apertural apparatus created through dorsal autothecal processes.

MORPHOLOGY

The precise morphology of the wimanicrustid colonies is unknown because most taxa have been described from minute fragments, usually isolated autothecae. Kozłowski (1971) described a single isolated specimen consisting of the prosicula and an incipient metasicula, which he tentatively assigned to the crustoids (Fig. 133.1–133.3). The prosicula is an ovoid vesicle (dome), proximally attached to the substrate by a

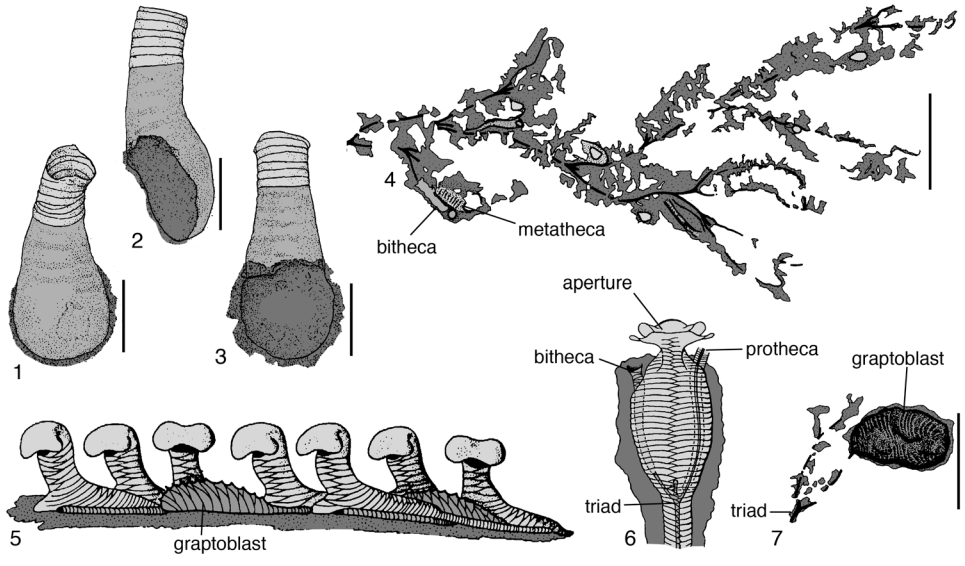


FIG. 133. The tubarium of the Wimanicrustidae. *1–3,* possible wimanicrustid sicula in different views, Vistula River Valley, Poland, scale bars, 0.1 mm (Kozłowski, 1971, fig. 4); *4, Bulmanicrusta*? KOZŁOWSKI, 1962, part of colony showing largely basal membranes, stolon system, and some parts of autothecae, scale bar, 1 mm (Mitchell, Wilson, & St. John, 1993, fig. 3,*6*); *5,* reconstruction of colony in lateral view, not to scale (adapted from Urbanek, 1983, fig. 4); *6,* reconstruction of thecal triad from above, not to scale (Kozłowski, 1962, fig. 1); *7,* ?*Bulmanicrusta* KOZŁOWSKI, 1962, fragment with graptoblast, scale bar, 1 mm (Mitchell, Wilson, & St. John, 1993, fig. 3,*7*).

concave and rough surface, surrounded by a marginal membrane. Distally, the dome produces an elongated necklike part. The metasicula consists of a number of annular fuselli, probably lacking an oblique suture. This sicula in many ways resembles the dome of the Rhabdopleuridae but differs by the presence of the necklike part raised above the substratum. It is unknown whether this specimen can be related to the Wimanicrustidae or represents a rhabdopleurid taxon. The specimen originated from glacial boulder O.544, Vistula River Valley, Poland, from which MIERZEJEWSKI (1986, p. 136) noted the presence of *Dictyonema* sp. and others, including specimens of *Rhabdopleurites primaevus* KOZŁOWSKI, 1967.

Later astogeny proceeded through triad formation to produce larger colonies (Fig. 133). Bifurcation through triads was described by KOZŁOWSKI (1962) and also by MITCHELL, WILSON, and ST. JOHN (1993). The *in situ* colonies of *Bulmanicrusta*? sp. (Fig. 133.4) encrusting the surface of a hardground from the Upper Ordovician of Ohio provide most of the available information concerning the colony shape and growth habits. *Bulmanicrusta*? sp. exhibit runner-type colonies made of radiating and irregularly branching stipes in which successive autothecae grow to alternate sides. The graptoblasts are situated mainly near the periphery of the colony at branch tips (Fig. 133.7). They develop as distal terminations of a stolotheca and appear to be associated with cessation of branch growth.

Wimanicrustid colonies are comprised of autothecae and bithecae, which are produced in triads, as is clearly visible in the preserved stolon system. The autothecae are the dominant element in construction of the wimanicrustid colony and are distinctly larger than the bithecae. The autothecae are made of a proximally more or less inflated portion and an erect distal portion producing a neck and an apertural apparatus. In its simplest form, the apertural apparatus is made of a hoodlike process, straight or curved over the aperture. The bithecae are slender, parallel-sided tubes, with their lower wall flat and

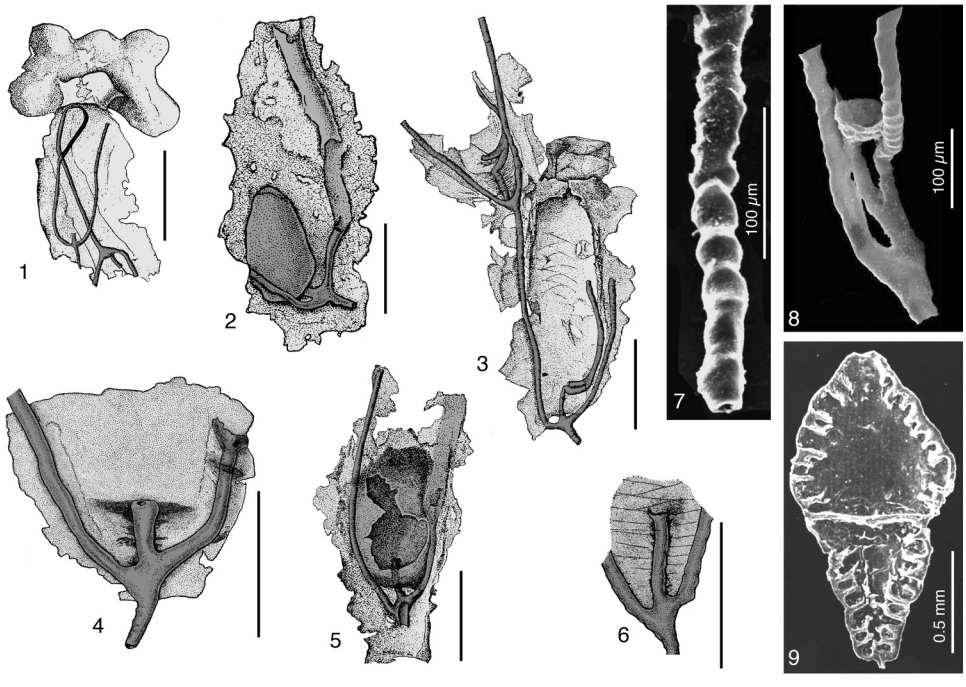


FIG. 134. The stolon system in Wimanicrustidae. *1, Bulmanicrusta modesta* KOZŁOWSKI, 1962, ventral view showing stolon system with triad budding; *2, 5,* triad budding with cyst and bitheca; *3*, *Bulmanicrusta modesta* KOZŁOWSKI, 1962, ventral view showing stolon system with triad budding; *4, 6, Wimanicrusta urbaneki* KOZŁOWSKI, 1962, details of triad budding (*1–6,* Kozłowski, 1962, fig. 2–3); *7–8, Bulmanicrusta latialata* KOZŁOWSKI, 1962, beaded stolon system (Mierzejewski, Kulicki, & Urbanek, 2005, fig. 2H); *9,* Inner cavity of graptoblast with transverse septum and hemiseptae (Mierzejewski, 2000b, fig. 2A). Scale bars, 0.1 mm in *1–6*; *7–9* as marked.

upper more or less convex. The apertures of the bithecae are devoid of any elaborations. (Fig. 133.6). The bithecae typically grow along the autothecae and open close to their apertures, but because of their great variation in length, these apertures might be an autotheca of the same or the next generation. A tendency toward right- and left-hand alternation of bithecae in successive triads can be observed.

The fusellum has distinct zigzag sutures on the dorsal side in both portions of the autothecae (Fig. 133.6), but the basal layer of the autothecae is devoid of any recognizable sutures. Bithecae have an irregular arrangement of their sutures and do not produce a zigzag suture. The differentiation of the fusellum and the ecto- and endocortex in the Wimanicrustidae has not been investigated in detail. Both types can be observed, but the ectocortex is much more common. URBANEK and MIERZEJEWSKI (1984) used transmission electron microscopy (TEM) investigation to differentiate cortex and fusellum, but this investigation was unable to determine whether cortical tissues developed as bandages because it was based on thin sections and did not provide an impression of surface features.

The stolon system has a typical triad budding system, in which the centrally placed autothecal stolon is distinctly shorter than the other stolons. As a rule, the triads are less regular than those in other dendroids and may be interpreted as two diads produced in rapid succession (MIERZEJEWSKI, KULICKI, & URBANEK, 2005) (Fig. 134). The well-sclerotized stolons, 20 to 35 μm in diameter, display a characteristic annulation not present in other graptolites (Fig. 134.7–134.8). The annulations have proved to be distinct in certain portions and much less pronounced

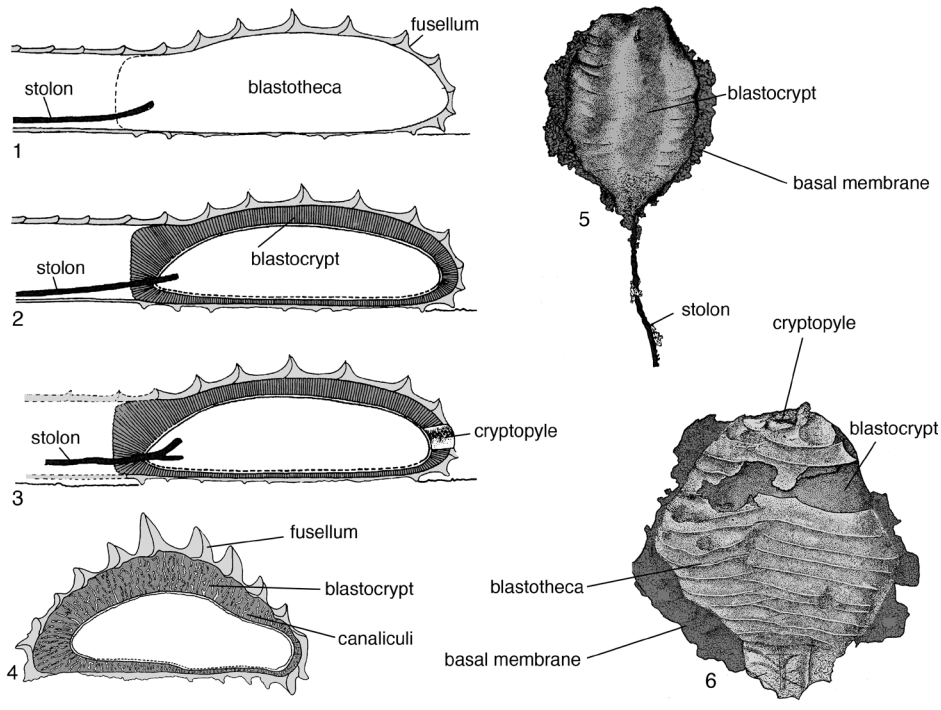


FIG. 135. Construction of the graptoblast. *1–3,* development of graptoblast (adapted from Urbanek, 1983, fig. 2); *4,* cross section of graptoblast showing canaliculi (adapted from Urbanek, Mierzejewski, & Rickards, 1986, fig. 2A); *5,* graptoblast showing basal membrane and chamber, fusellum not preserved (adapted from Kozłowski, 1962, fig. 7); *6,* graptoblast showing basal membrane and part of fusellum with dorsal zigzag suture (adapted from Kozłowski, 1962, fig. 8).

in other parts of the stolon and at places are almost smooth. Transverse sections of the stolon in *Bulmanicrusta latialata* KOZŁOWSKI, 1962 examined with TEM reveal a thick wall (about 6 µm) made of homogenous, electron-dense material and a thin inner layer comprised of loose-layered and granular material (URBANEK & MIERZEJEWSKI, 1984). The lumen of the stolon may contain organic matter in the form of filaments or globular bodies.

Cysts or vesicular bodies, varying greatly in size and shape, have been recognized inside many autothecae (Fig. 134.2, 134.5). In extreme cases, they fill the entire cavity of the autotheca, adhering tightly to its wall, but frequently are much smaller. They possess thick, blackish, and structureless walls. KOZŁOWSKI (1962) suggested they may represent the envelopes of degenerate zooids and are herein interpreted as comparable to the dormant buds of *Rhabdopleura.*

GRAPTOBLASTS

Graptoblasts (Fig. 135) were first described by KOZŁOWSKI (1949) as isolated ovoid bodies bearing traces of fusellar structure, associated with graptolite remains from the late Tremadocian fauna of Wysoczki, Poland. KOZŁOWSKI (1962) was also the first to recognize graptoblasts attached to the distal part of stolons in crustoid colonies, supported by MITCHELL, WILSON, and ST. JOHN (1993). The appendix of graptoblasts was called filum by KOZŁOWSKI (1949), but can be identified as the remnant of the stolon (KOZŁOWSKI, 1962). According to KOZŁOWSKI (1962), an opening, the cryptopyle, was formed secondarily by resorption of the distal graptoblast wall by the encysted individual or individuals (Fig. 135.3).

The graptoblast displays a two-layered construction formed from fusellar tissue outside and electron-dense crassal tissue inside (Fig. 135.1–135.3). The outer, primary

layer is called the blastotheca (Fig. 135.1). The inner component corresponds to KOZŁOWSKI's non-transparent blackish layer and was named the blastocrypt (URBANEK & RICKARDS, 1974; URBANEK, MIERZEJEWSKI, & RICKARDS, 1986), It possessed numerous and characteristic, vertically oriented and frequently branching canaliculi (Fig. 135.4). Their diameter typically varies from 0.02 nm to 0.04 nm. Some canaliculi are open to the inner cavity. The stolon may reach deep into the cavity of the graptoblast. The inner surface of the blastocrypt is covered by the inner lining, an essentially homogenous, electron-dense material sometimes with traces of layering. In some graptoblasts, the inner cavity became subdivided by the transverse septum (Fig. 134.9) into an anterior and posterior chamber (i.e., genus *Graptoblastus* KOZŁOWSKI, 1949). MIERZEJEWSKI (2000a) used SEM technique to demonstrate that the transverse septum is two-layered, each layer being the continuation of the inner lining either from the anterior or posterior chamber.

According to URBANEK (1983), graptoblasts may be reinterpreted as closed, resting terminal portions of thecae, housing encysted dormant buds (Fig. 135.1–135.4). Their role in the life cycle of crustoid graptolites may be best compared with hibernaculae of ctenostomate bryozoans. In one of the early Silurian graptoblasts he investigated, MIERZEJEWSKI (2000a) recognized numerous incomplete septae (which he called hemiseptae) produced by folds of the inner lining. These were spread more or less evenly in both chambers (Fig. 134.9). However, on the basis of this finding, one cannot conclude whether hemiseptae are normal structures or rare abnormalities.

Wimanicrusta KOZŁOWSKI, 1962, p. 43 [**W. cristaelingulata;* OD]. Apertural lobe linguiform; neck short or absent; triad budding; other details of colony unknown. *Lower Ordovician–Upper Ordovician:* Estonia, Poland, Sweden (Öland) (glacial erratic boulders).——FIG. 136,*6a–d*. **W. cristaelinguata*, holotype (*a–b*) and fragment (*c–d*) in dorsal and ventral views, scale bars, 0.1 mm (Kozłowski, 1962, fig. 24A–B).

Bulmanicrusta KOZŁOWSKI, 1962, p. 31 [**B. latialata;* OD]. Wimanicrustid with runner-type colony, showing triad budding; large apertural lobes with median and auriculate lateral folds; neck distinct or absent. *Middle Ordovician* (*Darriwilian*)*–Upper Silurian* (*Ludlow*): Baltic Region, ?USA.——FIG. 136,*1a–d*. **B. latialata; 1a–b,* holotype (Kozłowski, 1962, pl. 2A–B); *1c–d,* thecal aperture in apertural (*c*) and adapertural (*d*) views, scale bars, 0.5 mm (Kozłowski, 1962, 15A–B).——FIG. 136,*1e–h. B. latialata scutellifera* KOZŁOWSKI, 1962; *1e–f,* two fragments in dorsal view (Kozłowski, 1962, pl. 4A–B); *1g–h,* holotype, thecal aperture in apertural (*h*) and adapertural (*g*) views, scale bars, 0.5 mm (Kozłowski, 1962, 16A–B).

Ellesicrusta KOZŁOWSKI, 1962, p. 38 [**E. longicollis;* OD]. Apertural lobe with slight lateral folds; long neck; details of colony unknown. *Middle Ordovician–Upper Ordovician:* Estonia (glacial erratic boulders).——FIG. 136,*2a–d*. **E. longicollis,* holotype in various views, scale bars, 0.5 mm (Kozłowski, 1962, fig. 21).

Holmicrusta KOZŁOWSKI, 1962, p. 41 [**H. sombrero;* OD]. Apertual lobe large, flattened; neck long; details of colony unknown. *Lower Ordovician–Middle Ordovician:* Poland (glacial erratic boulders).——FIG. *136,3a–d*. **H. sombrero,* holotype in various views, scale bars, 0.2 mm (Kozłowski, 1962, fig. 23).

Hormograptus ÖPIK, 1930, p. 8, *pro Thallograptus* ÖPIK, 1928, p. 35, *non Thallograptus* RUEDEMANN, 1925b, p. 35 [**Thallograptus sphaericola;* OD]. Runner-type encrusting colony; tubarium details unknown. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Estonia.——FIG. 137,*1a–b*. **H. sphaericola* (RUEDEMANN), TUG 1317, holotype and enlargement of part, scale bars, 1 mm (new; provided by Ursula Toom).

Lapworthicrusta KOZŁOWSKI, 1962, p. 44 [**L. aenigmatica;* OD]. Apertural lobe small; autothecae slender without interthecal membrane; neck absent; details of colony unknown. *Middle Ordovician* (*Darriwilian*): Poland (glacial erratic boulders).——FIG. 136,*5a–b*. **L. aenigmatica,* holotype, two fragments of a single colony, scale bars, 0.5 mm (Kozłowski, 1962, fig. 26).

Ruedemannicrusta KOZŁOWSKI, 1962, p. 39 [**H. geniculata;* OD]. Apertural lobe distinct with small auriculate lateral folds; neck long, curved, with strong internal ridges; details of colony unknown. *Middle Ordovician–Upper Ordovician:* Poland, Estonia (glacial erratic boulders).——FIG. 136,*4a–c*. **R. geniculata,* holotype, scale bars, 0.1 mm (Kozłowski, 1962, fig. 22).

UNRECOGNIZABLE WIMANICRUSTID TAXA

The following taxa represent unidentifiable preservational forms, too imperfectly known for taxonomic description and placement. The genera *Graptoblastus* KOZŁOWSKI, 1949 and *Graptoblastoides* KOZŁOWSKI, 1949 are now identified as the resting stages of the Wimanicrustidae and not identified as separate graptolite genera (see KOZŁOWSKI,

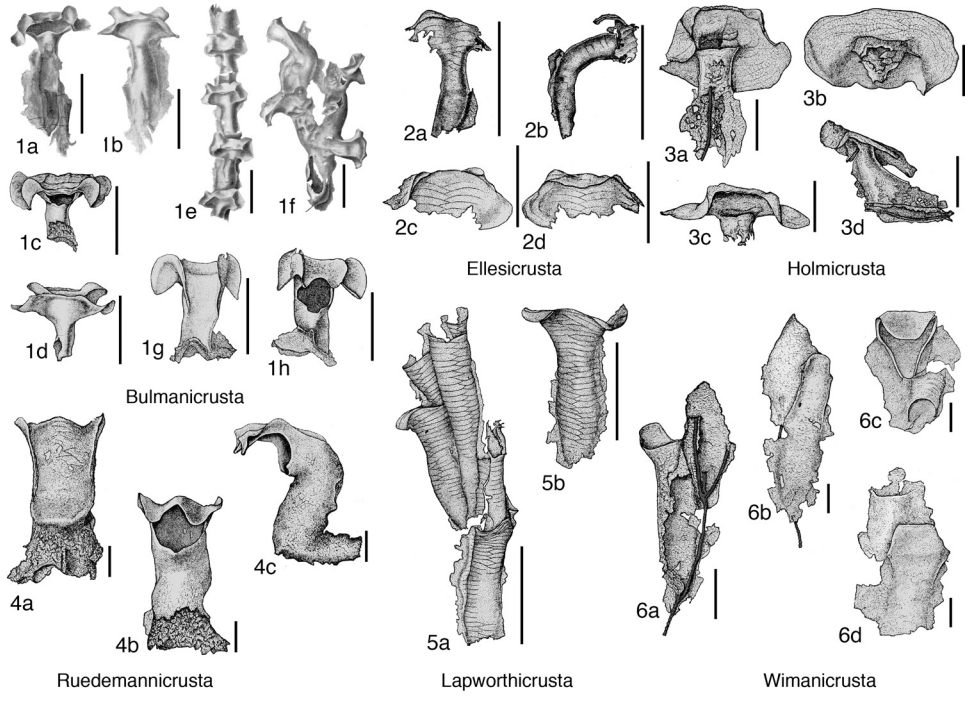


FIG. 136. Wimanicrustidae (p. 219).

1962; URBANEK, 1983) but are listed herein in the interest of being complete. A connection of the known graptoblasts to certain genera of the Wimanicrustidae has not been established; and, thus, these cannot be referred to any genus in particular.

Graptoblastus KOZŁOWSKI, 1949, p. 210 [**G. planus;* OD]. Ovoid to vesicular body with flat base, convex upper wall; dorsally distinct zigzag suture usually visible; formed from electron-dense material having numerous canaliculi; septum separates internal chamber into two partitions; indication of stolon on one end, cryptopyle on other end. [The taxon represents a resting stage or graptoblast in a parataxonomic context and not a valid graptolite genus (see KOZŁOWSKI, 1962, p. 18).]——FIG. 137,*6a–c*. **G. planus,* holotype in dorsal and ventral view, ZPAL G.I/1-290, scale bars, 0.1 mm (Kozłowski, 1949, pl. 37,*3*).

Graptoblastoides KOZŁOWSKI, 1949, p. 216 [**G. nowaki;* OD]. Ovoid to vesicular body with flat base, convex upper wall; dorsally, distinct zigzag suture visible; formed from electron-dense material having numerous canaliculi; single internal chamber; indication of stolon on one end, cryptopyle on other end. [The taxon represents a resting stage or graptoblast in a parataxonomic context and not a valid graptolite genus (see KOZŁOWSKI, 1962, p. 18)].——FIG. 137,*5a–b*. **G. nowaki,* holotype in dorsal and ventral view, ZPAL G.I/1-290, scale bars, 0.1 mm (Kozłowski, 1949, pl. 39,*1*).

Maenniligraptus MIERZEJEWSKI, 1985, p. 196 [**M. ursulae;* OD]. Encrusting taxon with tubular thecae, devoid of erect parts and any apertural apparatus; stolons with diad and triad budding; stolon with annular and helical thickenings; details of colony unknown. [The taxon is very poor and specifically indeterminate. MIERZEJEWSKI (1982) identified this material as a camaroid and suggested that similar organic material from pre-Devonian samples with the inner rings and spiral thickenings may have been mistaken for tracheid-like tubes characteristic of land plants.] ?*Ordovician:* Poland (glacial erratic boulder).——FIG. 137,*2a–b*. **M. ursulae,* fragments of holotype, scale bars, 0.1 mm (Mierzejewski, 1985, pl. 7,*8*).

Urbanekicrusta MIERZEJEWSKI, 1985, p. 194 [**U. reversa;* OD]. Dorsal apertural process long with wide lobe; neck long; bithecae unknown (absent?); details of colony unknown. [The taxon is unrecognizable due to poor preservation and fragmentation, but clearly represents pterobranch remains, possibly with triad budding.] *Silurian* (*Wenlock*): Poland, Sweden (glacial erratic boulders).——FIG. 137,*3a–b*. **U. reversa,* holotype, scale bar for *3a,* 1 mm, *3b,* scale bar, 0.1 mm (Mierzejewski, 1985, pl. 5).

Xenocyathus EISENACK, 1982, p. 630, *nom. dub.* [**X. stolonifer;* M]. [This taxon is represented as stolon fragments with triad budding and may be identified as a wimanicrustid (MIERZEJEWSKI, 1984).

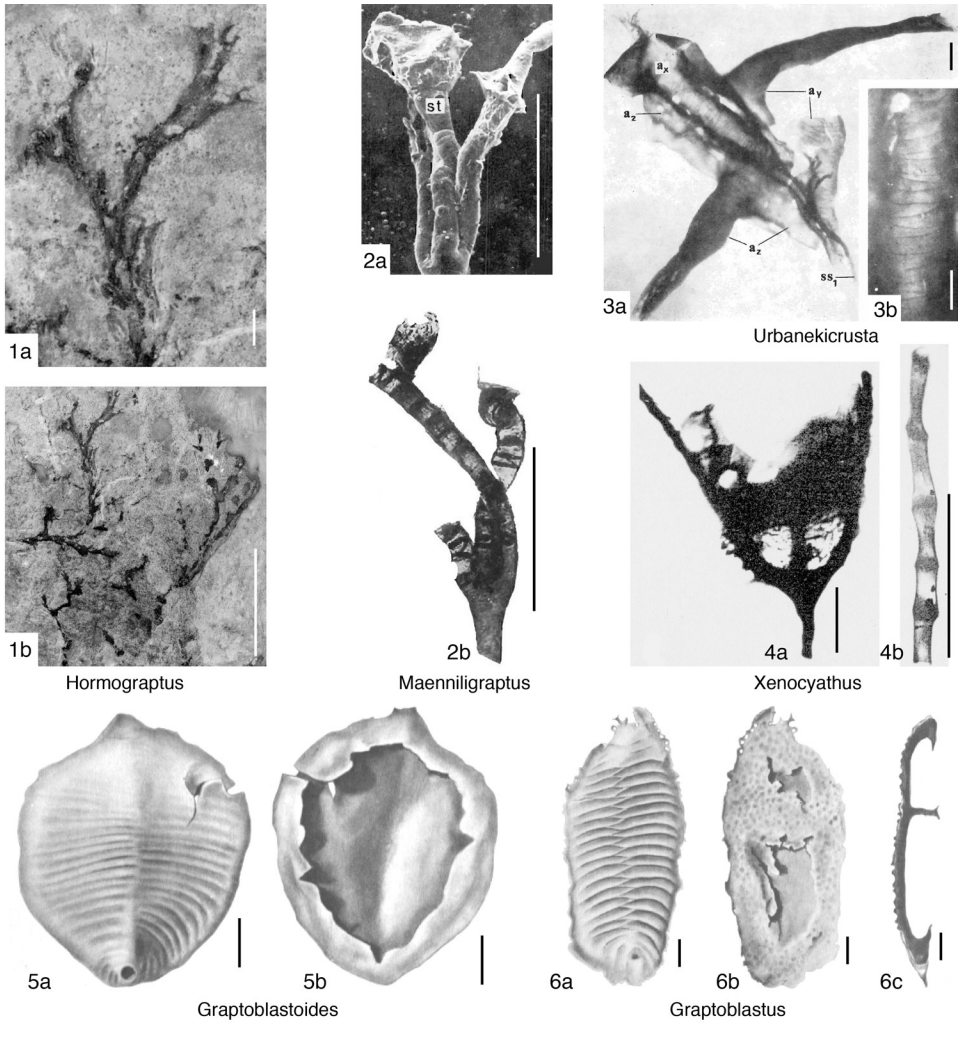


FIG. 137. Wimanicrustidae, uncertain genera (219–221).

The material cannot be related to any identifiable wimanicrustid genus.] *Ordovician* (*Sandbian*)–*Silurian* (*Wenlock*): Estonia, Finland, *Ordovician;* Sweden (Gotland) (glacial erratic boulders), *Silurian* (*Wenlock*).——FIG. 137,*4a–b*. **X. stolonifer,* Upper Ordovician, Estonia; *4a,* holotype, scale bar, 0.1 mm; *4b,* beaded stolon, scale bar, 0.1 mm (Eisenack, 1982, fig. 2,*4*).

Family CYSTICAMARIDAE Bulman, 1955

[Cysticamaridae BULMAN, 1955, p. 42; incl. Bithecocamaridae BULMAN, 1955, p. 42]

Encrusting, sigmophyllic Graptolithina producing autothecae as characteristic camara with erect neck or collum; stolon usually embedded in extracamaral tissue on surface of camara; bithecae may be present in some. *Lower Ordovician* (*Tremadocian*)–*Upper Ordovician* (*Sandbian*): Finland, Poland (glacial erratic boulders), Russia, Sweden.

The Cysticamaridae represent a small group of benthic, encrusting graptolites. Most of the material originated from the famous locality Wysoczki in the Holy Cross Mountains of Poland, where they are known mainly from glacial boulders (KOZŁOWSKI, 1949), but rare additional specimens were

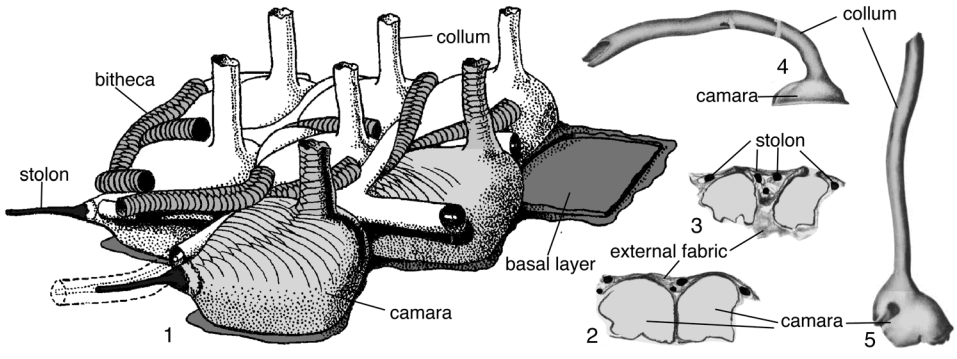


FIG. 138. Morphology of the Cysticamaridae. *1, Bithecocamara* KOZŁOWSKI, 1949, reconstruction (adapted from Bulman, 1955, fig. 26); *2–3,* Sections through the thecae of *Cysticamara accollis* KOZŁOWSKI, 1949 showing the presence of a stolon system (adapted from Kozłowski, 1949, pl. 29; *4–5,* two isolated cysticamarid fragments with long collum (adapted from Kozłowski, 1949, pl. 31).

collected from a few localities in Scandinavia (e.g., SKEVINGTON, 1963a; MIERZEJEWSKI, 2003). Very little is known about their colony construction and evolutionary relationships because the material is based on highly fragmented specimens.

MORPHOLOGY

The Cysticamaridae possess characteristically inflated autothecal tubes, camara with an erect tube, and a collum or neck (Fig. 138). The basal layer is smooth and constructional details are not visible. The collum is fairly slender as compared to the inflated camara, but both have conspicuous zigzag sutures. A considerable elongation of the collum has been recognized in a couple of fragments (Fig. 138.4–138.5). The development of the thecal apertures is uncertain in most taxa due to preservational aspects but may be quite simple. Commonly, the apertures indicate fragmentation and loss of the actual apertural margins through the presence of irregular rims.

Cross sections of *Cysticamara accollis* KOZLOWSKI, 1949 (Fig. 138.2–138.3) and *Bithecocamara gladiator* KOZLOWSKI, 1949 indicate the presence of a stolon system. The stolon system is encased in extrathecal fabric. It is positioned above the camara and is not visible externally. Thus, it has been verified only from thin sections of a few members. There is no information on the development of the stolon system as a diad or triad development as isolated stolon fragments have not been described. The description of bithecae in *Bithecocamara* suggests a thecal differentiation, but this is not known from other taxa, as these are typically based on small colony fragments that are commonly isolated metathecae.

KOZŁOWSKI (1949) differentiated bithecae in *Bithecocamara gladiator* as slender tubes without erect growth from the camarate autothecae with their characteristic colla. The development and differentiation of auto- and bithecae in most Cysticamaridae is uncertain, considering that the development of the stolon system has not been described. BULMAN (1955) erected the Bithecocamaridae based on the presence of bithecae in *Bithecocamara gladiator*. A thecal differentiation is unknown in other taxa of the family, but it may be argued that the preservation and fragmentation is too incomplete to recognize these details.

URBANEK and MIERZEJEWSKI (1991) described the ultrastructure of *Tubicamara coriacea* KOZŁOWSKI, 1949. TEM studies reveal fusellum and endo- and ectocortex to be present. The endocortex is thought to be underdeveloped and may be missing in

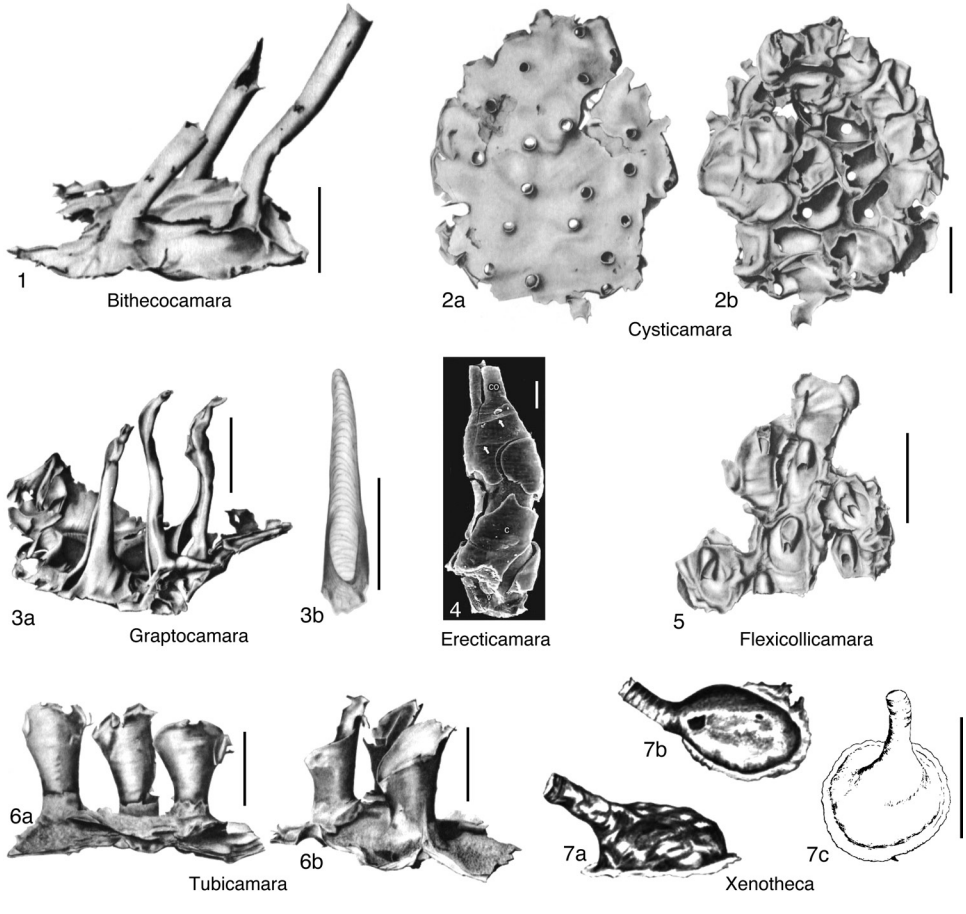


FIG. 139. Cysticamaridae (p. 223–224).

many cysticamarids. MIERZEJEWSKI (2000b) described the wall construction of *Xenotheca* in some detail and described the verrucose fabric as a previously unrecognized material on the outside of the taxon, very likely occluding the thecal apertures (MIERZEJEWSKI, 2003).

Bithecocamara Kozłowski, 1949, p. 176 [*B. gladiator; OD]. Thigmophilic tubarium with densely arranged camarae; autothecae with well-developed collum, but apertural modifications unknown; indications of stolon system inside extracamaral fabric above camarae; differentiated into two types of thecae, of which smaller one, which lacks collum, is termed bitheca. Lower Ordovician (Tremadocian): Poland.——Fig. 139.1. **B. gladiator,* holotype, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 24,1a).

Cysticamara KOZŁOWSKI, 1949, p. 183 [**C. accollis;* OD] [=*Syringotaenia* Obut, 1953, p. 54 (type, *S. bystrovi,* M), syn. by BULMAN, 1970, p. 50]. Thigmophilic tubarium with densely arranged camarae; autothecae with slightly elevated, thickened rim, but without collum; indications of stolon system inside extracamaral fabric above camarae. [VISKOVA & IVANTSOV, 1999, p. 25 referred *Syringothenia* (misspelling) to the bryozoan family Alcyonidiidae.] *Lower Ordovician* (*Tremadocian*)–*Middle Ordovician* (*Darriwilian*): Poland, Sweden, Russia.——FIG. 139,*2a–b*. **C. accollis,* holotype in dorsal (*a*) and ventral (*b*) views, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 28,*1–1a*).

Erecticamara MIERZEJEWSKI, 2000c, p. 241 [**E. maennili;* OD]. Tubarium unknown; slender, bottle-shaped or subconidal autothecae more or less differentiated into erect, broad proximal part (camara), provided with narrow distal part (collum); aperture devoid of any kind of apertural processes; bottom of camara convex with small camaral processes or in form of small, flat sole; fuselli irregular, no zigzag suture formed; indications of stolon system present.

Middle Ordovician (*Darriwilian*): Poland (glacial erratic boulder).——Fig. 139,*4*. **E. maennili,* holotype, ZPAL G/XXIV/5, isolated theca, scale bar, 0.1 mm (Mierzejewski, 2000c, fig. 1e).

Flexicollicamara Kozłowski, 1949, p. 182 [**F. bryozoaeformis;* OD]. Thigmophilic tubarium with densely arranged camarae; collum strongly bent back ventrally and fused to upper wall of camara; stolon system unknown. [The taxon is known from two fragments of which only one was ever illustrated.] *Lower Ordovician* (*Tremadocian*): Poland (glacial erratic boulder).——Fig. *139,5*. **F. bryozoaeformis,* holotype, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 28,*4*).

Graptocamara Kozłowski, 1949, p. 187 [**G. hyperlinguata;* OD] [=*Camarotubus* Mierzejewski, 2001, p. 371 (type, *C. graptocamaraeformis,* OD), syn. herein]. Thigmophilic tubarium with densely arranged camarae; autothecae with elongated rutellate apertural process, lacking collum; stolon system poorly known. *Lower Ordovician* (*Tremadocian*)–*Middle Ordovician* (*Darriwilian*): Poland, Sweden.——Fig. 139,*3a–b*. **G. hyperlinguata; 3a*, holotype, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 30,*6*). *3b*, isolated apertural process showing fuselli, scale bar, 0.5 mm (Kozłowski, 1949, pl. 30,*5*).

Tubicamara Kozłowski, 1949, p. 188 [**T. coriacea;* OD]. Thigmophilic tubarium with densely arranged camarae; funnel-shaped collum with ventral apertural process; abundant cortical tissue; stolon system unknown. *Lower Ordovician* (*Tremadocian*): Poland.——Fig. 139,*6a–b*. **T. coriacea,* holotype in two views, ZPAL GI/1-290, scale bars, 0.5 mm (Kozłowski, 1949, pl. 30,*1a–b*).

Xenotheca Eisenack, 1938b, p. 239, *non Xenotheca* Arber & Goode, 1915, p. 96 (Devonian plant) [**X. klinostoma;* OD] [?=*Xenokalymma* Eisenack, 1968, p. 306 (type, *X. trematophora,* OD), syn. herein]. Tubarium shape unknown; tubarium known from isolated metathecae formed as robust camarae with semi-erect collum; indications of stolon system present. *Middle Ordovician* (*Darriwilian*): Finland, Poland (glacial erratic boulder).——Fig. 139,*7a–c*. **X. klinostoma; 7a,* holotype (Eisenack, 1938b, fig. 21); *7b,* paratype (Eisenack, 1938*b*, fig. 22); *7c*, neotype, GPIT Tr. 5, Nr. 17 (Eisenack, 1970, fig. 1). Scale bar, 1 mm for all.

Family DITHECODENDRIDAE Obut, 1964

[Dithecodendridae Obut, 1964, p. 306 (misquoted as Obut, 1957); incl. Siberiograptidae Obut, 1964, p. 306 (misquoted as Obut, 1957); Bulmanidendridae Obut, 1974, p. 12]

Graptolithina with erect-growing tubarium, with multiple dichotomous branchings; thin-walled metathecae isolated, tubular, or slightly widening towards aperture; thecae arranged alternately or irregularly on slender to robust stem. *Cambrian* (*Miaolingian–Furongian*): Australia, Canada, USA, Spain, Poland (glacial erratic boulders), Sweden, Russia (Siberia).

The Dithecodendridae Obut, 1964 is a group of benthic graptolites with an erect growth of the colony and isolated, trumpet-like to parallel-sided, long metathecae. All taxa are formed from an organic material, but only in rare cases has the presence of the fusellum been demonstrated (e.g., *Tarnagraptus;* Maletz, Steiner, & Fatka, 2005) (Fig. 140). They possess isolated metathecae with thin fusellum and a robust stem (Fig. 140.1), probably thickened with considerable amounts of cortical tissues. Nothing is known about the style of budding, and the presence of a stolon system has not been demonstrated. Sdzuy (1974) described and illustrated holdfast structures (termed Basal-Scheibe) in a number of taxa, including *Tarnagraptus palma* Sdzuy, 1974 and *Tarnagraptus thomasi* Sdzuy, 1974, but most remains are fragmented stipes without of an attachment. Similarities to the Mastigograptidae include the stolon systems with triad budding and isolated, thin-walled thecae (Bates & Urbanek, 2002).

Obut (1960, p. 149) erected the order Dithecoidea based on the assumed diad budding in the included genera. Most of the genera are known from fragments, and details of their development are not available. Obut (1974) added the order Archaeodendrida Obut, 1974 for the genera *Archaeodendrum* Obut, 1974 (a possible hydroid; Rickards & Durman, 2006, p. 58) and *Archaeolafoea* Chapman, 1919 (included in the Rhabdopleuridae; see p. 210). Bulman (1970) listed most of the genera included here in the Dithecodendridae under the category, "taxonomic position uncertain."

Johnston, Johnston, and Powell (2009) described larger, complexly branched dithecodendrids from the *Bolaspidella* Zone (Drumian to lower Guzhangian; Peng, Babcock, & Cooper, 2012) of the Chancellor Basin, British Columbia, Canada, and documented fusellar construction in the material (Fig. 140.5–140.6). The speci-

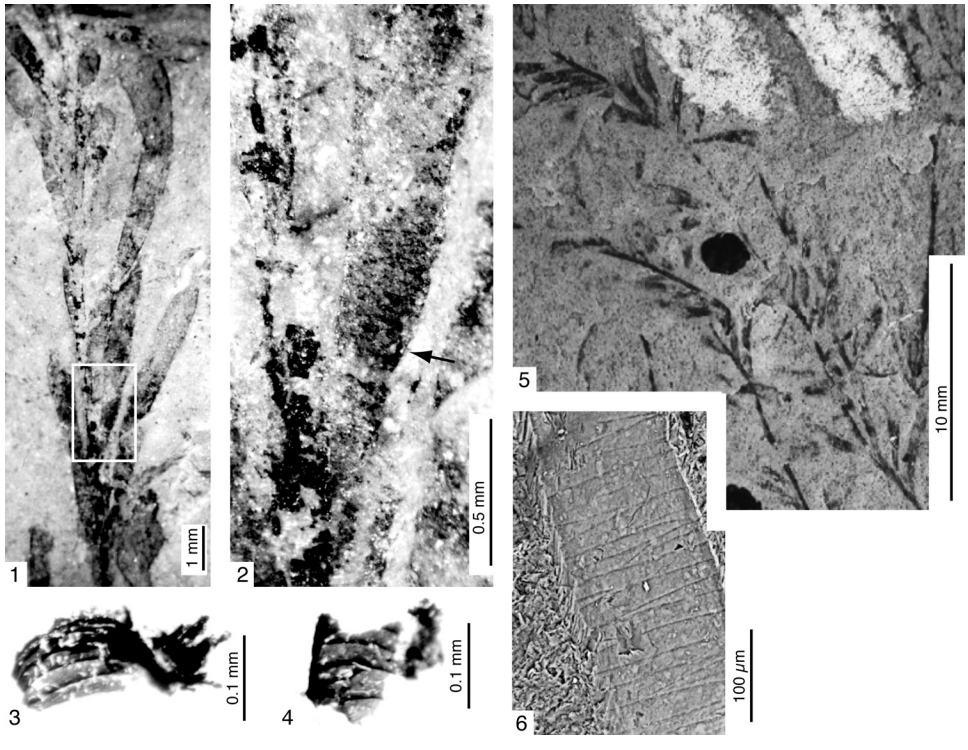


FIG. 140. Tubarium details of the Dithecodendridae. *1–2, Tarnagraptus cristatus* SDZUY, 1974, SMF 30021; *1*, part of holotype showing thin-walled metathecae and indications of robust stem; *2,* magnified part of (*1*) showing indications of fuselllar construction (*arrow*); *3–4,* chemically isolated fragments of *Tarnagraptus palma* SDZUY, 1974, from SMF 30002, showing fuselli (*1–4,* Maletz, Steiner, & Fatka, 2005, fig. 6); *5–6*, Dithecodendridae indet., Duchesnay unit, British Columbia, Canada, part of colony (*5*) and detail showing imprints of fuselli (*6*) (Johnston, Johnston, & Powell, 2009, fig. 7).

mens represent some of the oldest and best-preserved Middle Cambrian graptolites presently known.

Dithecodendrum Obut, 1964, p. 306 [**D. sibiricum;* OD]. Slender, elongate colony with tubular thecae; thecae isolated distally, possibly arranged biserially. *Cambrian* (*Miaolingian, Drumian*): Russia (Siberia). [The genus is based on a single flattened stipe fragment].——FIG. 141,*2*. **D. sibiricum,* IGiG 960, holotype, scale bar, 1 mm (Rickards & Durman, 2006, fig. 58c).

Bulmanidendrum OBUT, 1974, p. 12[**B. magnificum;* OD]. Stipe(s)? flexuous, robust, with long, slightly widening, alternately arranged thecae, proximally adnate and isolate distally. [A fusellar structure is not recognized (RICKARDS & DURMAN, 2006, p. 65)**,** therefore the graptolithic nature of this genus is uncertain.] *Middle Cambrian* (*Miaolingian, Drumian*): Russia (Siberia).——FIG. 141,*1*. **B. magnificum*, holotype, IGiG 592/5, scale bar, 5 mm (Rickards & Durman, 2006, fig. 55).

Karasidendrum SENNIKOV, 1998, p. 17 [**K. aspidograptoides;* OD]. Slender tubarium with regularly and dichotomously branching stipes; details of thecae not available. *Cambrian* (*Miaolingian, Drumian*): Russia (Siberia). [The illustrations are poor and unclear. No fuselli are visible to ascertain the graptolitic nature of the taxon].——FIG. 141,*6*. **K. aspidograptoides*, holotype, scale bar, 5 mm (Sennikov, 1998, pl. 1,*3*).

Ovetograptus SDZUY, 1974, p. 131 [**O. gracilis;* OD]. Dithecodendrids with bushy growth; metathecae parallel sided and widely spaced; stolon system unknown. *Cambrian, Miaolingian* (*Wuliuan–Drumian*): Spain.——FIG. 141,*7*. **O. gracilis,* holotype, SMF 30028, scale bar, 5 mm (new).

Protodendrum SENNIKOV, 1998, p. 16 [**P. paniculiformis;* OD]. Possible dithecodendrid with slender stem and crown of densely spaced tubular thecae; details of tubarium unknown. *Cambrian* (*Miaolingian, Drumian*): Russia (Siberia). [The taxon is based on poor material and could be a dithecoid. Assignment was based only on age].——FIG. 141,*5a–b*. **P. paniculiformis,* holotype, scale bars, 5 mm (Sennikov, 1998, pl. 1,*1–2*).

Siberiodendrum OBUT, 1964, p. 306 [**S. robustum;* OD]. Robust dithecodendrid fragment with densely

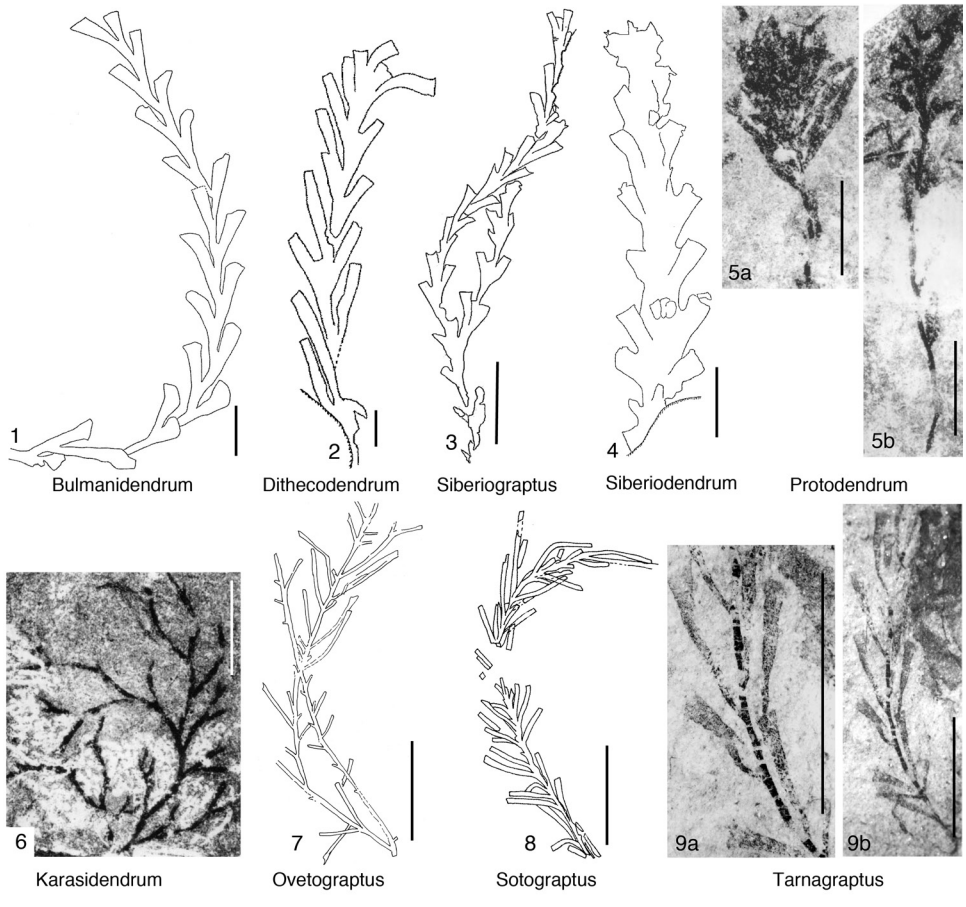


FIG. 141. Dithecodendridae (p. 225–226).

spaced, wide, probably parallel-sided thecae; thecae probably arranged biserially; tubarium shape unknown. *middle Cambrian–upper Cambrian:* Russia (Siberia). [The taxon is known from a single fragment. Its precise locality and age are unknown. RICKARDS & DURMAN (2006, p. 71) referred the taxon to the hydroids.]——FIG. 141,*4. *S. robustum,* IGiG 960, holotype, scale bar, 5 mm (Rickards & Durman, 2006, fig. 62).

Siberiographtus OBUT, 1964, p. 306 (there cited as OBUT, 1963) [**S. kotujensis;* OD] [=*Palaeodiphasia* SONG, RUTHENSTEINER, LYU, LIU, WANG & HAN, 2021, p. 2 (type, *S. simplex* LIN, 1985), syn. herein]. Tubarium slender, with large, distally isolate thecae; thecae arranged biserially. [The identity of *Palaeodiphasia simplex* as a hydroid relies on a reinterpretation of the poorly preserved type material and remains equivocal.] *upper Cambrian:* Russia (Siberia).——FIG. 141,*3. *S. kotujensis,* IGiG 960, holotype, scale bar, 5 mm (Rickards & Durman, 2006, fig. 39).

Sotograptus SDZUY, 1974, p. 130 [*S. flexilis;* OD]. Dithecodendrids with bushy growth; metathecae barely widening aperturally; stipes surrounded by initial parts of thecae; stolon system unknown. *Cambrian, Miaolingian* (*Wuliuan–Drumian*): Spain.——FIG. 141,*8. *S. flexilis,* holotype, SMF 30026, scale bar, 5 mm (Sdzuy, 1974, fig. 17).

Tarnagraptus SDZUY 1974, p. 124 [**T. palma;* OD]. Dithecodendrids with bushy growth; thin-walled metathecae distinctly widening; stolon system unknown. *Cambrian, Miaolingian* (*Wuliuan–Drumian, Paradoxides paradoxissimus* Biozone): Spain.——FIG. 141,*9a–b. *T. palma,* holotype, SMF 30023, specimen and detail showing preservation of robust stipes and thin-walled metathecae, scale bars, 5 mm (new).

Family CYCLOGRAPTIDAE Bulman, 1938

[Cyclograptidae BULMAN, 1938, p. 22] [=Tubidendridae KOZŁOWSKI, 1949, p. 160; *non* Tubidendridae NUTTING, 1905, p. 940 (a family of Hydrozoa), emend. SCHUCHERT, 2003]

Encrusting Graptolithina with tubular thecae; erect-growing short stipes may form from thecorhiza; thecal differentiation may be

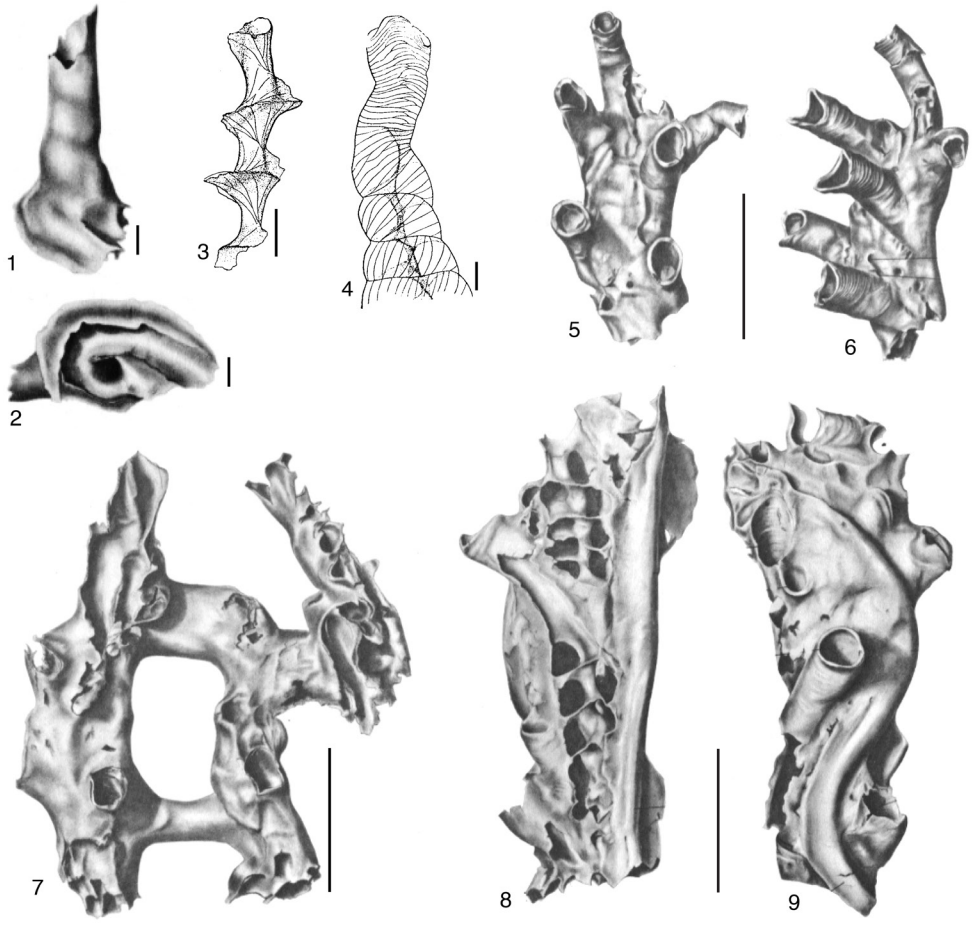


FIG. 142. Morphology of the Cyclograptidae. *1–2*, *Dendrotubus wimani* KOZŁOWSKI, 1949, details of coiled median part of thecae; *3–9*, *Tubidendrum bulmani* KOZŁOWSKI, 1949; *3*, internal helicoidal structure; *4*, coiled median part of theca; *5–6*, fragment showing thecal orientation; *7*, bridges connecting stipes; *8–9*, fragment with coiled thecae and external tubes; *1–4*, scale bars, 0.1 mm; *5–9*, scale bars, 1 mm (*1–9*, Kozłowski, 1949, see fig. 50a–b and pl. 19–20).

present, but rarely expressed through differences in size; stolon system might be quite variable; branching apparently by diads with irregular succession at variable spacing. *Lower Ordovician* (*Tremadocian*)*–Upper Ordovician* (*Sandbian*): Finland, Poland (glacial erratic boulders), Russia, Sweden.

The Cyclograptidae include mostly taxa formerly referred to the order Tuboidea by KOZŁOWSKI (1949). BULMAN (1938) erected the family for benthic taxa with a basal disk and numerous erect stipes, but BULMAN (1950b) considered the family Cyclograptidae as a synonym of Idiotubidae and did not even mention Cyclograptidae in the earlier Treatise volumes (BULMAN, 1955, 1970). MIERZEJEWSKI (1978, p. 562) discussed the validity of the taxon and questioned the monophyly of the family Cyclograptidae, but found it impossible to provide a better solution. The details of the tubarium formation are typically known from small fragments chemically isolated from limestones and cherts. It is quite difficult to relate these fragments with material from shales and to understand their construction.

MORPHOLOGY

The colony shape of most Cyclograptidae is not well established and BULMAN (1970) considered encrusting to flabellate and bushy

forms to be represented. The thecae grew upward from the thecorhiza as individuals or in groups, forming complex stems.

The genera *Cyclograptus*, *Galeograptus,* and *Discograptus* are known from larger and more complete colonies. They have a rounded thecorhiza with erect growing groups of thecae and may be closely related. Erect stipes on the thecorhiza may have one or two branching divisions, and the stipes remained relatively short. *Galeograptus* has conothecae and bithecae concentrated in the thecorhiza, but these are not present in the erect stipes (BULMAN & RICKARDS, 1966).

KOZŁOWSKI (1949) illustrated possible bithecae in *Calycotubus*, but these appear to be based on the diameter of the openings on the thecorhiza only. The so-called bithecae may actually be initial parts of aborted or broken thecal tubes. Nothing is known on the presence of a stolon system, budding style, and other tubarium details. Even the origins of individual autothecae and thecal connections are unknown.

Thecae may produce anastomosis and thecal bridges to connect the stipes laterally (Fig. 142.7) through which tubular thecae grow from one stipe to an adjacent one in *Tubidendrum bulmani* KOZŁOWSKI, 1949 and possibly in others. The apertures of the autothecae are commonly oriented to one side of the stipe, interpreted as the ventral side, showing a possible serial arrangement (Fig. 142.5–142.6).

According to BULMAN (1938), the tubaria of the Cyclograptidae are differentiated into autothecae and numerous bithecae with a highly irregular distribution. The identification of the bithecae is made solely on the size of the thecal tubes and the simple straight apertures, whereas the autothecae typically bear short rutella and are larger. A spiral development of the median parts of the thecae has been described for *Tubidendrum bulmani* and *Dendrotubus wimani* KOZŁOWSKI, 1949 (Fig. 142.1–142.4; Fig. 142.8–142.9). This development may include a variable number of coils, but is not present in all taxa referred to the Cyclograptidae.

KOZŁOWSKI (1949) described a thecal dimorphism in *Tubidendrum,* in which special thecae, called microthecae, possess a narrow terminal portion with an oblique aperture facing the opposite side of the stipe from that of normal autothecae. Dimorphic thecae are also present in *Galeograptus* in which umbellate thecae form an umbrella-shaped structure shielding the aperture of the preceding theca (BULMAN & RICKARDS, 1966; BULMAN, 1970). The shields of these umbellate thecae fill the cavity formed by the ring of stipes in the proximal region of the specimens with a vesicular mass of tissue. Umbellate thecae are only known from thin sections of *Galeograptus wennersteni* WIMAN, 1901.

KOZŁOWSKI (1949) described the diad development of the stolon system of *Tubidendrum* from serial sections of the holotype. A diad budding system is known from *Kozlowskitubus* (Fig. 143,*7a*), in which the initial thecae grew in a circle around the erect sicula, and all thecae bud from the left side of the stolon. MIERZEJEWSKI (1978) described similar construction for *Dendrotubus wimani*. BULMAN and RICKARDS (1966) discussed a diad stolon system in *Reticulograptus* WIMAN, 1901 from serial sections, but the taxon is now referred to the Acanthograptidae. The stolon system is poorly known in most Cyclograptidae and is documented largely from serial sections. Thus, important information on its construction is not available.

Cyclograptus SPENCER, 1883, p. 365 [**C. rotadentatus* SPENCER, 1884, p. 592; M] [=*Rodonograptus* POČTA, 1894, p. 204 (type, *R. astericus,* M), syn. by BULMAN, 1970, p. 48]. Tubarium discoidial, erect portions of autothecae grouped into 20 to 30 peripheral sheaves bifurcating at mid-length; thecae tubular, elongated; thecal differentiation and stolon system unknown. *Silurian* (*Wenlock*): Canada, Czech Republic.——FIG. 143,*4a*. **C. rotadentatus,* lectotype, ROM 21623, scale bar, 1 mm (Bulman, 1970, fig. 29,*3*).——FIG. 143,*4b*. *C. astericus*, ?lectotype, scale bar, 1 mm (Počta, 1894, pl. 8,*11*).

Calycotubus KOZŁOWSKI, 1949, p. 156 [**C. infundibulatus;* OD]. Encrusting taxon with strongly widening, robust autothecae, bearing regular zigzag sutures and forming irregular associations; simple, straight apertures or slight development of rutellum on one side; fuselli robust and regular, invariably developed as half rings with two zigzag sutures. *Lower Ordovician* (*Tremadocian*): Poland (glacial

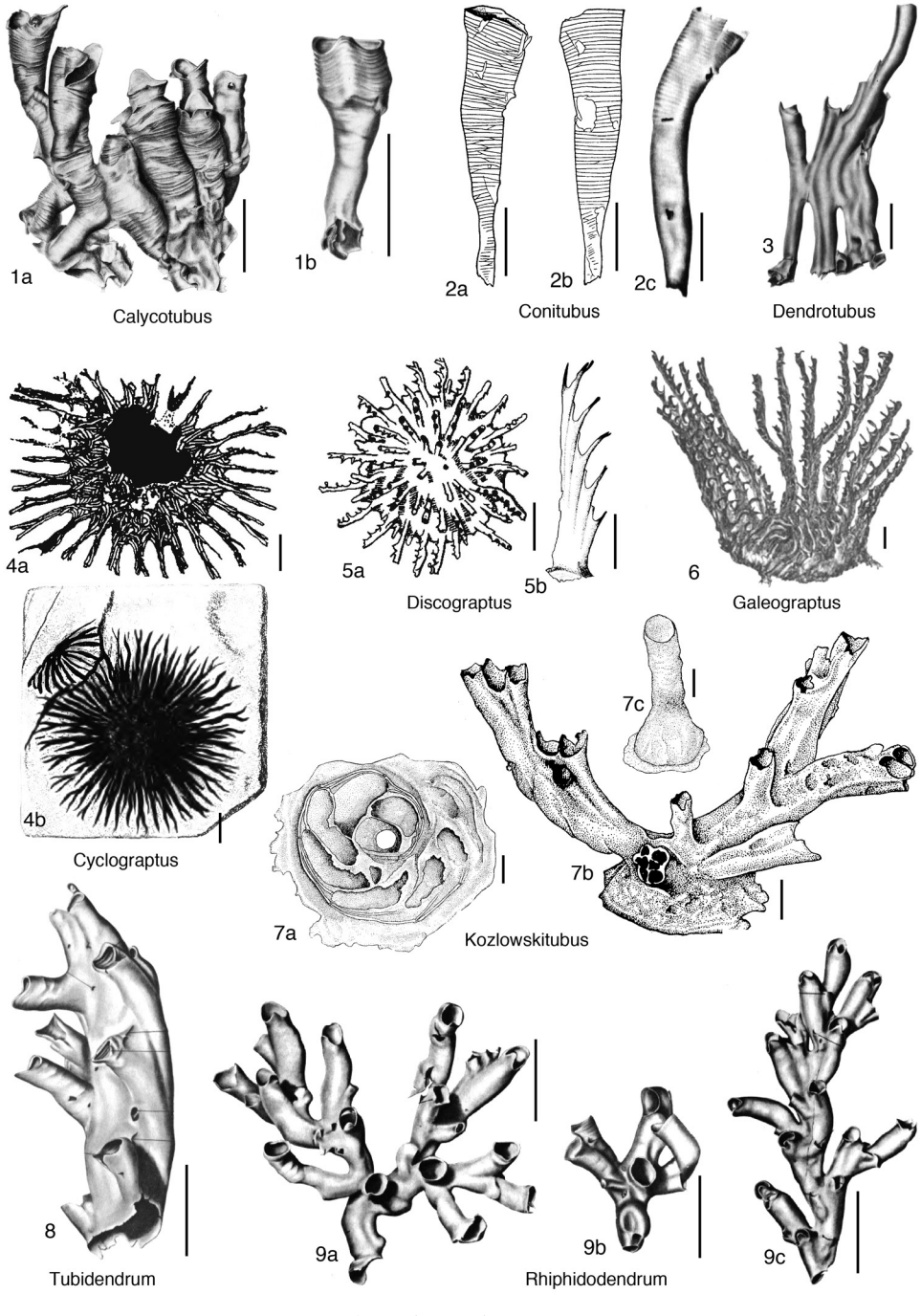


FIG. 143. Cyclograptidae (p. 228–231).

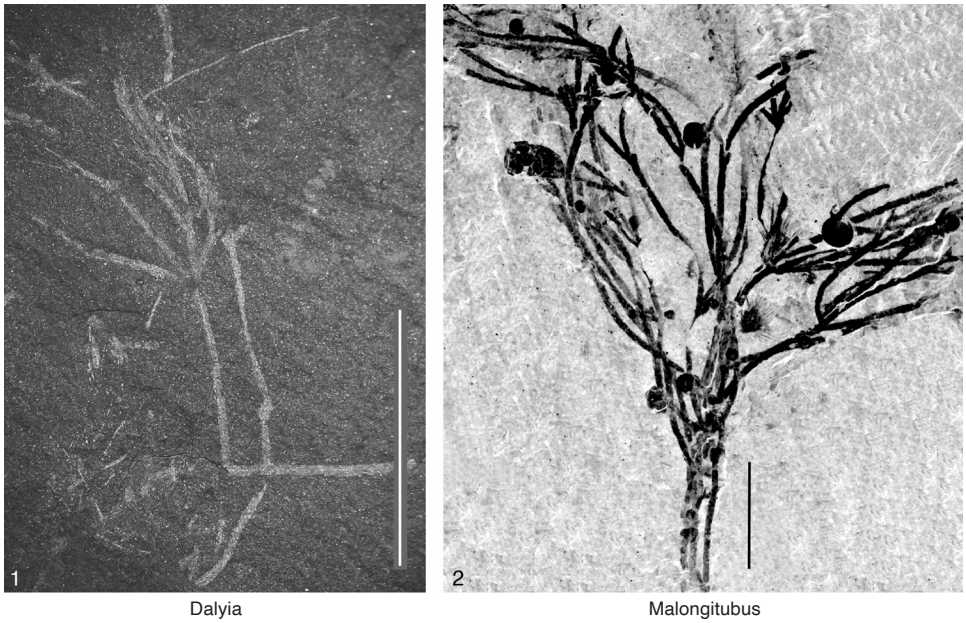


FIG. 144. Graptolithina? *incertae sedis* (p. 231).

erratic boulder).——FIG. 143,*1a–b*. **C. infundibulatus,* holotype, ZPAL GI/1-290, scale bars, 0.5 mm (Kozłowski, 1949, pl. 18,*1–2*).

Conitubus KOZŁOWSKI, 1949, p. 159 [**C. siculoides;* OD]. Gradually widening autotheca with irregular sutures; colony shape unknown. [The taxon consists of isolated autothecae of uncertain origin, thus, may be useless. It could be identical to *Sphenoecium* CHAPMAN & THOMAS, 1936]. *Lower Ordovician* (*Tremadocian*): Poland.——FIG. 143,*2a–c*. **C. siculoides;* holotype in different views, ZPAL GI/1-290, scale bars, 0.5 mm (Kozłowski, 1949, fig. 46).

Dendrotubus KOZŁOWSKI, 1949, p. 153 [**D. wimani;* OD]. Encrusting tubarium with tubular thecae; erect portions of autothecae forming irregularly distributed groups; thecae typically serially arranged; proximal portions of thecae commonly coiled into helical spiral. *Lower Ordovician* (*Tremadocian*): Poland.——FIG. 143,*3*. **D. wimani,* holotype, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 16,*8*).

Discograptus WIMAN, 1901, p. 191 [**D. schmidti;* OD]. Tubarium discoidal, erect portions of autothecae in more or less radially arranged groups on upper surface of thecorhiza; thecae tubular, elongated; bottle-shaped sicula with first thecae growing in circular pattern around it; thecal differentiation and stolon system unknown; thecae with prominent dorsal and ventral rutella; presence of conothecae uncertain. *Upper Ordovician* (*Katian*): Sweden (Gotland).——FIG. 143,*5a–b*. **D. schmidti; 5a,* lectotype, PMU G 786, scale bar, 1 mm (Bulman, 1970, fig. 29.*2*); *5b*, stipe fragment, scale bar, 0.5 mm (Bulman & Rickards, 1966, fig. 46B).

Galeograptus WIMAN, 1901, p. 189 [**G. wennersteni;* OD]. Tubarium encrusting, discoidal, erect portions of autothecae in more or less radially arranged groups on upper surface of thecorhiza; bithecae and conothecae confined to thecorhiza; thecae tubular, with extended dorsal and ventral rutella. *Upper Ordovician* (*Katian*): Sweden. [Lectotype preserved as series of thin sections, also indicating the presence of umbrella-shaped apertural modifications; BULMAN and RICKARDS, 1966, p. 61].——FIG. *143,6*. **G. wennersteni,* holotype, PMU G 93, specimen preserved as serial sections, scale bar, 1 mm (Wiman, 1901, pl. 8,*8*).

Kozlowskitubus MIERZEJEWSKI, 1978, p. 571 [**Dendrotubus erraticus* KOZŁOWSKI, 1963, p. 104; OD]. Encrusting and erect-growing taxa with simple, tube-shaped thecae without apertural elaborations; sicula bottle-shaped, erect, in distal part with spiral line; proximal thecae spirally coiled around sicula; irregularly developed branches comprise thecal bundles arising from thecorhiza and thecae formed on branches. *Upper Ordovician* (*Katian*)–*Silurian* (*Ludlow*): Poland (glacial erratic boulder).——FIG. 143,*7a–c*. **K. erraticus* (KOZŁOWSKI), scale bars, 0.1 mm; *7a–7b,* holotype in different views (Kozłowski, 1963, fig. 4,*9*); *7c,* sicula (Kozłowski, 1963, fig. 3).

Rhiphidodendrum KOZŁOWSKI, 1949, p. 133 [**R. samsonowiczi;* OD]. Multiramous, erect colony with irregular branching from three first order stipes; autothecae and bithecae tubular; stolon system unknown. *Lower Ordovician* (*Tremadocian*): Poland

(glacial erratic boulder).——Fig. 143,*9a–c.* **R. samsonowiczi,* ZPAL GI/1-290; *9a,* holotype; *9b,* proximal end; *9c,* stipe fragment; scale bars, 0.5 mm (Kozłowski, 1949, pl. 10).

Tubidendrum Kozłowski, 1949, p. 160 [**T. bulmani;* M]. Colony erect, conical or flabellate; irregularly developed stipes connected by bridges through single thecal tubes; thecae concentrated on one side of stipe but not serially arranged; two types of thecae, larger (?autothecae) and smaller ones (?bithecae), formed possibly through diad budding; tubular thecae with ventral apertural lip (rutellum); autothecae helically coiled in median part. *Lower Ordovician* (*Tremadocian*): Poland.——Fig. 143,*8.* **T. bulmani,* holotype, ZPAL GI/1-290, scale bar, 1 mm (Kozłowski, 1949, pl. 21,*1*).

GRAPTOLITHINA? *INCERTAE SEDIS*

A few apparently colonial genera are here tentatively identified as Graptolithina? *incertae sedis* following Maletz and Steiner (2015), even though the final recognition of fusellar construction for their complex fossils is lacking and the material is poorly preserved. They differ considerably in the construction of their tubaria from the remaining taxa of the Graptolithina, as thecal apertures are recognized only at the distal end of the stipes and not at the branching segments. It is impossible to refer the material to the recognized families included in the Graptolithina.

Dalyia Walcott, 1919, p. 237 [**D. racemata;* OD]. Colonial organism with long, slender, almost parallel-walled thecal tubes(?) and prominent internal thread; axes both erect and creeping, with whorls of thecal tubes radiating at specific branching points; circular attachment structures at base of branching points. *Cambrian* (*Miaolingian, Wuliuan, Ptychagnostus praecurrens* Biozone): Canada.——Fig. 144,*1.* **D. racemata,* lectotype, USNM 354117, Burgess Shale, loc. 35K, British Columbia, Canada, scale bar, 10 mm (Maletz & Steiner, 2015, fig. 16).

Malongitubus Hu, 2005, p. 185 [**M. kuangshanensis;* OD] [=?*Cambrohydra* Hu, 2005, p. 188 (type, *C. ercaia,* OD), syn. herein]. Colonial organism(?) formed from parallel-sided tubes(?), branching at irregular distances to form whorls of radiating tubes of next order; number of tubes forming at branching division variable from two to at least six; distal tubes may be open-ended; length of the longest tubular branch measures at least 6 cm. *Cambrian* (*Series 2, Stage 3*, *upper Eoredlichia–Wutingaspis* Zone): China.——Fig. 144,*2.* **M. kuangshanensis,* holotype, NIGP 165032, Kuangshan, Yunnan Province, China, scale bar, 10 mm (Hu, 2005, cover).

ORDER DENDROIDEA

Jörg Maletz

Order DENDROIDEA Nicholson, 1872

[Dendroidea Nicholson, 1872a, p. 101; *ex* section Dendroidea Nicholson, 1872a, p. 101] [=Cladophora Hopkinson in Hopkinson & Lapworth, 1875, p. 634; *non* Inocaulida Bouček, 1957, p. 145, herein (dasycladacean algae); =Mastigograptida Obut & Sobolevskaya, 1967, p. 58, herein]

Benthic graptoloids with erect, bushy, cone- or fan-shaped tubarium; thecae typically serially arranged along stipes with regularly placed bithecae based on triad budding system; thecal development variable from tube shaped and aperturally isolated to distinctly widening and with ventral rutellum; anastomosis, dissepiments, or thecal bridges may connect stipes laterally; sicula possibly tubular with helical line but development unknown in most taxa. *Cambrian* (*Miaolingian*)–*Carboniferous, Serpukhovian* (*Arnsbergian*): worldwide.

Dendroidea includes most of the benthic graptoloids with an erect tubarium, possessing a triad-budding system with distinct thecal differentiation. The families Dendrograptidae, Callograptidae, and Mastigograptidae are separated due to the shape and organization of their autothecae. Bushy growth, however, also appears in some Cyclograptidae (see Maletz, 2019d), in which the encrusting part may be reduced in size, but the included species do not have triad budding. The genera of the dendroid families are typically defined from tubarium fragments and are based on general constructional features. However, the final shape of their tubaria remains unknown. The differentiation into various genera and families has varied considerably through time, and the attribution of the hundreds of described species to a certain genus and family is often arbitrary and in need of re-evaluation. Proximal ends and siculae are rarely known in enough detail to understand the real phylogenetic relationships of the taxa. The thecal development is unknown in most species, and the inclusion into a certain genus is based on the tubarium shape, thus remains tentative. Therefore, the precise biostratigraphic ranges of most genera cannot be evaluated.

Hopkinson in Hopkinson and Lapworth (1875) differentiated the family Callograptidae (genera *Dendrograptus, Callograptus, Dictyograptus, Desmograptus*) from the family Ptilograptidae (*Ptilograptus*) among the Dendroidea. The family name Callograptidae has rarely been used afterward (e.g., Bouček, 1957), but Mu (1953) defined a subfamily Callograptinae within the family Dendrograptidae. Mu and others (2002) used the subfamily Callograptinae for the genera *Callograptus, Aspidograptus, Desmograptus,* and *Syrrhipidograptus*.

Chapman, Rickards, and Grayson (1993) and Chapman, Durman, and Rickards (1996) used the thecal style and tubarium shape to differentiate and sort the genera into a number of families, but little information on the important initial colony development exists to support these taxa as phylogenetically meaningful. Mitchell and others (2013) did not provide any indication or opinion on the differentiation of the dendroid benthic graptolites. The authors differentiated the Eugraptolithina as a holophyletic group, united by the presence of a helical line in the erect prosicula, excluding the benthic, encrusting taxa. The term should not be confused with the Eugraptoloida of Maletz, Carlucci, and Mitchell (2009), referring to the traditional Graptoloidea lacking bithecae, excluding the planktic Anisograptidae.

MORPHOLOGY

All Dendroidea produce erect-growing colonies starting from a disk-like proximal attachment site, called a basal disk or holdfast, which is known only from a few taxa.

Wiman (1896) illustrated the proximal end of *Dictyonema cavernosum* Wiman, 1896 with an irregularly formed attachment disk (Fig. 145.3), and Bates and Urbanek (2002) illustrated the basal disk of *Mastigograptus* sp. cf. *M. tenuiramosus* (Walcott, 1883), indicating the growth on a ridged underground, possibly a brachiopod shell.

The sicula is known from very few taxa and may be tubular in form with an upward-directed aperture (Fig. 145.1) possessing a helical line in the prosicula and distinct fusellar half rings in the metasicula. Initially, the flat base of the prosicula is attached to a surface and in later stages is covered by cortical material forming the basal disk. The dendroid colonies then may either develop a bushy form through a number of proximal branching divisions, forming the main stipes of the colony or, alternately, a single stem that branches only at some distance from the proximal end, forming a more treelike shape (Fig. 145.4). During the later growth of the colony, various shapes can develop. The stipes are either oriented in a single plane in fan-shaped or cone-shaped tubaria or the branches develop more irregularly in three-dimensional bushy or treelike colonies (Fig. 145.3–145.7). The diagenetic flattening of the colonies in the sediments and fragmentation due to postmortem transport often make these shapes difficult to recognize and distinguish.

The development and differentiation of thecae is recognized mainly from chemically isolated material and has a triad budding system (Wiman, 1895, 1896; Bulman, 1927b; Kozłowski, 1949) in which each autotheca is associated with a bitheca (Fig. 146.3a–b, Fig. 146.4). The bithecae originate on alternating sides on their mother thecae (Maletz, Lenz, & Bates, 2016). Triad budding has been demonstrated from chemically isolated material in the Mastigograptidae by Andres (1961, 1977) (Fig. 146.1b), but a morphological differentiation of autothecae and bithecae is not present. Bates and Urbanek (2002) described important details of the construction of the stolon system in stem fragments of *Mastigograptus* sp. and verified the presence of triad budding in this taxon. Triad budding in the Callograptidae has only been verified in *Desmograptus micronematodes* (Spencer, 1884) (see Saunders & others, 2009). Three-dimensionally preserved isolated material of *Koremagraptus* has triad budding, but the differentiation of autothecae and bithecae is nearly impossible in the ropy stipes with strongly elongated thecae (Bulman, 1945).

The thecal style varies considerably between the various groups of the Dendroidea. The thecae are parallel sided and typically elongated in the Callograptidae (Fig. 146.2), forming a ropy appearance of the stipes of the tubarium. Thecal apertures are typically raised above the stipes and form isolated tubes and compound twigs. The thecal apertures may be oriented either to all sides or toward one side, identified as the ventral side of the stipe. In the Mastigograptidae (Fig. 146.1), the delicate and thin-walled metathecae originate from slender to robust branches and appear to be largely isolate, gradually widening toward their apertures. It is unclear whether the thecal apertures have a preferred orientation. The Dendrograptidae (Fig. 146.3) have serially arranged thecae, in which all metathecal apertures are ventrally oriented in one single row. The thecae gradually widen toward their apertures and commonly have a ventral apertural lip or rutellum. The rutellum may be modified into a complex apertural construction. The thecal development is largely identical to the development in the bithecate Anisograptidae (Fig. 146.4) with a distinct difference in thecal size between autothecae and bithecae.

EVOLUTION

Very little is known about the evolutionary patterns of the Dendroidea. Chapman, Durman, and Rickards (1996) discussed a general middle Cambrian origin of the main groups of the Graptolithina. Rickards and Durman (2006) provided an overview on the Cambrian graptolites known at the time, indicating that a number of taxa

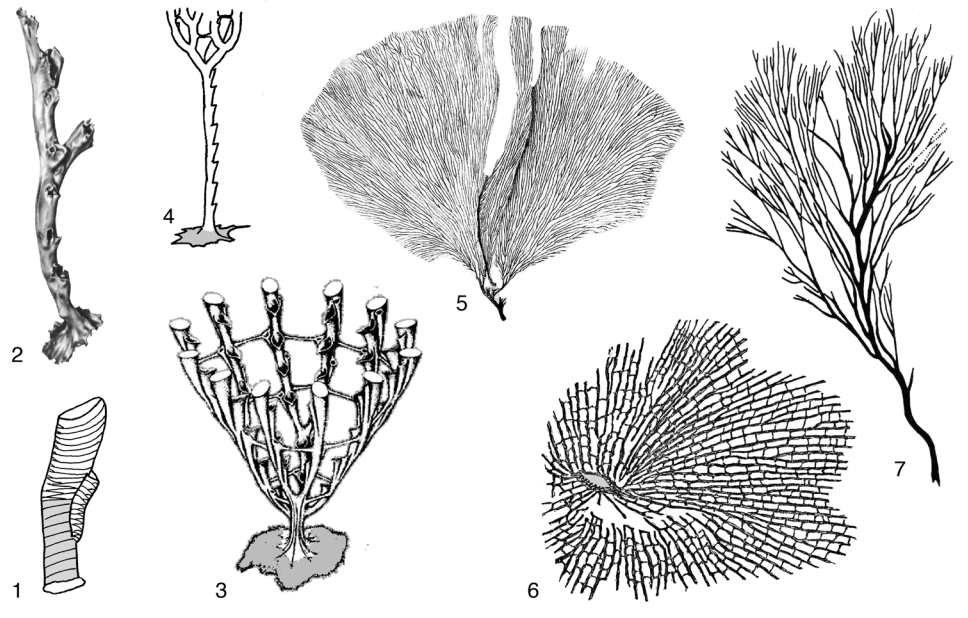


Fig. 145. Astogeny and tubarium shape of the Dendroidea. *1–2, Dendrograptus communis* Kozłowski, 1949; *1,* sicula with bud of th1 (adapted from Kozłowski, 1949, fig. 1); *2,* stem with part of attachment disk and one distal branching (Kozłowski, 1949, pl. 6,*5*); *3, Dictyonema cavernosum* Wiman, 1896, reconstruction of cone-shaped colony (from Mierzejewski website); *4, Dictyonema* sp. with long stem (adapted from Bulman, 1928, fig. 2F); *5, Callograptus elegans* Hall, 1865, fan-shaped colony (Hall, 1865, pl. 19,*2*); *6, Dictyonema retiforme* (Hall, 1843), holotype, cone-shaped benthic colony, attachment site marked in gray (Hall, 1865, fig. 10); *7, Dendrograptus fruticosus* Hall, 1865, bushy colony (Bulman, 1970, fig. 16,*1a*). Illustrations not to scale.

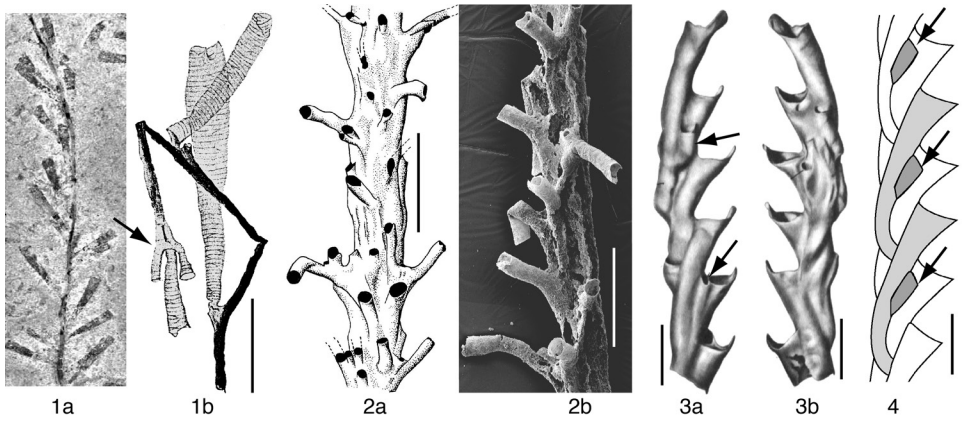


Fig. 146. Thecal style in the Dendroidea. *1a,* ?*Mastigograptus* sp., Marjum Formation, Utah, Miaolingian, Cambrian (LoDuca & Kramer, 2014, fig. 2,*2*); *1b, Mastigograptus* sp., *arrow* points to triad budding, glacial boulder, Ostseekalk, Upper Ordovician, Germany (Andres, 1977, fig. 13); *2a, Acanthograptus musciformis* (Wiman, 1901), Upper Ordovician, Gotland, Sweden (Bulman & Rickards, 1966, fig. 20); *2b, Acanthograptus divergens* Skevington, 1963a, LO 11412t, Middle Ordovician, Öland, Sweden (new); *3a–b, Dendrograptus communis* Kozłowski, 1949, Lower Ordovician, Tremadocian, Poland, specimen shown from both sides, *arrows* (*a*) show bithecae (adapted from Kozłowski, 1949, pl. 6,*8*, 6,*8a*); *4,* Anisograptidae, thecal style showing bithecae (*arrows*) (adapted from Maletz, Lenz, & Bates, 2016, fig. 16,*1*). Scale bars, 1 mm in all figures.

were already present in the Miaolingian (Cambrian). Many taxa were only identified by their general tubarium shape because they were poor and fragmentary in preservation. Maletz (2019a) indicated the presence of the Dithecodendridae during the Cambrian, Series 2 (Stage 4) and the appearance of the Dendrograptidae in the Miaolingian. A considerable diversification of the Dendrograptidae and Callograptidae might have taken place during the late Cambrian. During the Ordovician and Silurian time intervals, the diversity of the Dendroidea remained high, but few groups survived into the Devonian and only the Callograptidae have been recognized with certainty from the Carboniferous (Chapman, Durman, & Rickards, 1996; Maletz & others, 2020).

Family DENDROGRAPTIDAE Roemer in Frech, 1897

[Dendrograptidae Roemer in Frech, 1897, p. 568; *ex* Dendrograptidi Roemer in Frech, 1897, p. 568] [=family Dendroidea Hopkinson, 1872, p. 503]

Benthic graptoloids with variable colony shape; erect, bushy, or fan-shaped tubarium; thecae serially arranged along stipes with regularly placed bithecae based on a triad budding concept; anastomosis or dissepiments present in some taxa; sicular and proximal development largely unknown; autothecae widening toward the apertures, possessing a ventral lip or rutellum, sometimes with complex apertural modifications. *Cambrian* (*Miaolingian*)–*Lower Devonian* (uppermost *Emsian* to lowermost *Eifelian,* possibly *Nowakia maureri* Biozone–*Novakia sulcata sulcata* Biozone): worldwide.

Dendrograptidae represent a paraphyletic taxon from which the derived planktic graptoloids originated. Allman (1872, p. 380) suggested the term Rhabdophora for the taxa "by the possession of a solid supporting rod," later identified as the nema by Lapworth (1897) (e.g., the planktic graptolites), and Hopkinson in Hopkinson and Lapworth (1875) separated the benthic taxa as the Cladophora. At the time, encrusting taxa were unknown to science, and all benthic taxa were supposed to be erect in growth. Hopkinson in Hopkinson and Lapworth, 1875 erected the new family Ptilograptidae for the genus *Ptilograptus* and referred *Dendrograptus* to the Callograptidae. Mitchell and others (2013, fig 6) interpreted the dendroids as a paraphyletic group including a number of genus level taxa that are here informally referred to a variety of family level taxa (e.g., Callograptidae, Dendrograptidae, Mastigograptidae).

Most taxa of the Dendrograptidae are poorly known from flattened shale material or isolated fragments, usually preserved as current-transported specimens. The proximal end development and sicular construction are unknown in most taxa. The erect growth of the colonies with the relatively simple aperturally widening thecae may be regarded as defining characters of Dendrograptidae. The thecae are invariably serially arranged on the stipes and possess the typical triad budding with bithecae on alternate sides of the stipes. Branching is often irregular and secondary connections between stipes through dissepiments and anastomosis are common.

Planktic dendroids (Fig. 147) have been described from a number of occurrences (Rickards, Hamedi, & Wright, 1994; Kraft & Kraft, 2007). They may be referred to the genus *Calyxdendrum* Kozłowski, 1960, a genus that Bulman (1970) identified as a member of the planktic Anisograptidae. *Pseudocallograptus* cf. *salteri* (Skevington, 1963a) from the Middle Ordovician of Öland (Sweden) possesses a sicula with a free nema, indicating a possibly planktic taxon but might be unrelated to *Calyxdendrum*. These planktic taxa should not be placed in the planktic Graptoloidea, as they likely represent a secondary, independent origination of a planktic life style (see Kraft & Kraft, 2007). It is preferred herein to keep them with the benthic Dendrograptidae, as they do not possess the defining characters of the planktic Anisograptidae.

MORPHOLOGY

The morphology of the tubaria of the Dendrograptidae is largely related to ecological influences of the attached colonies and their environmental conditions. The basic shape of the dendrograptid tubarium depends on the branching mode and direction of growth of the stipes. Three main types can be differentiated: the disorderly developed bushy shape, the fan shape, and the conical shape (see Fig. 145). In all these shapes, taxa with and without a thickened stem are known. The colony shape may be influenced considerably by the late-stage addition of cortical material, and thecal style may be considerably masked to the extent that the original thecal shape is not recognizable (see BATES & others, 2011).

A proximal development of the Dendrograptidae is known from a few juvenile specimens of the genus *Dendrograptus* and *Graptolodendrum*. The sicula is tubular with a flat base for attachment (Fig. 145.1). The prosicula can be differentiated through the spiral line, and the metasicula has fusellar half rings and regularly placed oblique sutures on the dorsal and ventral sides in *Dendrograptus communis* KOZŁOWSKI, 1949. However, in *Graptolodendrum,* full fusellar rings are present and the sutures are irregularly placed. A very irregular development of fusellar rings also occurs in the more triangular sicula of *Calyxdendrum,* in which a free nema is also present. The origin of th1[1] is variable and may be in the prosicula (*Dendrograptus communis, Calyxdendrum*) or in the metasicula (*Graptolodendrum*). The first dicalycal theca may be th1[2] or a later one in specimens with a stem. The details are not available for most species and genera.

One of the characteristic features of many Dendrograptidae is the secondary connection between stipes. These connections are regarded as a means of keeping the stipes at a certain distance to prevent competition for the zooids. Dissepiments are variably developed rods formed initially from fusellar tissue overlain by cortical material

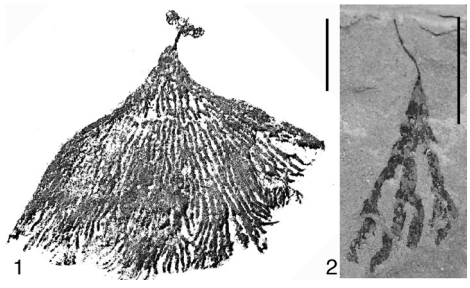


FIG. 147. Planktic Dendrograptidae. *1, Calyxdendrum ghodsiae* (RICKARDS, HAMEDI, & WRIGHT, 1994), holotype, Dapingian, Iran (Rickards, Hamedi, & Wright, 1994, fig. 2); *2, Calyxdendrum titanus* (KRAFT, 1990) note the long nema, Dapingian, *Tetragraptus abbreviatus* Biozone, Czech Republic, scale bars, 5 mm (Kraft & Kraft, 2007, fig. 1).

(URBANEK & MIERZEJEWSKI, 2009). They are sometimes very thin and delicate but can also be fairly robust and then appear similar to the bridges in the Callograptidae. Dissepiments form straight, perpendicular connections between stipes, but obliquely developed dissepiments are also common. Dissepiments are characteristic for dendroids previously included in the genus *Dictyonema* (see BULMAN, 1970; ERDTMANN, 1982a). The material described by URBANEK and MIERZEJEWSKI (2009) consists of Middle to Upper Ordovician fragments and a specific identification of the material is difficult. Dissepiments are also typical for the planktic anisograptid *Rhabdinopora* (see ERDTMANN, 1982a; COOPER & others, 1998). A second way of connecting stipes is the growth of thecal tubes as bridges, common in the Callograptidae (identified as Acanthograptidae in MALETZ, 2019c). These may easily be mistaken as dissepiments when flattened. A different way of stipe interaction is the temporary fusion of adjacent stipes or the transfer of thecae, called anastomosis and pseudanastomosis (RICKARDS & LANE, 1997).

The stipes are constructed by parallel-sided, slender bithecae and aperturally widening autothecae with or without apertural modifications. There appears to be

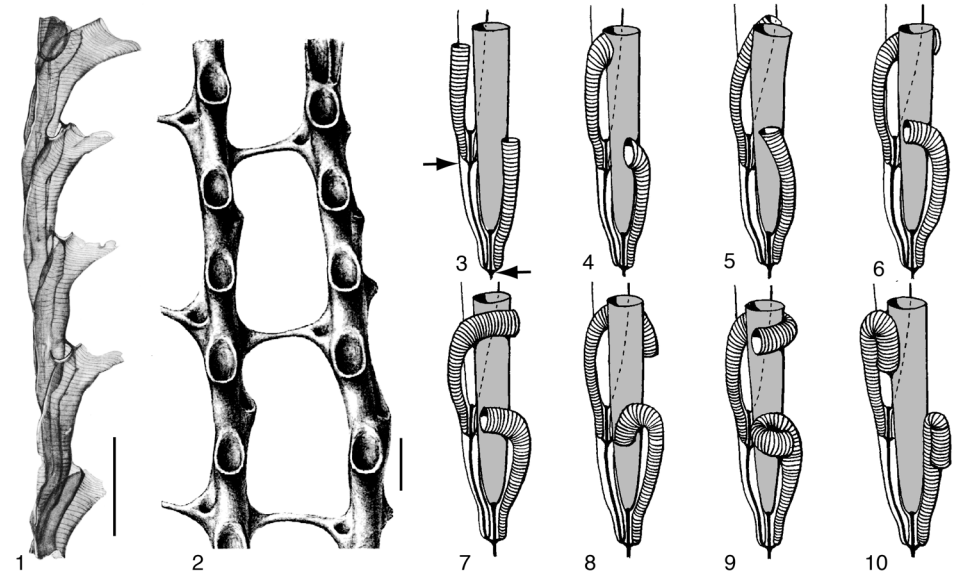


FIG. 148. The stipe and thecal development in the Dendrograptidae. *1,* ?*Dictyonema* aff. *estlandicum* BULMAN, 1933, GSM 71879, stipe fragment showing thecal style and fusellar construction, Katian, Laggan Burn, Girvan, UK, scale bar, 1 mm (Bulman, 1945, pl. 1,*1*); *2, Rhabdinopora flabelliformis* (EICHWALD, 1840), stipe fragment with dissepiments, scale bar, 1 mm (Bulman, 1933, pl. 1,*6*); *3–10,* reconstructions to show bithecal growth, bithecae shown with parallel lines, not representing fusellar construction; *3, Rhabdinopora flabelliformis* (EICHWALD, 1840), *arrows* indicate the presence of triad budding, which is present in all taxa; *4, Dictyonema peltatum* WIMAN, 1895; *5, Dictyonema cotyledon* BULMAN, 1933; *6, Dictyonema rarum* WIMAN, 1895; *7, Callograptus infrabithecalis* KOZŁOWSKI; *8, Dictyonema inconstans* BULMAN, 1933; *9, Dendrograptus cofeatus* KOZŁOWSKI, 1949; *10, Dictyonema wysoczkianum* KOZŁOWSKI, 1949 (*3–10,* Bulman, 1955, fig. 10).

considerable variation in the development of the bithecae (Fig. 148.3–148.10); but for most taxa, the precise development of the bithecae is uncertain.

THECAL DEVELOPMENT

Thecal development is unknown in many Dendrograptidae, but well-preserved fragments have been found during the last hundred years. BULMAN (1933a) described a number of taxa from chemically isolated Scandinavian material and provided the best information on the three-dimensional construction of dendroid thecae. The thecae develop with a typical triad budding system of autothecae and alternately originating daughter thecae and bithecae. The largely parallel-sided bithecae typically open at the aperture of the previous autotheca (Fig. 146). The autothecae widen distinctly toward the aperture and are commonly connected with their dorsal side to the ventral side of the next theca of the stipe. The ventral side of the aperture is provided with a rutellum of variable dimension and shape. In some species, the apertural part of the thecae is isolated (e.g., *Dictyonema wimani* BULMAN, 1933), but the typical shape of the autothecae of the Dendrograptidae is retained. The bithecae are either simple tubes, opening adjacent to the autothecal apertures, or they are growing in various shapes around the autothecae (Fig. 148). Little is known about the patterns of distribution of certain styles of bithecae, but the early planktic Anisograptidae, derived from the Dendrograptidae, possess fairly simple, straight bithecae (Fig. 146.4).

EVOLUTION

Even though hundreds of species have been referred to the various genera of the Dendrograptidae, ranging from the upper

Cambrian to at least the Devonian, little is known of the phylogeny of the family. It appears reasonable that the clade produced the stem leading to the planktic Graptoloidea (see ERDTMANN, 1982a), but further information on evolutionary pattern and changes in the Dendrograptidae is not available.

Dendrograptus HALL, 1858, p. 143 [**Graptolithus hallianus* PROUT, 1851, p. 189; SD HALL, 1862, p. 21] [=*Odontocaulis* LAPWORTH, 1881, p. 175 (type, *O. keepingii,* OD), syn. herein; =*Ophiograptus* POULSEN, 1937, p. 24 (type, *O. inexpectans,* OD), syn. by BULMAN, 1970, p. 38]. Erect, bushy dendrograptid with loosely branching stipes; stem of variable length may be present; tubular sicula with spiral line in prosicula known from one species; origin of first theca in pro- or metasicula. *Cambrian, Furongian* (*Jiangshanian*)–?*Devonian:* worldwide.——FIG. 149,*1a.* **D. hallianus* (PROUT), CMC IP83197, Potsdam Sandstone, Afton, Minnesota, USA, scale bar, 5 mm (Bulman, 1970, fig. 16.1b).——FIG. 149,*1b. D. inexpectans* (POULSEN, 1937), holotype, scale bar, 1 mm (Poulsen, 1937, fig. 11).——FIG. 149,*1c. D. keepingii* (LAPWORTH, 1881), holotype, Llandovery, Aberystwyth, Wales, UK, scale bar, 5 mm (Bulman, 1928, fig. 1; specimen not identified).

Airograptus RUEDEMANN, 1916, p. 20 [**Dictyonema furciferum* RUEDEMANN, 1904, p. 606; OD]. Flabellate or shrub-like dendrograptid tubarium; thecae with low inclination and furcate or peltate ventral apertural processes; proximal development unknown; circular attachment disk known from juveniles; bithecae regularly developed, inconspicuous to strongly bulbous; dissepiments slender, irregularly developed. *Cambrian* (*Furongian*)–*Middle Ordovician* (*Dapingian, Didymograptellus bifidus* Biozone): China, Sweden, Canada, USA.——FIG. 149,*2a–b*. **A. furciferus* (RUEDEMANN); *2a,* NYSM 6838, small specimen with attachment disk, Bellefonte, Pennsylvania, USA, scale bar, 1 mm (Ruedemann, 1916, fig. 7); *2b,* holotype, fragment, Deep Kill, New York, USA, scale bar, 5 mm (Ruedemann, 1904, fig. 28).——FIG. 149,*2c. A.* aff. *furciferus* (RUEDEMANN), NIGP 134654, Dayangcha, Jilin Province, northeastern China, specimen showing colony shape, scale bar, 5 mm (Zhang & Erdtmann, 2004b, fig. 5a).

Aspidograptus BULMAN, 1934, p. 70 [**Clematograptus implicatus* HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 652; OD]. Cone-shaped to fan-shaped dendrograptid branching laterally from ?four curved principal stipes; lateral branches close set, irregularly produced, bifurcating repeatedly. *Cambrian, Furongian* (*Paibian*)–*Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone): UK, Argentina, Czech Republic, China, Tasmania.——FIG. 149,*4a–c*. **A. implicatus* (HOPKINSON IN HOPKINSON & LAPWORTH); *4a,* SM A5325, lectotype, Whitesand Bay, St. David's, Wales, UK, scale bar, 5 mm (selected by BULMAN, 1934, p. 71) (Hopkinson in Hopkinson & Lapworth, 1875, pl. 34,*1*); *4b,* SM A5326, Shelve, Shropshire, UK, scale bar, 5 mm (Bulman, 1970, fig. 16,*5*); *4c,* SM A5319, stipe fragment possibly belonging to the species, Shelve, Shropshire, UK, scale bar, 1 mm (Bulman, 1934, fig. 37).

Calyxdendrum KOZŁOWSKI, 1960, p. 109 [**C. graptoloides;* M]. Possibly biradiate, multiramous dendrograptid with thick free nema; autothecae conical, bithecae opening into autothecal cavities. *Middle Ordovician* (*Dapingian, Tetragraptus abbreviatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Poland (glacial boulder), Czech Republic, Iran.——FIG. 149,*3a–d*. **C. graptoloides*, glacial erratic boulder, Poland; *3a,* prosicula and early part of metasicula, scale bar, 0.1 mm; *3b,* holotype, proximal end in reverse view, scale bar, 0.5 mm; *3c,* stipe fragment showing triad budding, scale bar, 0.5 mm; *3d,* stipe fragment with several branchings, scale bar, 0.5 mm (Kozłowski, 1960, fig. 1, 3, 10, and 11, respectively).

Capillograptus BOUČEK, 1957, p. 42; *ex Callograptus* (*Capillograptus*) BOUČEK, 1957, p. 42 [*?*Callograptus dichotomous* POČTA, 1894, p. 182; M]. Fan-shaped to conical dendrograptid with slender stipes; thecae simple with low inclination and prominent ventral apertural spines; few thin dissepiments irregularly distributed in colony. *Silurian* (*Wenlock, Cyrtograptus radians* Biozone–*Pridoli, Monograptus ultimus* Biozone): Czech Republic.——FIG. 149,*5a*. **C. dichotomous* (POČTA), paratype, scale bar, 5 mm (Bouček, 1957, fig. 16a).——FIG. 149,*5b–c*. *C. pilosus* BOUČEK, 1957, fragments showing dissepiments and ventral apertural spines, scale bars, 5 mm, 1 mm, respectively (Bouček, 1957, fig. 16c–d).

Graptolodendrum KOZŁOWSKI, 1966b, p. 4 [**G. mutabile;* OD]. Erect, multiramous dendrograptid with metasicular origin of $th1^1$; metasicula with irregular development of fuselli and without dorsal and ventral zigzag suture; regular triad budding with bithecae of branching divisions on same side, position changing at branching points. *Middle Ordovician* (upper *Darriwilian* or *Sandbian, Dicellograptus vagus* or *Nemagraptus gracilis* Biozone): Poland (glacial boulder only).——FIG. 149,*8a–d*. **G. mutabile; 8a,* holotype, scale bar, 1 mm (Kozłowski, 1966b, fig. 1.*1*); *8b–c*, sicula with first theca and first triad, $th2^1$ covered behind $th1^1$ in *5b,* scale bars, 0.5 mm (Kozłowski, 1966b, fig. 13a–b); *8d,* prosicula and initial part of metasicula. scale bar, 0.5 mm (Kozłowski, 1966b, fig. 10).

Licnograptus RUEDEMANN, 1947, p. 196 [**L. elegans;* OD]. Robust erect dendrograptid with short thickened stem and several main branches bearing groups of subparallel fanlike extended stipes; thecae with low inclination and long apertural spines. *Lower Ordovician* (*Tremadocian–Floian*): Canada.——FIG. 149,*6a–b*. **L. elegans; 6a,* holotype, scale bar, 10 mm (Bulman, 1970, fig. 16.7); *6b,* detail showing spined thecal apertures, scale bar, 5 mm (Ruedemann, 1947, pl. 16,*5*).

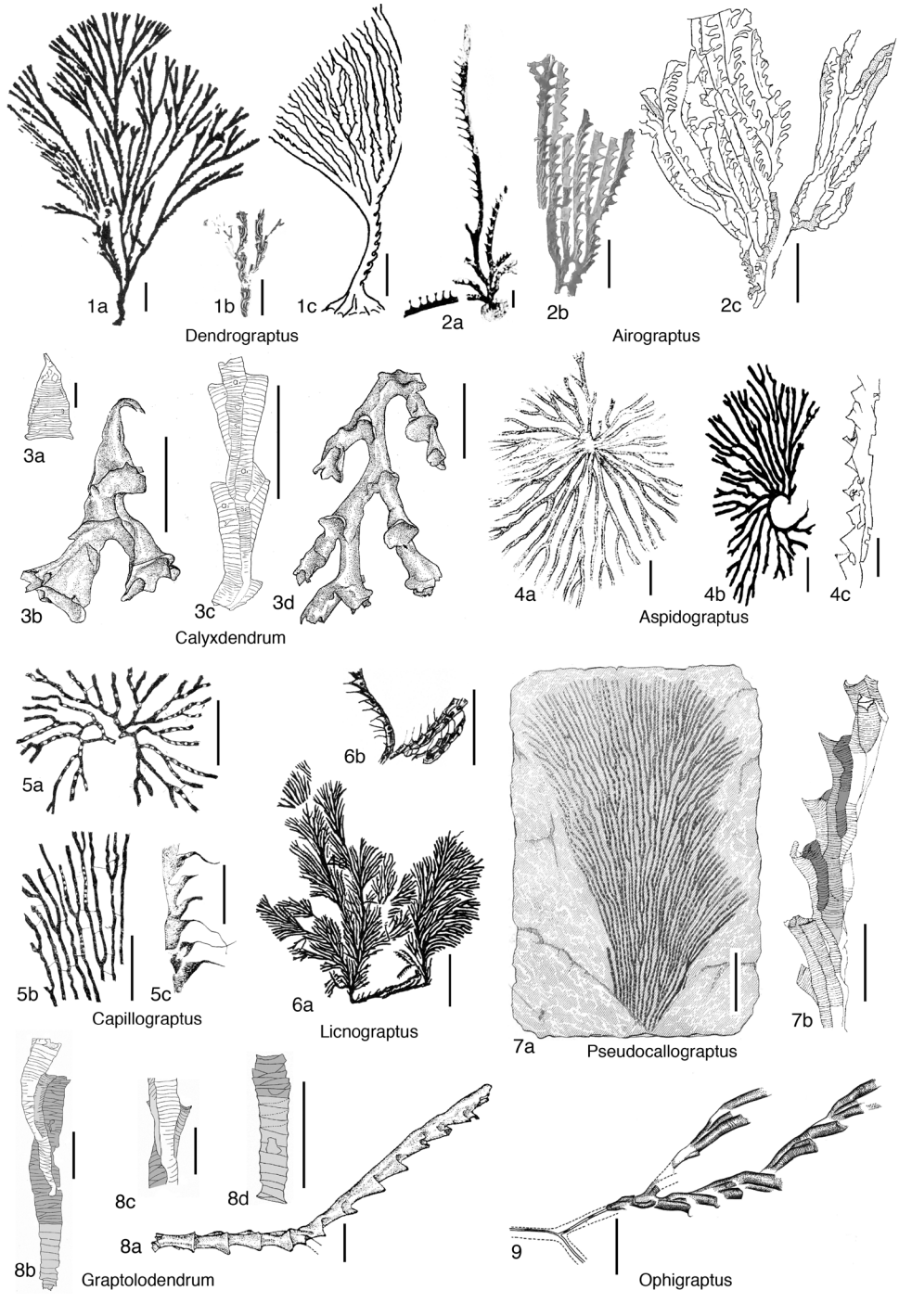


FIG. 149. Dendrograptidae (p. 239–241).

Ophigraptus Jaeger, 1992, p. 125 [**O. hercyniae;* OD]. Erect, slender dendrograptid with monoprogressive branching forming several zigzag-shaped main branches; some of the lateral branches also with monoprogressive branching divisions; distances between branchings regular, probably consisting of two or three autothecae each; proximal end unknown; thecae simple with low inclination and straight apertures; bithecae small and tubular. *Lower Devonian* (uppermost *Emsian* to lowermost *Eifelian,* possibly *Nowakia maureri* to *Novakia sulcata sulcata* biozones; see Alberti & others, 1996, p. 275): Germany.——Fig. 149,*9*. **O. hercyniae,* MB.G. 811, detail of holotype, Buntenbock, Harz, Germany, scale bar, 1 mm (Jaeger, 1992, fig. 1).

Pseudocallograptus Skevington, 1963**a**, p. 19 [**Callograptus salteri* Hall, 1865, p. 135; OD]. Fan-shaped robust dendrograptid; autothecae and bithecae possibly slender, elongate, with increased overlap and low inclination; producing ropy appearance of stipe and unusual association of thecal apertures; autothecae generally denticulate. [The diagnosis is based on chemically isolated fragments from Sweden, and the relationship to *Callograptus salteri* from Canada remains uncertain (see Skevington, 1963a, p. 25).] *Lower Ordovician* (*Floian, Didymograptellus bifidus* Biozone)–*Middle Ordovician* (*Darriwilian, Didymograptus murchisoni* Biozone): Sweden, Canada, Argentina.——Fig. 149,*7a*. **P. salteri* (Hall), GSC 955a, syntype, larger colony fragment, Gros Maule, Québec, Canada (probably in error for Lévis, Québec, Canada), scale bar, 10 mm (Hall, 1865, pl. 19,*5*).——Fig. 149,*7b*. *Pseudocallograptus* sp. cf. *P. salteri* showing thecal overlap and development of bithecae, Öland, Sweden, scale bar, 1 mm (adapted from Skevington, 1963a, fig. 23a).

Family CALLOGRAPTIDAE Hopkinson, in Hopkinson & Lapworth, 1875

[Callograptidae Hopkinson, in Hopkinson & Lapworth, 1875, p. 663] [=Acanthograptidae Bulman, 1938, p. 20; =Pseudodictyonemidae Chapman, Rickards, & Grayson, 1993, p. 308; =Stelechocladiidae Chapman, Rickards, & Grayson, 1993, p. 307; =?Ptilograptidae Hopkinson in Hopkinson & Lapworth, 1875 p. 633; =?Nephelograptidae Bouček, 1957, p. 83 (misspelled Nephellograptidae in Bouček, 1957, p. 5); *non* Inocaulidae Ruedemann, 1947, p. 230, Mierzejewski, 1986, p. 165]

Benthic graptoloids with variable shape of colonies, from erect, bushy, cone-, or fan-shaped; commonly complex stipe development of ropy appearance; anastomosis, dissepiments or thecal bridges may connect stipes; thecae tube shaped, with isolated autothecal apertures; development of twigs common; regularly placed bithecae based on a triad budding concept, but no size differentiation of bithecae; proximal development and details of fusellar construction unknown. *Cambrian* (*Miaolingian*)–*Carboniferous* (*Upper Mississippian, Serpukhovian, Arnsbergian*): worldwide.

The Callograptidae include a characteristic group of multiramous benthic graptolites with a typically complex development of their stipes from slender tubular thecae. Rickards and Durman (2006, fig. 18, 20) described the Callograptidae (as Acanthograptidae) as a monophyletic group in their study. They regarded the presence of multiserial stipes as the defining synapomorphy of the group. This character is herein regarded as a feature of derived callograptids; earlier taxa (e.g., *Callograptus* Hall, 1865) have less complex development but share the simple parallel-sided thecae with isolated apertures. The proximal development and sicula are unknown for all included taxa. Triad budding indicates the presence of thecal differentiation, but the recognition of bithecae is not possible through size differences as it is in the Dendrograptidae.

A number of taxa previously included in the Inocaulidae Ruedemann, 1947 may turn out to represent callograptids. The type species of the genus *Inocaulis*—*Inocaulis plumulosa* Hall, 1865—may represent a dasycladacean alga or at least not a graptolite (Mierzejewski, 1986). *Thallograptus succulentus* (Ruedemann, 1904), the type species of *Thallograptus* Ruedemann, 1925b, is regarded as a dasycladacean alga, whereas many other taxa included in this genus (e.g., Bouček, 1957; Chapman, Durman, & Rickards 1996) have to be referred to other callograptid genera. *Thallograptus phycoides* (Spencer, 1884) was illustrated by Bulman (1970, fig. 22,*2*) as characteristic of the genus *Thallograptus* but identified as *Thallograptus cervicornis* (Spencer, 1884).

Specimens of the Callograptidae are easily misidentified as land plants in poor, flattened material, as was convincingly demonstrated by Kenrick, Kvaček, and Bengtson (1999), who recognized the graptolitic relationships of *Boiophyton* Obrehl, 1959. The same is indicated for the genus *Saxonia* Roselt,

1962 herein. Lundblad (1972) redescribed *Psilophyton*? *hedei* Halle, 1920 from the Gorstian (Silurian) of Gotland (Sweden) as a dendroid graptolite. The species can be regarded as a member of the Callograptidae based on the isolated tubular thecal apertures visible in the material and may belong to *Boiophyton* (see Kenrick, Kvaček, & Bengtson, 1999).

MORPHOLOGY

The Callograptidae include mostly robust, erect-growing graptoloids with a variably fan-shaped to cone-shaped tubarium reaching a considerable size. Typical bushy forms may appear but are rare. Specimens may be as much as 30 cm or more in diameter in cone-shaped colonies, but mostly small colonies or fragments are found as preserved specimens. These have generally been transported, and few specimens have been found *in situ.* Fragments may be difficult to identify to species level, as features of proximal and distal pieces may differ considerably in dimensions. In all callograptids, dorsal and ventral sides of the stipes can be differentiated, because even in complexly developed taxa, thecal apertures may be oriented ventrally and laterally but never dorsally.

Large differences are present in the complexity of the development of the stipes and their connections. Taxa may develop large colonies without even connecting adjacent stipes (e.g., *Callograptus*), but more commonly, dissepiments or thecal bridges connect the individual stipes (e.g., *Dictyonema*). Maletz (2019c) recognized the growth of thecae crossing the gap to an adjacent stipe as thecal bridges. There may be bridges constructed by a single thecal tube, but also multiple thecae may cross at a point. Urbanek and Mierzejewski (2009) quoted the presence of dissepiments in *Ptiograptus,* for example, but it is clear now that the stipe connections in *Ptiograptus* are formed as thecal bridges (Maletz, 2019c, p. 152).

Anastomosis has been described in a few taxa (Fig. 150.2, Fig. 150.4), but may be difficult to separate from accidental connections of the stipes of the colonies in the sediment. Bulman (1945, pl. 1,*2*) illustrated the anastomosis in an isolated fragment of *Koremagraptus kozlowskii* Bulman, 1945. Rickards and Lane (1997) described the transfer of thecae from one stipe to another as pseudanastomosis.

Twigs can be regarded as an important character of the Callograptidae. However, many taxa only have isolated apertural parts of the thecae, and twigs are lacking (Fig. 150.3). Through the evolution of the Callograptidae, more thecae have joined the laterally growing isolated autothecal apertures. These became elongated and the twigs (Fig. 150.5) formed as short and complex extensions or lateral stipes. The colony shapes appear more similar to those of the Dendrograptidae in these forms without twigs (Fig. 150.1). Maletz and Kozłowska (2013) illustrated partial relief specimens of *Acanthograptus sinensis* Hsü and Ma, 1948 with slender and parallel-sided, tubelike thecae, typical of Callograptidae. The specimens have paired thecal origins, indicating the presence of triad budding (Fig. 150.5). A differentiation of potential autothecae and bithecae is impossible in this material, as there is no obvious size difference in the thecae. Thecae are generally straight and curve outward only toward their apertures, but a number of thecae have irregular curved paths (Fig. 150.6). The development of the thecae in more slender stipes with fewer overlapping thecae and a more regular development is evident in *Callograptus elegans* (Hall, 1865) (Fig. 150.4).

EVOLUTIONARY RELATIONSHIPS

Little is known about the evolutionary relationships of the Callograptidae. Chapman, Durman, and Rickards (1996) concluded that *Thallograptus* (now identified as a dasycladacean alga) might have been the earliest taxon of the Callograptidae and originated in the upper Cambrian but also stated that the

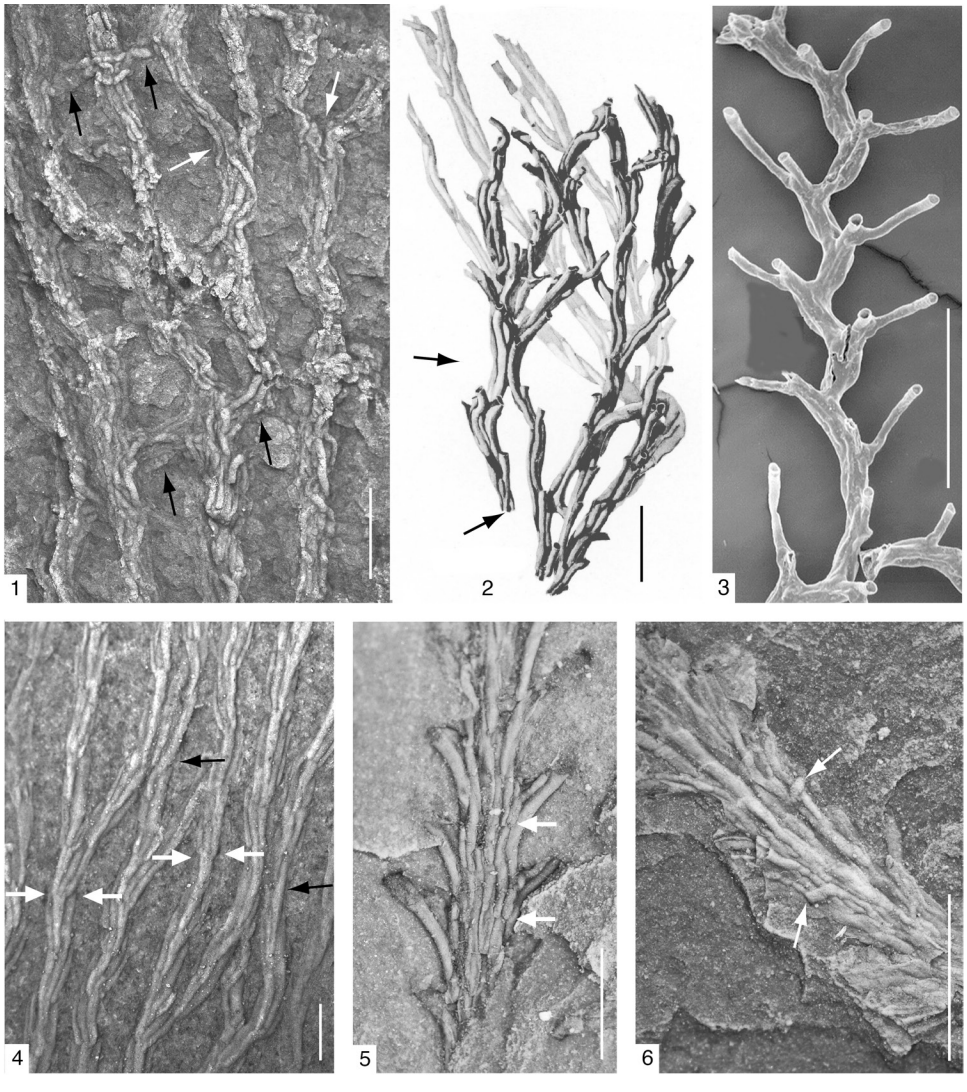


Fig. 150. Stipe development and connections in the Callograptidae. *1, Dictyonema fournieri* (Ubaghs, 1941), fragment in dorsal view, latex cast showing bridges (*black arrows*) and branching (*white arrows*), scale bar, 1 mm (new); *2, Koremagraptus kozlowskii* Bulman, 1945, arrows indicate anastomosis, scale bar, 1 mm (adapted from Bulman, 1945, pl. 1,*2*); *3, Ptilograptus* sp., GSC 119695, ventral view, showing alternating growth of long autothecae, Wenlock, Snowblind Creek, Cornwallis Island, Arctic Canada (Lenz & Kozłowska-Dawidziuk, 2001, pl.1,*12,* as *Acanthograptus*); *4, Callograptus elegans* Hall, 1865, GSC 955a, lectotype, latex cast showing dorsal view of stipes with triad budding (*white arrows*) and anastomosis (*black arrows*), Lévis, Quebec (new); *5–6, Acanthograptus sinensis* Hsü & Ma, 1948, PKUM02-0627, 0629, specimens showing twigs and irregular growth (*black arrows* in *6*) of thecal tubes (*arrows* indicate triad budding in *5*), Tianjianling, Hubei Province, China (Maletz & Kozłowska, 2013, fig. 5b,d). Scale bars, 1 mm for all images.

early forms of the Callograptidae are poorly known. RICKARDS and DURMAN (2006) listed the biostratigraphic ranges of Cambrian graptolites and listed the first occurrence of *Acanthograptus* (thus, the Callograptidae) from the *Goniagnostus nathorsti* Biozone of the Drumian (Miaolingian), based on *Acanthograptus banksi* QUILTY, 1971 from Tasmania. MITCHELL and others (2013) suggested a sister group relationship to the Dendrograptidae and Mastigograptidae, but their analysis was based on a low resolution, as it was not aimed at differentiating clades within the Dendroidea.

Callograptus HALL, 1865, p. 133 [**C. elegans,* SD MILLER, 1889, p. 175]. Tubarium conical, flabellate or irregular with or without a thecate stem; stipes branching dichotomously, attaining a subparallel to parallel orientation quickly; autothecae tubular, slightly to strongly isolate aperturally; bithecae indistinct, tubular. *Cambrian* (*Furongian*)–*Carboniferous:* worldwide.——FIG. 151,*3*. **C. elegans,* GSC 956a, lectotype, Lévis, Quebec, Canada, scale bar, 10 mm (Hall, 1865, pl. 19,*2*).

Acanthograptus SPENCER, 1878, p. 461, original spelling as *Acanthograpsus* changed in ICZN Opinion 650, 1963 [**Acanthograpsus granti;* M] [=*Xylonograptus* SENNIKOV, 1976, p. 108 (type, *X. regularis,* M), syn. herein; =*Paracanthograptus* WANG in WANG & others, 1987, p. 365 (English text, p. 548–549) (type, *P. sanxianensis,* OD), syn. herein (synonym of *Thallograptus* in MU & others, 2002, p. 104)]. Erect, possibly bushy or fan-shaped callograptid with complex development of stipes; apertural parts of slender isolated autothecal tubes, inclined to main stipes. ?*Cambrian* (*Miaolingian, Drumian*, *Goniagnostus nathorsti* Biozone)–*Silurian* (*Ludlow, Gorstian, Saetograptus chimaera* Biozone): worldwide.——FIG. 151,*1a.* **A. granti,* Hamilton, Ontario, Canada, type specimen whereabouts unknown, scale bar, 10 mm (Ruedemann, 1908, pl. 6,*4*).——FIG. 151,*1b. A. arborescens* (BOUČEK, 1957), specimen showing branching pattern, scale bar, 10 mm (Bull, 1987, fig. 10b).——FIG. 151,*1c. A. musciformis* (WIMAN, 1901), reconstruction of distal part of stipe showing thecal growth, scale bar, 1 mm (Bulman, 1970, fig. 21,*1b*).

Alternograptus BOUČEK, 1956, p. 131 *ex Callograptus* (*Alternograptus*) BOUČEK, 1956, p. 131 [**C.* (*A.*) *holubi;* OD]. Bushy callograptid with slender, possibly monoprogressive stipes showing isolated thecal apertures; proximal development unknown. *Lower Ordovician* (*Dapingian, Tetragraptus reclinatus abbreviatus* Biozone): Czech Republic.——FIG. 151,*2a–b.* **A. holubi; 2a,* holotype, proximal end (Bouček, 1956, fig. 2a); *2b,* fragment showing thecal apertures (Bouček, 1956, fig. 2c). Scale bars, 1 mm.

Callodendrograptus DECKER, 1945, p. 28 [**C. sellardsii;* OD]. Callograptid with bushy tubarium; compound stipes and tubular thecae with isolated, ventrally oriented apertures; details unknown. *Cambrian* (*Furongian, Jiangshanian, Ellipsocephaloides* Biozone–*Idahoia* Biozone)–*Ordovician:* USA.——FIG. 151,*5*. **C. sellardsii,* cotype, Point Peak Member, Wilberns Formation, Texas, USA, scale bar, 1 mm (Decker, 1945, pl. 4,*5*).

Desmograptus HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 668; *ex Dictyograptus* (*Desmograptus*) HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 668 [**D.* (*D.*) *cancellatus;* M] [=*Rhizograptus* SPENCER, 1878, p. 460, original spelling as *Rhizograpsus* changed in ICZN Opinion 650, 1963, syn. by RUEDEMANN, 1947, p. 224 (type, *R. bulbosus,* M), BULMAN, 1970, p. 38; =*Syrrhipidograptus* POULSEN, 1924, p. 4 (type, *S. nathorsti,* M), syn. by BULMAN, 1970, p. 38]. Tubarium may be conical or fan-shaped; simple to compound stipes; regular, dominant anastomosis; dissepiments rare; autothecae tubular, denticulate to isolate aperturally; bithecae much smaller. *Lower Ordovician* (*Tremadocian*)–?*Devonian:* worldwide.——FIG. 152,*1a.* **D. cancellatus*, holotype, SM A17507, scale bar, 10 mm (Bulman, 1970, fig. 16,*2*).——FIG. 152,*1b, D. bulbosus* (SPENCER, 1878), holotype, Silurian, Niagara Limestone, Hamilton, Ontario, Canada, scale bar, 10 mm (Spencer, 1884, pl. 4,*4*).——FIG. 152,*1c–d. D. nathorsti* (POULSEN, 1924), holotype, Katian, Bornholm, Denmark. scale bars, 10 mm, 1 mm, respectively (Poulsen, 1924, fig. 2a–b).

Dictyonema HALL, 1851, p. 401 [**Gorgonia*? *retiformis* HALL, 1843, p. 115; SD MILLER, 1889, p. 185]; [=*Dictyograptus* HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 667 (type not designated), syn. herein; =*Dictyonema* (*Pseudodictyonema*) BOUČEK, 1957, p. 69 (type, *Dictyonema graptolithorum* POČTA, 1894, p. 196, OD), syn. by MALETZ, 2019c, p. 152; *non Dictyonema* ADGARDH in KUNTH, 1822, p. 1 (lichens, Agaricales, family Hygrophoraceae), see PARMASTO, 1978; DAL-FORNO & others, 2013; LÜCKING & others, 2013]. Tubarium conical to fan-shaped; conical tubaria varying from almost cylindrical to almost discoidal; stipes straight, subparallel to parallel, branching dichotomously; stipes united by regularly or irregularly produced thecal bridges formed from single or multiple thecal tubes; stipes compound, formed from complexly overlapping slender, tubular thecae; thecal apertures isolate, openings oriented ventrally; sicular and proximal development unknown. [A number of species currently referred to *Dictyonema* (e.g., *D. peltatum, D. cotylodon, D. rarum,* and others) will need to be moved to a genus of the family Dendrograptidae due to their thecal development that is unlike that of the callograptid *Dictyonema*.] *Cambrian* (*Miaolingian*)–?*Carboniferous:* worldwide.——FIG. 151,*4a–b.* **D. retiformis* (HALL); *4a*, holotype, AMNH 1671, scale bar, 10 mm (Hall, 1865, fig. 10); *4b*, NYSM 7112, detail of

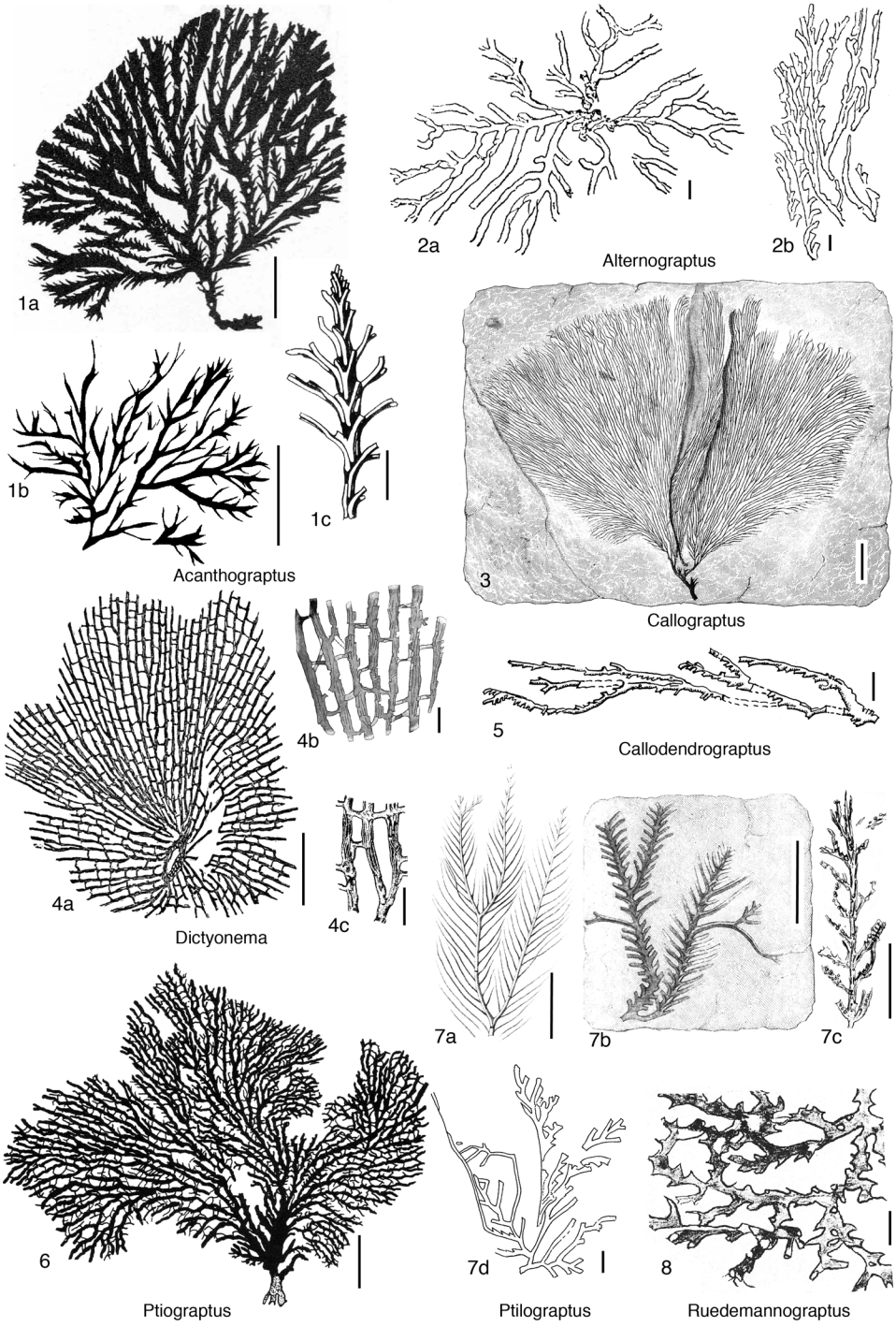


FIG. 151. Callograptidae (p. 244–247).

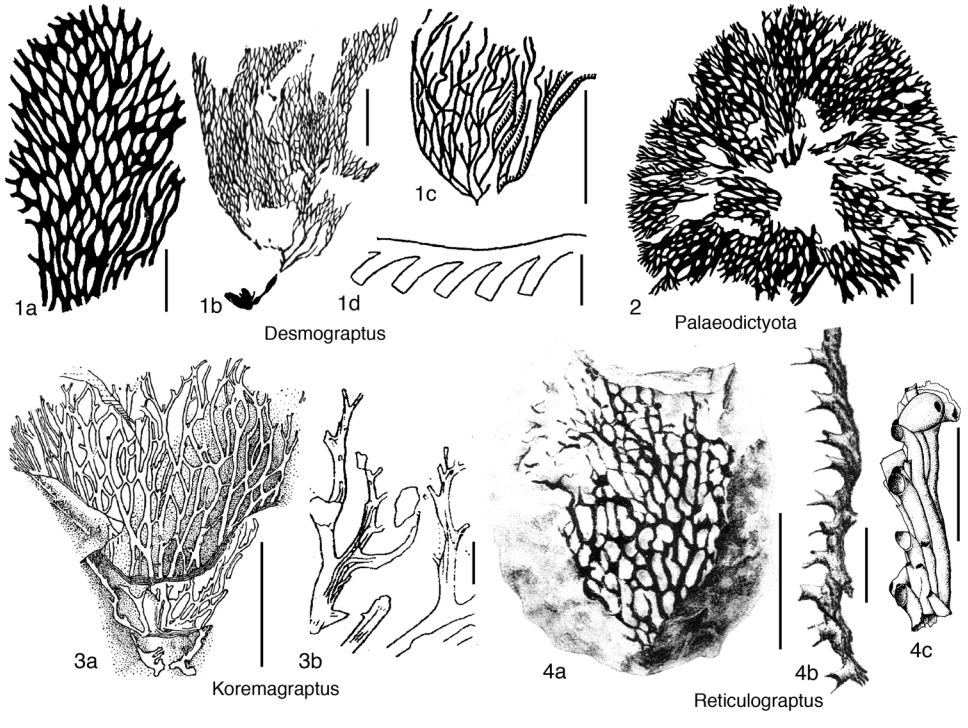


FIG. 152. Callograptidae (p. 244–247).

stipe fragment showing complex thecal overlap and bridge development, scale bar, 1 mm (Ruedemann, 1908, fig. 64).——FIG. 151,*4c. D. graptolithorum* POČTA, 1894, fragment with complex stipes, scale bar, 1 mm (Bouček, 1957, fig. 27b).

Koremagraptus BULMAN, 1927a, p. 345 [**K. onniensis* BULMAN, 1927a, p. 345; M] [=*Coremagraptus* BULMAN, 1942, p. 285 (misspelling); =*Archaeodictyota* OBUT & SOBOLEVSKAYA, 1967, p. 55 (type, *A. draguovi,* OD); syn. by BULMAN, 1970, p. 43; =*Dyadograptus* OBUT, 1960, p. 147 (type, *D. praecursor,* OD), syn. by BULMAN, 1970, p. 43]. Tubarium conical or flabellate; branches complex, with several stolonal chains; branches and twigs anastomosing irregularly; thecae very long, tubular, usually adnate for much of their length but isolated at the apertures. ?*Cambrian* (*Furongian*)–*Lower Devonian* (*Lochkovian*): worldwide.——FIG. 152,*3a.* **K. onniensis*, holotype, scale bar, 10 mm (BULMAN, 1927b, fig. 1).——FIG. 152,*3b. K. fibratus* BULMAN, 1927a, holotype, SMF XXIV C 115a, fragment showing complex stipes, scale bar, 1 mm (Bulman, 1927b, fig. 2,*1*).

Palaeodictyota WHITFIELD, 1902, p. 399 [**Inocaulis ramulosus* WHITFIELD, 1902, p. 399, *non* SPENCER, 1884, =*Inocaulis anastomotica* RINGUEBERG, 1888, p. 131; SD RUEDEMANN, 1908, p. 200]. Resembling *Koremagraptus* but without projecting thecae and twigs; branches probably composite but stolonal system unknown. *Silurian–Middle Devonian:* Canada, USA, Europe.——FIG. 152,*2. P. anastomotica* (RINGUEBERG), typical colony, Rochester Shale, Silurian, Lockport, New York, USA, scale bar, 10 mm (Ruedemann, 1908, pl. 6,*4*).

Ptilograptus HALL, 1865, p. 139 [**P. plumosus;* SD MILLER, 1889, p. 201, misspelled *Ptylograptus* in SPENCER, 1878, p. 462] [=*Stelechograptus* RUEDEMANN, 1908, p. 279 (type, *S. rectus,* OD), syn. herein]; =*Denticulograptus* SCHMIDT, 1940, p. 122, *ex Ptilograptus* (*Denticulograptus*) SCHMIDT, 1940, p. 122 (type, *Ptilograptus acutus* HOPKINSON & LAPWORTH, 1875, p. 662, OD), syn. herein; =*Zigzagigraptus* YU, 1962, p. 49 (type, *Z. yunnanensis,* OD), syn. by ZHANG & others, 2009, p. 311]. Tubarium with several orders of monoprogressive branches; isolated metathecae to complex twigs and stipes form later order extensions; thecal details and development unknown. *Middle Ordovician* (*Dapingian, Didymograptellus bifidus* Biozone)–*Silurian* (*Wenlock, Cyrtograptus radians* Biozone): Australia, Czech Republic, Canada, USA.——FIG. 151,*7a.* **P. plumosus,* lectotype (designated herein), scale bar, 10 mm (Hall, 1865, pl. 21,*1*).——FIG. 151,*7b. P. geinitzianus* HALL, 1865, GSC 561b, scale bar, 10 mm (Hall, 1865, pl. 21,*6*).——FIG. 151,*7c. P. rectus* (RUEDEMANN, 1908), holotype, scale bar, 10

mm (Ruedemann, 1947, pl. 42,*9*).——Fig. 151,*7d. P. yunnanensis* (Yu), holotype, scale bar, 1 mm (adapted from Yu, 1962, pl. 1,*2*).

Ptiograptus Ruedemann, 1908, p. 175 [**P. percorrugatus;* OD]. Fan-shaped tubarium with robust, compound stipes; attachment and stem development unclear; dichotomously branched stipes connected through numerous bridges; bridges may form secondary stipes. Possibly *Middle Devonian* (*Eifelian, Paraspirifer acuminatus* Biozone): USA.——Fig. 151,*6. *P. percorrugatus,* NYSM 7348, holotype, waterlime at Louisville, Kentucky, USA, scale bar, 10 mm (Bulman, 1970, fig. 16,*6*) [The limestone looks like Louisville Limestone and the specimen may be of Silurian age.]

Reticulograptus Wiman, 1901, p. 189 [**R. tuberosus;* OD] [=*Marsipograptus* Ruedemann, 1936, p. 385 (type, *M. bullatus,* OD), syn. by Bulman, 1970, p. 47]. Callograptid with probably fan-shaped tubarium, showing anastomosis; thecal details unknown; conothecae may be present. *Lower Ordovician* (*Tremadocian*)–*Silurian* (*Wenlock*): Sweden, Canada, USA.——Fig. 152,*4a–b. *R. tuberosus; 4a,* holotype, scale bar, 10 mm (Wiman, 1895, pl. 12,*9*); *4b*, stipe fragment, scale bar, 1 mm (Wiman, 1895, pl. 12,*12*).——Fig. 152,*4c. R. thorsteinssoni* Bulman & Rickards, 1966, GSC 20322, fragment showing conothecae, scale bar, 1 mm (Bulman & Rickards, 1966, fig. 38B).

Ruedemannograptus Termier & Termier, 1948, p. 174; *pro Streptograptus* Ruedemann, 1947, p. 197; *non Streptograptus* Yin, 1937 (Monograptidae) [**Streptograptus tenuis* Ruedemann, 1947, p. 198; SD Bulman, 1970, p. 57]. Irregularly branched dendroid tubarium with projecting thecae alternately opening to the sides of the stipes. *Ordovician* (*Sandbian*)–?*Middle Devonian* (*Givetian,* middle *Polygnathus varcus* Biozone): Morocco, Czech Republic, Germany, USA.——Fig. 151,*8. *R. tenuis* (Ruedemann), part of holotype, scale bar, 1 mm (Ruedemann, 1947, pl. 14,*9*).

TAXA PREVIOUSLY IDENTIFIED AS EARLY LAND PLANTS

These taxa are separated herein, as they are described from small, largely unbranched fragments originally referred to as land plant remains. They clearly have complex stipe and isolated tubular extensions that may represent thecal tubes. To date, there is no evidence of fusellar construction in this material to support the inclusion in the Graptolithina.

Boiophyton Obrhel, 1959, p. 536 [**B. pragense;* OD]. Large, bushy, erect callograptid with complex development of stipes; long and slender autothecal apertures inclined to main stipes, not forming compound twigs. *Middle Ordovician* (*Darriwilian*, *Corymbograptus retroflexus* Biozone)–*Silurian, Ludlow* (*Gorstian*): Czech Republic, Sweden.——Fig. 153,*3a–c. B. aculeatus* (Počta, 1894), *3a,* pyritic stipe fragment showing thecal details, Lodenice, *Cyrtograptus radians* Zone, scale bar, 1 mm (Bouček, 1957, pl. 15,*7*); *3b,* specimen showing isolated thecal tubes, Kopanina beds, Silurian (Ludlow), scale bar, 1 mm (Bouček, 1957, pl. 15,*5*); *3c,* holotype of *Psilophyton hedei* (Halle, 1920) now identified as a specimen of *B. aculeatus,* NRM-S 010022, Hemse Marl (Silurian, Ludlow), southeast of Petesviken, parish of Hablingbo, Gotland, Sweden, scale bar, 10 mm (Kenrick, Kvaček & Bengtson, 1999, fig. 3D).——Fig. 153,*3d–e. *B. pragense,* holotype, NM-D418, specimen (*e*) and enlargement (*d*), Praha-Vokovice, Czech Republic, Darriwilian, scale bars, 1 mm (Kenrick, Kvaček & Bengtson, 1999, fig. 3a–b).

Bowerophylloides Edwards, Morel, Poiré, & Cingolani, 2001, p. 7 [**B. mendozaensis;* OD]. Unbranched stipe fragments with radiating tubular extensions. [The taxon was originally described as a plant fossil, but Kraft & Kvaček (2017, p. 185) suggested it to be a possible animal.] *Devonian* (possibly *Lochkovian*): Argentina.——Fig. 153,*1. *B. mendozaensis,* holotype, Devonian, Argentina, scale bar, 1 mm (Edwards, & others, 2011, pl. 1,*16*).

Saxonia Roselt, 1962, p. 323 [**S. microphylla;* OD]. Robust, dichotomously branching stems of considerable length reaching 0.5–0.7 cm in width; slender projecting tubes. *Silurian* (*Ludlow*): Germany.——Fig. 153,*2. *S. microphyla*, holotype, Ölsnitz, Vogtland, Germany, scale bar, 5 mm (Roselt, 1962, pl. 1,*1*).

Family MASTIGOGRAPTIDAE Obut & Sobolevskaya, 1967

[Family Mastigograptidae Obut & Sobolevskaya, 1967, p. 58]

Bushy dendroid colonies with slender stipes formed from stolonal strands; metathecae arranged in pairs, distinctly widening; fuselli formed as complete fusellar rings with irregularly placed sutures; triad budding present; auto- and bithecae not differentiated by size; sicular development poorly known. *Middle Ordovician* (*Darriwilian*)–*Upper Ordovician* (*Katian*): worldwide.

Mastigograptidae is likely a monophyletic clade differing from all other graptolites through their slender stems with a tightly adhering tube covering the stolon system and the thin-walled, distinctly widening and completely isolated metathecal tubes. Rickards and Durman (2006) included *Mastigograptus*

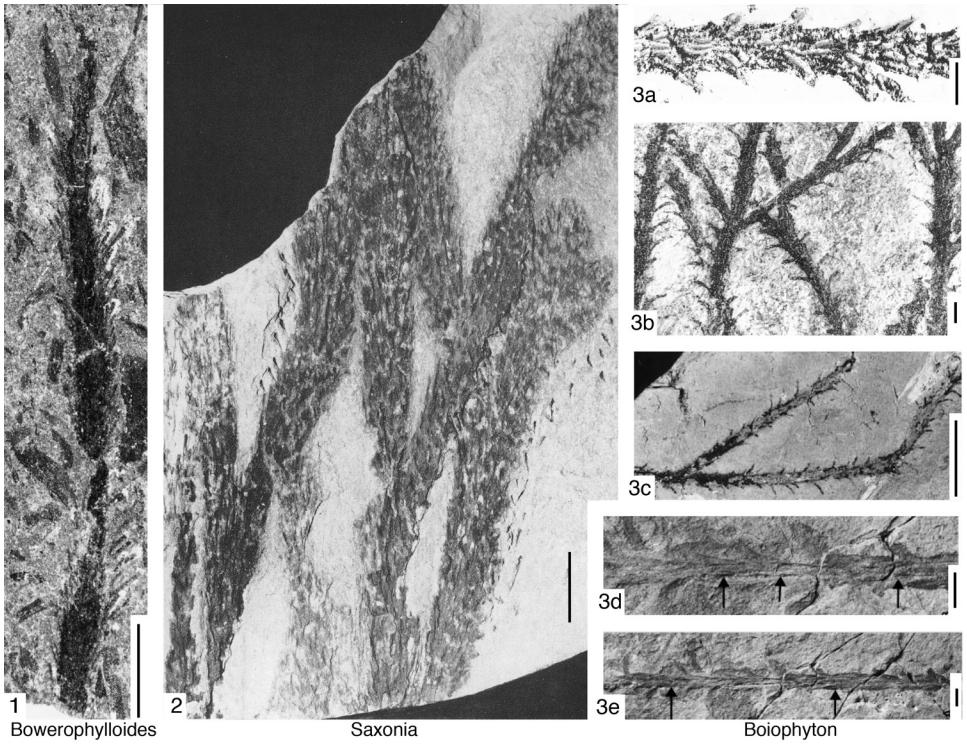


FIG. 153. Possible Callograptidae, previously identified as plants (p. 247).

in Dithecoidea (Dithecodendridae), but this relationship cannot be supported without the knowledge on the thecal origin and development the members of the Dithecodendridae. Unfortunately, this group is known exclusively from flattened shale material and details are not available. All records of the Mastigograptidae from the Cambrian are questionable and may represent members of the Dithecodendridae.

The family Mastigograptidae is based on two closely related genera with a typical triad budding system. The taxa are known from isolated three-dimensionally preserved specimens found in glacial boulders in northern Germany and Poland. Their origin and phylogenetic relationships are uncertain, but the development of a typical triad budding system strongly indicates an inclusion in Dendroidea.

RUEDEMANN (1908) for the first time recognized the conical thecae in *Mastigograptus tenuiramosus* (WALCOTT, 1883) in material from the Eden Shale of Kentucky, USA (now the Kope Formation), not visible in the type of WALCOTT (1883). The identification of this material with *M. tenuiramosus* is uncertain and the inclusion of the material from Ordovician glacial erratics of Europe in *Mastigograptus* has been questioned by OBUT and SOBOLEVSKAYA (1967). Cambrian taxa with isolated metathecae are generally included in the Dithecodendridae (MALETZ, 2019c), based on the assumed diad budding (OBUT, 1960), which has not been verified.

MORPHOLOGY

Specimens of the Mastigograptidae indicate a loosely branching bushy shape with widely spaced paired autothecae. The stipes are robust and strongly thickened with extrathecal cortical material. The colonies are anchored to the sediment surface or fossil

shells by a distinct attachment disk developed from cortical material (Fig. 154.4), in which the erect sicula is hidden. The holdfast of a number of specimens of *Mastigograptus* has an ornamentation indicating that the specimens were attached to ribbed brachiopods (e.g., EISENACK, 1934; BATES & URBANEK, 2002).

BATES and URBANEK (2002) provided some general information on the initial segment of the *Mastigograptus* colonies, which they presumed to represent the sicula. However, important details of the sicular development are not available due to the strong cortical overgrowth of the proximal ends. The authors interpreted the structure as a cylindrical sicula similar to the sicula of the dendroid graptolites but different from the embryonic vesicle of *Rhabdopleura* or the conical sicula of *Dendrotubus*. The sicula opens upward as in Dendrograptidae, and a possible origin of th1 appears in the lower to middle part of the sicula. Later development is unknown, even though the general triad budding has been documented (BATES & URBANEK, 2002).

The thecae are formed from thin-walled fusellar rings (Fig. 154.1–154.2). They are conical, widening distinctly toward their simple straight apertures. The fusellar rings have full-ring development with irregularly placed sutures. The prothecal parts may have swollen initial parts (Fig. 154.3) but are simple in other species.

Mastigograptus RUEDEMANN, 1908, p. 210 [**Dendrograptus tenuiramosus* WALCOTT, 1883, p. 21; OD]. Bushy dendroid colonies with slender, elongated stipes formed from stolonal strands; isolated metathecae arranged in pairs, distinctly widening; thecae formed from complete fusellar rings with irregularly placed sutures; triad budding present; auto- and bithecae not differentiated by size; sicular development poorly known. *Upper Ordovician* (*Sandbian–Katian*): USA, Germany, Poland (glacial boulder).——FIG. 155,*1a–b*. **M. tenuiramosus* (WALCOTT)*; 1a,* holotype, Utica Slate, Trenton, New York, USA, scale bar, 10 mm (Walcott, 1883, pl. 1,*4*); *1b,* specimens showing conical thecae; scale bar, 1 mm (part of Ruedemann, 1908, pl. 11,*1*).

Micrograptus EISENACK, 1974, p. 665 [* *M. fragilis;* OD]. Bushy dendroid colonies with slender, elongated stipes formed from stolonal strands; isolated metathecae arranged in pairs, distinctly widening; thecae formed from complete fusellar rings with irregularly placed sutures; triad budding present; auto- and bithecae probably not differentiated by size. *Middle Ordovician* (*Darriwilian*)*–Upper Ordovician* (*Sandbian*): Estonia, Finland.——FIG.155,*2a–c*. **M. fragilis, 2a,* holotype, glacial boulder, southern Finland; *2b,* specimen with thecal bud; *2c,* specimen possibly belonging to the species, showing regrowth of theca, Estonia; scale bars, 0.1 mm (Eisenack, 1974, fig. 1,*3–4*).

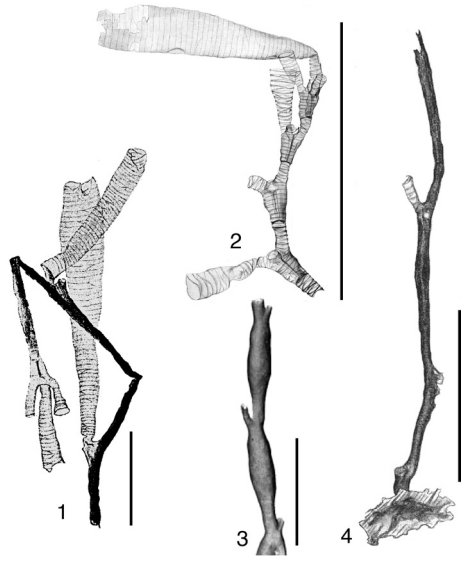


FIG. 154. Morphology of Mastigograptidae. *1,3–4, Mastigograptus* sp. *1,* stipe fragment with triad (Andres, 1977, fig. 13); *3,* stolon with swollen central part (inverted photo, Bates & Urbanek, 2002, fig. 3G); *4,* proximal end with attachment and short stipe showing bases of thecae (Andres, 1961, fig. 2a); *2, Micrograptus* sp., stipe fragment showing four closely spaced branching divisions (Andres, 1977, fig. 21). Scale bars, 1 mm.

DENDROIDEA INDET

The following taxa most likely belong to the Dendroidea. They are based on highly incomplete fragments and preserve little detail of their development. The genus *Archaeoantennularia* was initially described as a hydrozoan, but MUSCENTE, ALLMON, and XIAO (2016) recognized fusellar construction in the taxon, supporting a graptolitic nature of the material. The available material has a quite special tubarium shape, not recognized in other dendroids. The denticulate or rutellate nature of the thecae in the erect tubarium may indicate an inclusion with the

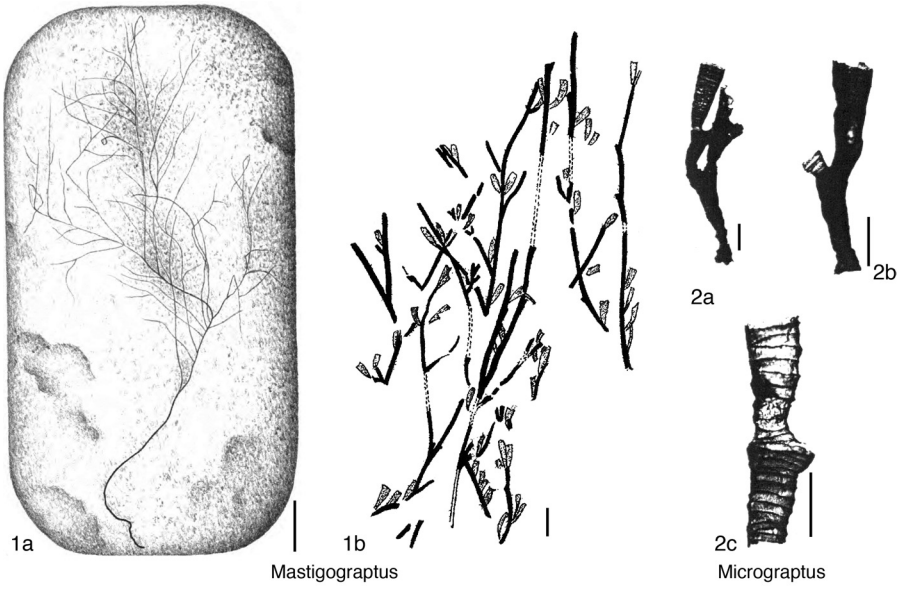


FIG. 155. Mastigograptidae (p. 249).

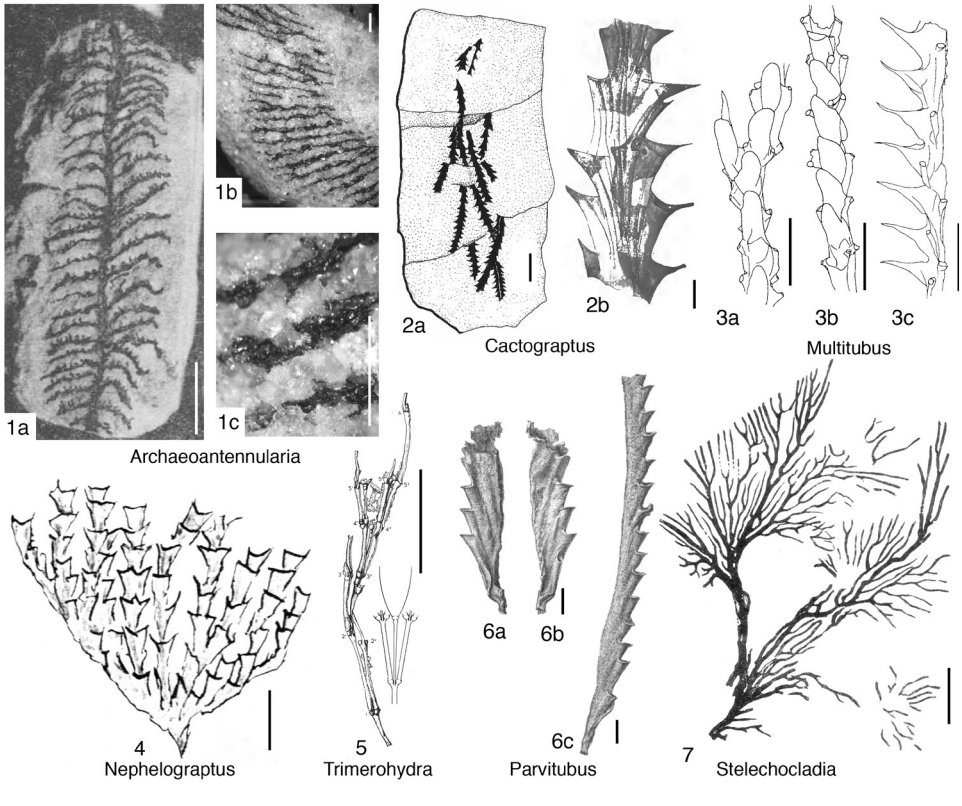


FIG. 156. Dendroidea indet (p. 251).

Dendroidea and possibly the Dendrograptidae when more details of its development are available.

The genus *Multitubus* is based on a few small stipe fragments with an apparently unusual development, and SKEVINGTON (1963a) even referred the genus to his new family Multitubidae. BULMAN and RICKARDS (1966) synonymized the genus with *Reticulograptus,* a suggestion that is without true evidence.

Archaeoantennularia DECKER, 1952, p. 656 [**A. byersi;* M]. Cylindrical tubarium with a central axis from which branches radiate in all directions; thecae appear to be denticular and not isolate apparturally; thecal differentiation and stolon system not recognized; details of colony unknown. *Middle Devonian:* USA (Michigan).——FIG.156,*1a–c*. **A. byersi,* Silvania Sandstone, Wayne County, Michigan, USA; *1a,* holotype, UMMP material, specimen strongly retouched, scale bar, 10 mm (Decker 1952, fig. 1); *1b–c,* metatype, SNOMNH OU622, fragments showing thecal style (new; provided by A. D. Muscente). Scale bars, 1 mm.

Cactograptus RUEDEMANN, 1908, p. 196 [**C. crassus;* OD]. Dichotomously branching, elongate stipes; prominent thecae projecting to both sides. *Cambrian, Miaolingian* (*Wuliuan, Ptychagnostus gibbus* Biozone)–*Silurian* (*Llandovery, Streptograptus crispus* Biozone–*Cyrtograptus centrifugus* Biozone): Kazachstan, Australia, USA.——FIG. 156,*2a–b*. **C. crassus,* holotype, NYSM 6860, specimen (*a*) and detail (*b*), Williamson Shale Formation, New York, USA (2*a,* Ruedemann, 1908, pl. 8,*1; 2b,* Ruedemann, 1908, fig. 99). Scale bars, 10 mm, 1 mm, respectively.

Multitubus SKEVINGTON, 1963a, p. 51 [**M. spinosus;* OD] Stipe fragments with serially arranged, spinose or rutellate autothecae and multiple capriciously distributed bithecae. *Middle Ordovician* (*Darriwilian*): Sweden.——FIG.156,*3a–c*. **M. spinosus,* holotype, fragments, Darriwilian, Öland, Sweden, scale bars, 1 mm (Skevington, 1963**a**, fig. 73–74).

Nephelograptus RUEDEMANN, 1947 p. 196 [**N. rectibrachiatus;* OD]. Fan-shaped tubarium with delicate dissepiments; thecae probably denticulate, oriented alternately to both sides; details of development unknown due to poor preservation. *Ordovician* (?*Katian*): USA (Tennessee).——FIG. 156,*4. **N. rectibrachiatus*, holotype, Ottosee Shale, Knoxville, Tennessee, USA. scale bar, 1 mm (Ruedemann, 1947, pl. 14,*26*).

Parvitubus SKEVINGTON, 1963a, p. 47 [**Azygograptus*? *oelandicus* BULMAN, 1936, p. 46; OD] Colony erect; branches with serially arranged autothecae, possibly with triad budding; bithecae restricted to one side of the stipe; opening into autothecae. *Middle Ordovician* (*Darriwilian*): Sweden.——FIG.156,*6a–c*. **P. oelandicus* (BULMAN), Öland, Sweden; *6a–b*, holotype viewed from both sides (Bulman, 1936, pl. 2,*23–24*); *6c,* paratype, long specimen (Bulman, 1936, pl. 2,*16*). Scale bars, 1 mm.

Stelechiocladia POČTA, 1894, p. 206 [**S. fruticosa* POČTA, 1894, p. 207; SD BOUČEK, 1957, p. 35 as *Dendrograptus* (*Stelechocladia*) *suffruticosus* BOUČEK, 1957, p. 36]. Bushy tubarium with strongly compound stipes; thecae elongate and in ropy bundles. *Ordovician, Sandbian–?Middle Devonian (Givetian,* middle *Polygnathus varcus* Biozone): Czech Republic.——FIG. 156,*7*. **S. fruticosa,* holotype, Silurian, Bohemia, scale bar, 10 mm (Bouček, 1957, pl. 2,*1*).

Trimerohydra KOZŁOWSKI, 1959a, p. 217 [**T. glabra;* OD]. Stolon system with distinct nodes, showing triad budding. *Ordovician:* Poland (glacial boulder). [BULMAN, 1970, p. 43, suggested a synonymy with *Koremagraptus*].——FIG. 156,*5. **T. glabra,* holotype, scale bar, 0.5 mm (Kozłowski, 1959a, fig. 1).

ORDER GRAPTOLOIDEA

Jörg Maletz, Blanca A. Toro, and Yuandong Zhang

Order GRAPTOLOIDEA Lapworth, 1875

[Graptoloidea Lapworth in Hopkinson & Lapworth, 1875, p. 633, *nom. transl*. Ruedemann, 1904, p. 573, *ex* section Graptoloidea] [=suborder Rhabdophora Allman, 1872, p. 380; =division Graptoloida Mitchell, Melchin, Cameron, & Maletz, 2013, p. 53]

Graptolites united by the retention of the nematophorous sicula in the adult stage as the defining synapomorphy. *Ordovician* (*Tremadocian, Rhabdinopora proparabola* Biozone)–*Devonian* (*lower Emsian, Uncinatograptus yukonensis* Biozone): worldwide.

In the past, all bithecae-bearing planktic taxa (family Anisograptidae) were included in the Dendroidea (Bulman, 1955, 1970) or in the Graptodendroidina (Mu & Lin in Lin, 1981) because they have close similarities to the construction of the benthic graptolites due to the presence of a typical triad budding system with development of bithecae along the stipes. Fortey and Cooper (1986) differentiated the Graptoloidea on a cladistic interpretation and based it on the presence of a free nema in the adult stage as the defining synapomorphy. These authors promoted the inclusion of all nematophorous graptolites into a single order and indicated that the loss of bithecae was polyphyletic within the Graptoloidea (Fig. 157), a notion supported by the analysis of Li and others (2007). Maletz, Carlucci, and Mitchell (2009) provided an analysis of the derived graptoloids but did not include enough taxa of the Anisograptidae to be able to shed light on the early divergence of the graptoloids. Mitchell and others (2013, p. 53) defined the Graptoloidea (as the division Graptoloida) as the taxon including all graptolites retaining a nematophorous sicula in the adult stage, and thus they provided a definition based on an easily recognizable synapomorphy but otherwise followed the interpretations of Fortey and Cooper (1986).

Early Graptoloidea share numerous tubarium characters with the Dendroidea, especially the stipe structure formed by triad budding (Wiman rule), in which each autotheca produces two daughter thecae—an autotheca and a bitheca (see Cooper & Fortey, 1983). Dicalycal thecae are inserted at various distances to produce branching of the stipes. The most obvious difference the Graptoloidea has from the benthic taxa is the development of a free nema and the differentiation of the conus and cauda of the prosicula (Hutt, 1974a).

A number of planktic dendroids have been described (Rickards, Hamedi, & Wright, 1994; Kraft & Kraft, 2007), among which *Calyxdendrum graptoloides* (Kozłowski, 1960) from the *Nemagraptus gracilis* Biozone is the best known and the only one available from chemically isolated material. These are not considered to be graptoloids but are regarded as examples of dendroids that independently developed a planktic life style.

Suborder GRAPTODENDROIDINA Mu & Lin, 1981

[Graptodendroidina Mu & Lin in Lin, 1981, p. 244]

Quadriradiate to biradiate planktic, nematophorous graptolites with a triad budding system of the thecae; bithecae reduced or even lost in stratigraphically younger taxa; colonies multiramous to biramous, pendent to reclined; dissepiments present in some taxa; autothecae simple, widening tubes with or without short ventral rutellum; thecal apertures may be isolated; prosicula with distinct differentiation of conus and cauda; origin of th1[1] in the middle part of

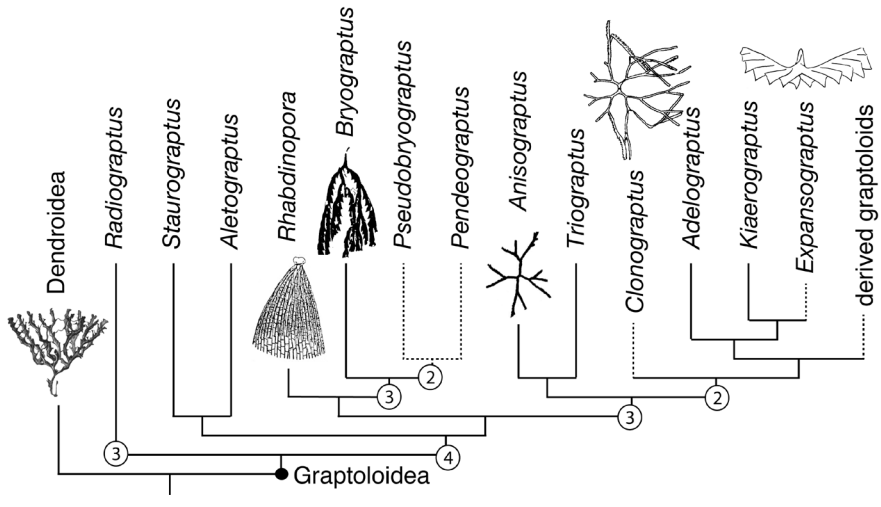


FIG. 157. Cladistic interpretation of early Graptoloidea by FORTEY and COOPER (1986), showing possible polyphyletic origin of non-bithecate graptoloids (*dotted lines*); circled numbers indicate origins of quadriradiate (*4*), triradiate (*3*), and biradiate (*2*) proximal development (new).

the conus; proximal end may possess one to three successive (proximal) dicalycal thecae with th1^2 as the first dicalycal theca; later dicalycal thecae adventitiously or regularly distributed. *Lower Ordovician* (*Tremadocian*, *Rhabdinopora proparabola* Biozone–*Floian, Sagenograptus murrayi* Biozone): worldwide.

The Graptodendroidina is a paraphyletic taxon from which all younger groups of the Graptoloidea originated. The group and its biostratigraphic range is poorly known, because few horizons in the upper Tremadocian time interval provide faunas bearing the younger members of the Graptodendroidina. Thus, the transition to the derived suborders of the order Graptoloidea (e.g., Dichograptina, Sinograpta) is only vaguely defined.

Family ANISOGRAPTIDAE Bulman, 1950

[Anisograptidae BULMAN, 1950, p. 79] [incl. Adelograptinae MU, 1974, p. 231; Rhabdinoporinae ERDTMANN, 1982a, p. 128; Psigraptidae LIN, 1981, p. 244; Muenzhigraptidae ZHAO & ZHANG, 1985, p. 16; Staurograptinae MU, 1974, p. 230]

Planktic nematophorous, multiramous graptoloids with a triad budding system; colony shape ranges from reclined through horizontal to declined and bell-shaped or pendent; bithecae distinctly smaller than autothecae; bithecae initially regular, but in later taxa irregular and commonly reduced or absent; autothecae simple, widening tubes, sometimes aperturally isolated; ventral rutella common; dissepiments present in a few taxa; proximal development type isograptid, quadriradiate to biradiate, variably dextral and sinistral; maeandrograptid type proximal symmetry with inclined sicula; prosicula with distinct differentiation of conus and cauda; origin of first theca in median part of conus; th1^2 is first dicalycal thecae, later dicalycal thecae adventitiously or regularly distributed. *Lower Ordovician* (*Tremadocian*, *Rhabdinopora proparabola* Biozone–*Floian*, *Sagenograptus murrayi* Biozone): worldwide.

The Anisograptidae form a paraphyletic stem group of the Graptoloidea (see Fig. 157). The Dichograptina and Sinograpta originated from this stem independently, but the details of the divergence of both groups have not been explored. MALETZ, CARLUCCI, and MITCHELL (2009) defined the supercohort Eugraptoloida as a monophyletic group through the defining synapomorphy, loss of bithecae along stipes, and indicated a monophyletic origin of the derived graptoloids. Their results are in direct conflict with the interpretation of FORTEY and COOPER

(1986) and LINDHOLM (1991) concerning the multiple independent loss of bithecae in the Anisograptidae.

MORPHOLOGY

The tubarium shape of the Anisograptidae is quite variable and ranges from pendent to horizontal and reclined. The stratigraphically earliest taxa (*Rhabdinopora*, *Staurograptus*) recall the multiramous, dissepimentous tubaria of the benthic Dendrograptidae. The stipes are connected by irregularly or regularly distributed dissepiments to keep them at a certain distance, most probably to prevent interaction and feeding competition of zooids from adjacent stipes (FORTEY & BELL, 1987).

All Anisograptidae possess a free nema (Fig. 158), indicating that the colonies are not attached to any object. Nemata can be branched or replaced by various features interpreted as float structures or described simply as nematularia with unknown function. The nematularia are not known from isolated material and their precise construction is uncertain. HUTT (1974a) described the distal end of the nema in *Adelograptus tenellus* (LINNARSSON, 1871) as open and interpreted it as a growing end of the colony. BATES (1987a) considered the growth to be similar to that of other spines of the colonies and suggested an incremental growth from fusellar or cortical components. RICKARDS (1975, 1996) discussed the construction of the nema and claimed that it is a hollow tube (actually referring to the cauda of HUTT, 1974a), later overgrown by the addition of fusellar tissue in the form of a spine. He identified this addition as the virgula. The virgula is herein regarded as a synonym of the nema. Early developments on the nema include various vanes or possibly vesicular bodies of uncertain construction (e.g., nematularia).

The sicula of the Anisograptidae is conical, gradually widening from the prosicula and typically bearing a short rutellum (Fig. 158.4). The prosicula is differentiated into two parts of approximately equal length,

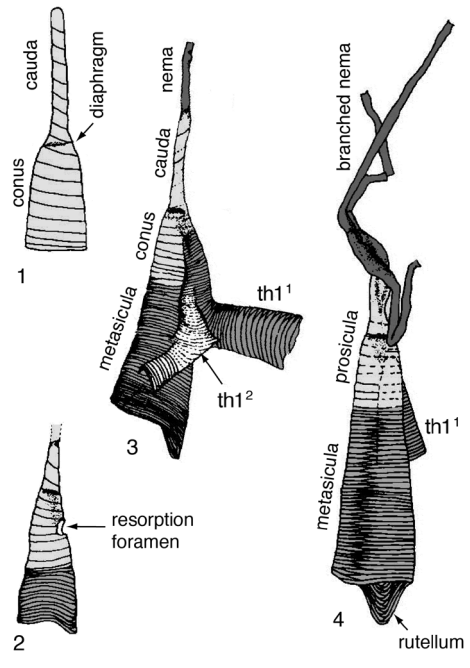


FIG. 158. Sicular development in Anisograptidae. *1,* prosicula showing conus and cauda, *arrow* indicates diaphragm; *2,* prosicula (*light gray*) with early metasicula (*dark gray*), resorption foramen for th1[1] indicated by *arrow; 3,* juvenile with complete sicula, part of th1[1] and crossing canal of th1[2], reverse view; *4,* sicula with complex nema (adapted from Hutt, 1974a).

the conus and cauda (HUTT, 1974a), separated by a diaphragm (Fig. 158.1). A highly regular development of fuselli with a dorsal and a ventral zigzag suture characterizes the metasicula of the Anisograptidae and of all derived Graptoloidea. The origin of the tube of th1[1] is through a resorption foramen in the upper half of the conus on the ventral side of the prosicula (Fig. 158.2). The length of the prosicula may be reduced, and the origin of th1[1] is close to the apex of the sicula (*Choristograptus* LEGRAND, 1964b).

The position of the dicalycal thecae defines the branching geometry of the graptoloid colonies. Dicalycal thecae are most densely distributed in the proximal end and more widely dispersed distally in most multiramous taxa. MALETZ (1992) described the proximal development of the Anisograptidae and provided a model for their construction.

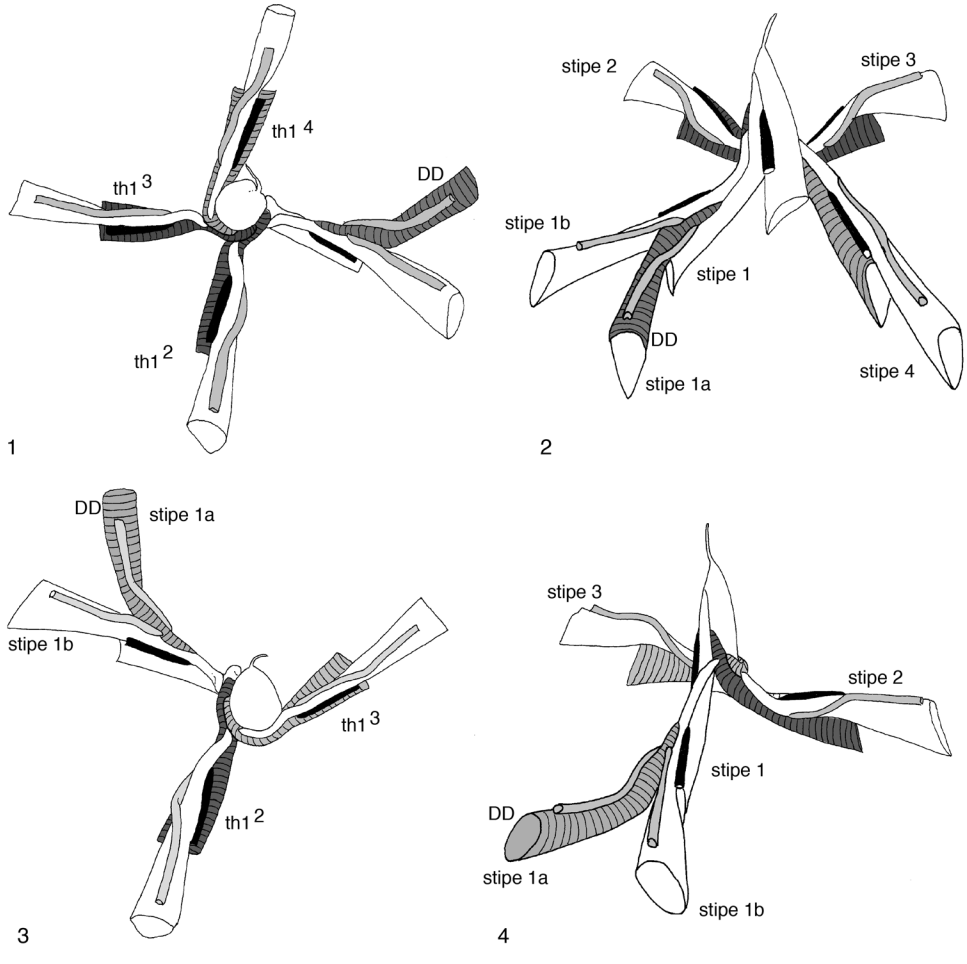


Fig. 159. Quadriradiate and triradiate proximal development. *1,* Quadriradiate development, dorsal view, showing successive, clockwise (dextral) origins of dicalyal thecae (th1^2, th1^3, th1^4) around the sicula; *2,* quadriradiate development, obverse view, showing sicular bitheca; *3,* triradiate development, dorsal view, showing two successive dicalycal thecae (th1^2, th1^3) originating in anticlockwise (sinistral) fashion; *4,* triradiate development, reverse view. Dicalycal thecae are striped and show various shades of gray: bithecae, *black*, first distal dicalycal theca, marked *DD* (adapted from Maletz, 1992, fig. 3).

Dicalycal thecae can be differentiated into proximal dicalycal thecae and distal ones. The first dicalycal theca is th1^2, defining an isograptid proximal development as the basic constructional unit of the proximal end of all Anisograptidae. Dicalycal thecae may be consecutive, but a dicalycal theca can only generate a single further dicalycal theca.

The successive dicalycal thecae, starting from the first dicalycal theca (th1^2), are identified as proximal dicalycal thecae, whereas distal dicalycal thecae are separated from proximal ones by at least one monocalycal theca. Earliest anisograptids (*Staurograptus*, *Rhabdinopora*) possessed three successive (proximal) dicalycal thecae and, therefore, developed a quadriradiate proximal end (Fig. 159.1–159.2). The successive dicalycal thecae all formed on one side of the growing stipe growing in a circular fashion around the sicula, either clockwise or anticlockwise. During the evolution of the Anisograptidae,

the number of proximal dicalycal thecae was reduced to two (triradiate development) and finally to one (biradiate development).

A biradiate proximal development is the standard in younger anisograptids and is present in non-bithecate multiramous to biramous graptoloids. The position of distal dicalycal thecae may be highly variable. Those closest to the proximal dicalycal thecae are th3[1] and th3[2]. This proximal construction has been termed the tetragraptid foundation (MALETZ, 1992, p. 299). It is typically developed in the multiramous dichograptids, especially in *Clonograptus* (see LINDHOLM & MALETZ, 1989) and derived taxa. A tetragraptid foundation also appears to be present in the anisograptid *Psigraptus* and in some adelograptids.

BULMAN (1925, 1927b) and STUBBLEFIELD (1929) first described bithecae in planktic graptolites. In earlier Anisograptidae, the bithecae alternated along the stipes, with the first bitheca associated with the sicula termed the sicular bitheca (Fig. 160.1). Bithecae are more irregularly placed along the stipes in some late taxa such as *Kiaerograptus kiaeri* (SPJELDNAES, 1963), and the typical alternation is lost (Fig. 160.2). LINDHOLM (1991) and WILLIAMS and STEVENS (1991) discussed the loss of bithecae in upper Tremadocian anisograptids. Lateral budding of the thecae, typical of the Dendroidea, is preserved in most members of the Anisograptidae, even when bithecae along the stipes are lost (Fig. 160.3). The sicular bitheca is the last remaining bitheca according to WILLIAMS and STEVENS (1991) and is present in *Hunnegraptus copiosus* LINDHOLM, 1991 (Fig. 160.4).

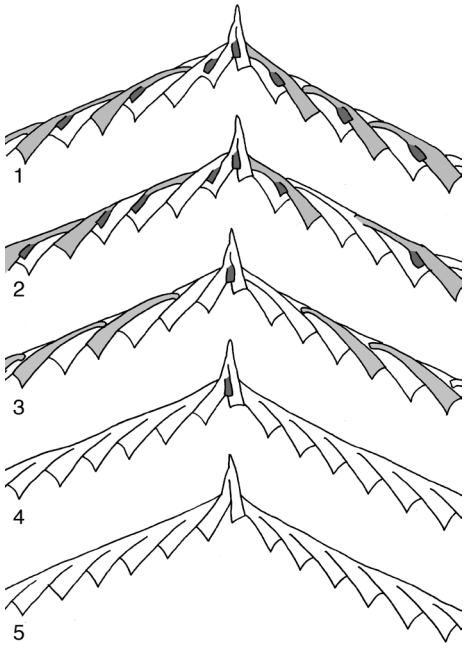


FIG. 160. Diagram illustrating the loss of bithecae in the Anisograptidae in obverse view to show presence/absence of sicular bitheca, proximal ends hypothetical. *1,* Stipes based on *Kiaerograptus*? *supremus* LINDHOLM, 1991; *2,* stipes based on fragment of *Kiaerograptus kiaeri* MONSON, 1925, with successive bithecae on one side; *3,* stipes based on fragment of ?*Clonograptus* sp. aff. *Clonograptus multiplex* (NICHOLSON, 1868d); *4,* stipes based on *Hunnegraptus copiosus* LINDHOLM, 1991, with sicular bitheca as the only remaining bitheca; *5,* stipes based on *Clonograptus multiplex* (NICHOLSON,1868d) (adapted from Lindholm, 1991, fig. 4).

EVOLUTION

The Anisograptidae represent the initial step in graptolites becoming successful planktic organisms. The earliest planktic form, *Rhabdinopora proparabola* (LIN, 1986), appeared close to the base of the Tremadocian, and species of *Rhabdinopora* have commonly been used to indicate the base of the Ordovician System. The genus *Rhabdinopora* quickly diversified and represents one of the most compelling examples of evolutionary conservatism in early Ordovician graptolites (see COOPER & others, 1998).

A clear trend in evolutionary simplification is illustrated by the successive loss of first-order stipes. The Anisograptidae evolved from initially quadriradiate to triradiate and finally to biradiate forms until a stabilization point was reached during the upper Tremadocian. All subsequently appearing graptoloids possess two first-order stipes and one single, proximal dicalycal theca, which is the typical biradiate development (see MALETZ, 1992). The exact points of change from a quadriradiate to triradiate and from triradiate to biradiate development have not

been documented, and the trends appear to be polyphyletic, according to the interpretation of FORTEY and COOPER (1986) and LI and others (2007) (see Fig. 157).

Upper Tremadocian faunas from the *Hunnegraptus copiosus* Biozone of Scandinavia (LINDHOLM, 1991) and the *Aorograptus victoriae* Biozone of western Newfoundland (WILLIAMS & STEVENS, 1991) indicate a breakdown of the typical dendroid triad budding structure along several lineages. Specimens of the sigmagraptine *Paradelograptus* initially still possess a sicular bitheca with a dorsal origin of all thecae along the stipes (MALETZ, 2014b, fig. 10), a condition similar to that in the dichograptine genus *Hunnegraptus* LINDHOLM, 1991. The genus *Paratemnograptus* possesses the plaited thecal overlap of the Anisograptidae and possibly bears a sicular bitheca, but bithecae along the stipes are not present. Thus, it may be possible to demonstrate the loss of bithecae and plaited overlap of thecae independently in the sinograptids and dichograptids.

The genus *Rhabdinopora* EICHWALD, 1855 and its type species *Rhabdinopora flabelliformis* (EICHWALD, 1840) are among the most controversial taxa of the planktic graptolites. For a long time, benthic and planktic graptolites with the typical mesh of *Rhabdinopora flabelliformis* have been included in the genus *Dictyonema*, before ERDTMANN (1982a) reestablished the genus *Rhabdinopora* for planktic taxa and separated the benthic species under the genus name *Dictyonema* HALL, 1851. HOPKINSON and LAPWORTH (1875, p. 667) changed *Dictyonema* to *Dictyograptus*, based on the notion that *Dictyonema* was "an old-established name for a genus of plants." The name was actually based on a group of lichens described as *Dictyonema* by ADGARTH (in KUNTH, 1822) (see PARMASTO, 1978). Graptolite material now referred to the genera *Dictyonema* and *Rhabdinopora* had originally been identified as *Gorgonia* LINNAEUS, 1758, due to their similarity to gorgonian soft corals. The bryozoan *Fenestella* LONSDALE in MURCHISON, 1839, is another fossil easily misidentified as a graptolite but is constructed from calcite instead of the organic material in the graptolites. SALTER (1858) described the genus *Graptopora* and referred to the species *Fenestella socialis* as the type, a taxon now identified as *Rhabdinopora flabelliformis socialis* (SALTER, 1858). At the time, the species was only known from a yet-unpublished manuscript and was first described and illustrated in SALTER (1866).

Rhabdinopora EICHWALD, 1855, p. 453 [**Gorgonia flabelliformis* EICHWALD, 1840, p. 207; SD BASSLER, 1911, p. 348] [=*Phyllograpta* ANGELIN, 1854, p. 4 (type, *Gorgonia flabelliformis* EICHWALD, 1840, p. 207, M); =*Graptopora* SALTER, 1858, p. 65 (type, *G. socialis,* OD, illustrated in SALTER, 1866, p. 331, pl. 4,1); =?*Damesograptus* JAHN, 1892, p. 645 (type, *Dictyonema* sp., DAMES, 1873, p. 383, OD); =*Dictyodendron* WESTERGÅRD, 1909, p. 62 (type, *Gorgonia flabelliformis* EICHWALD, 1840, p. 207, OD); =*Heterograptus* ZHAO & ZHANG in LIN 1986, p. 241 (type, *H. radiatus,* OD) non *Heterograptus* HERNÁNDEZ SAMPELAYO, 1960, p. 33; *nomen oblitum*] [*non Graptopora* ULRICH, 1882, p. 148, *nom. nud.*, =*Graptodictya* ULRICH, 1882, p. 165 (type, *Ptilodictya perelegans,* ULRICH 1878, p. 94, SD, BASSLER, 1953, p. 137, Bryozoa); *non Graptopora* LANG, 1916, p. 405 (type, *G. scripta,* OD; =*Graptoporella* BASSLER, 1953, p. 189, Bryozoa)]. Pendent, multiramous anisograptid with irregularly to regularly distributed dissepiments; proximal development quadriradiate. *Lower Ordovician* (*lower Tremadocian, Rhabdinopora proparabola* Biozone–*Adelograptus* Biozone): worldwide.——FIG. 161,*1a–b*. **R. flabelliformis* (EICHWALD)*; 1a,* neotype (BULMAN, 1966, p. 408, BULMAN, 1967), NHMUK PM Q 1392, Pakerort, north of Paldiski, Estonia (Bulman, 1966, fig. 1); *1b,* LO 4144t, proximal end, Paldiski, Estonia (Bulman, 1966, fig. 2a). Scale bars, 10 mm.—— FIG. 161,*1c*. *R. proparabola* (LIN, 1986), holotype of *Heterograptus radiatus* ZHAO & ZHANG in LIN, 1986, CCG G8456, Dayangcha, Jilin, China, scale bar, 5 mm (Lin, 1986, fig. 96,*1*).

Adelograptus BULMAN, 1941, p. 114 [**Bryograptus*? *hunnebergensis* MOBERG, 1892b, p. 92; OD; =*Dichograptus*? *tenellus* LINNARSSON, 1871, p. 794, MALETZ & ERDTMANN, 1987, p. 180] [=*Clonograptus* (*Paraclonograptus*) ZHAO & ZHANG, 1985, p. 15, *nom. nud.,* herein]. Biradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; cortical overgrowth of proximal part of stipes in gerontic specimens; bithecae on alternate sides of stipes; slender, gradually widening thecae, commonly with short rutellum. *Lower Ordovician* (*upper Tremadocian, Adelograptus tenellus* Biozone–*Hunnegraptus copiosus* Biozone): Algeria, ?Australia, China, Sweden, Norway, UK, Canada, USA, Argentina, Bolivia.——FIG. 162,*5a–b,d*. *A. tenellus* (LINNARSSON, 1871); *5a*, neotype, SGU 4497a–b,

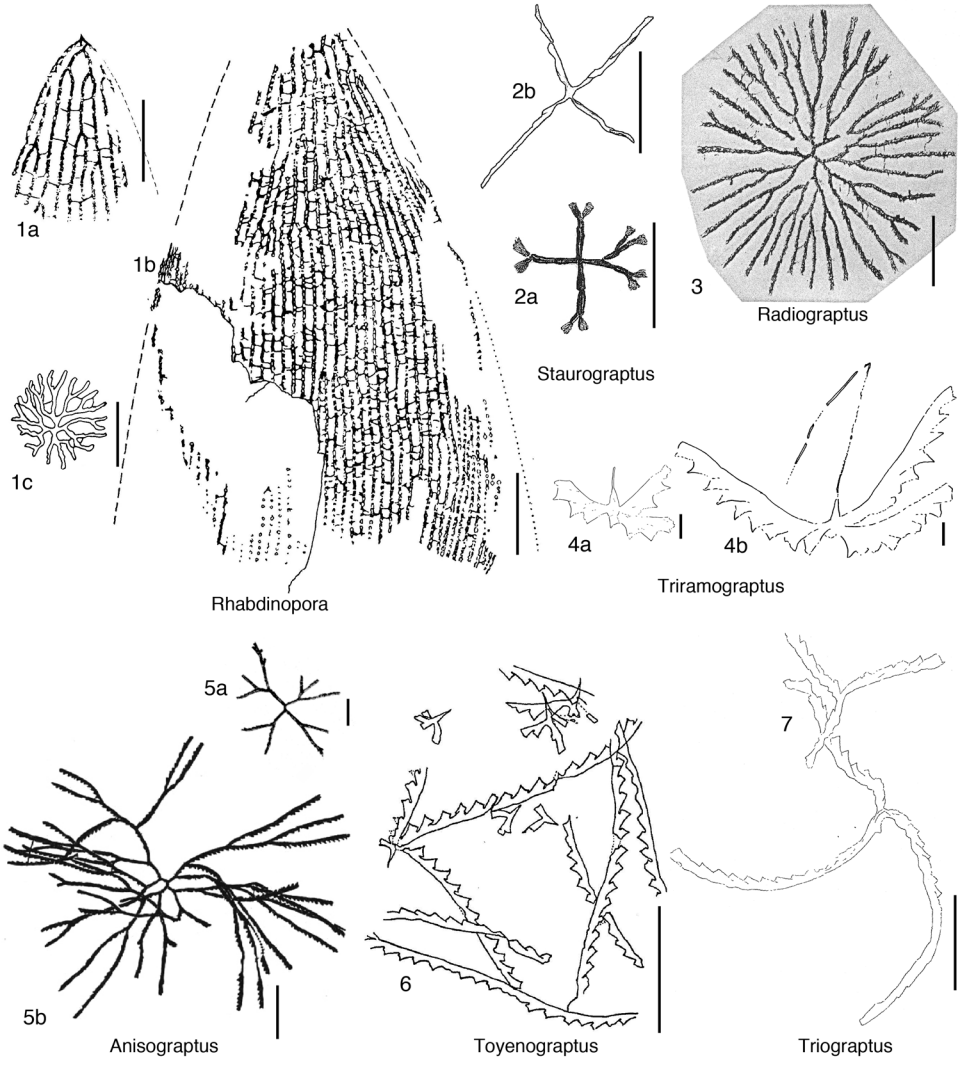


FIG. 161. Anisograptidae (p. 258–263).

scale bar, 5 mm (Maletz & Erdtmann, 1987, pl. 1A); *5b*, SGU 4506, lectotype of **Bryograptus? hunnebergensis* (selected herein), scale bar, 5 mm (Maletz & Erdtmann, 1987, p 188); *5d,* SM A82770, Shineton Shale, Shropshire, UK, scale bar, 1 mm (Maletz, 1992, fig. 1F).——FIG. 162,*5c. A. messaoudi* LEGRAND, 1964a, proximal end, obverse view showing sicular bitheca, scale bar, 1 mm (adapted from Legrand, 1964a, fig. 3a).

Ancoragraptus JACKSON & LENZ, 2003, p. 141 [**Adelograptus*? *bulmani* SPJELDNAES, 1963, p. 127; OD]. Biradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; short bithecae on alternate sides of stipes; slender, gradually widening thecae commonly with short rutellum; tubular sicula and typically a number of proximal thecae isolated aperturally; bithecae may be reduced or missing along the stipes. *Lower Ordovician* (*upper Tremadocian, Aorograptus victoriae* Biozone): China, South Korea, Norway, Canada, Argentina.——FIG. 164,*1a–c. *A. bulmani* (SPJELDNAES); *1a,* holotype, PMO 72835a, Slemmestad, Norway; *1b,* PMO 214.032, proximal end in obverse view showing sicular bitheca; *1c,* PMO 214.028, multiramous colony; scale bars, 1 mm (new).

Anisograptus RUEDEMANN, 1937, p. 61 [**A. matanensis;* OD]. Triradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced. *Lower Ordovician* (*lower Tremadocian,*

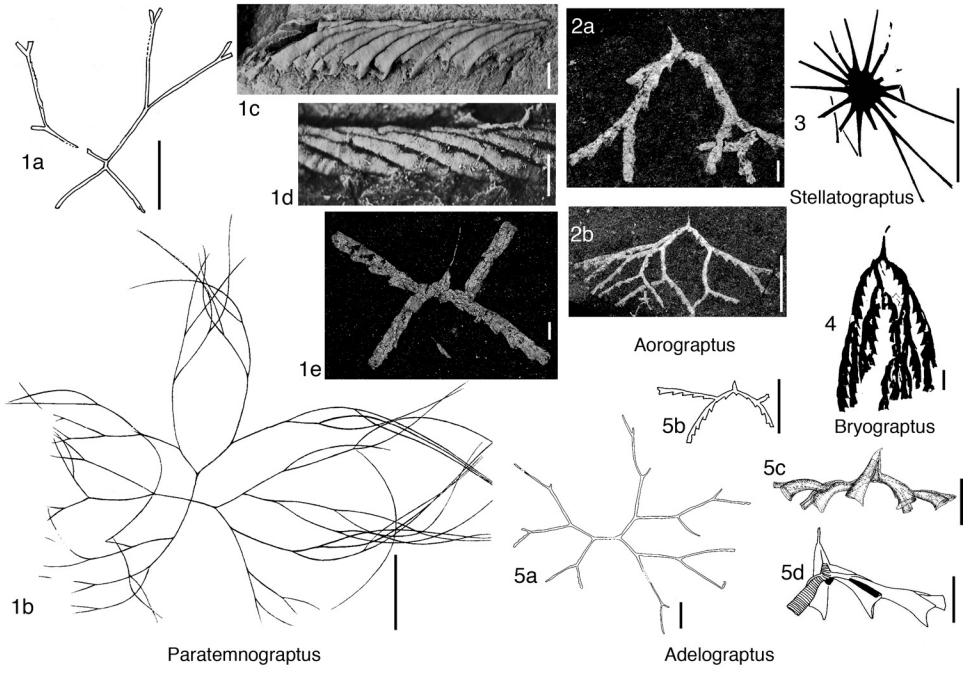


FIG. 162. Anisograptidae (p. 258–263).

Anisograptus matanensis Biozone–*Rhabdinopora flabelliformis anglica* Biozone): worldwide.——FIG. 161,*5a*.**A. matanensis,* holotype, NYSM 6841, Matane, Quebec, Canada, scale bar, 5 mm (Ruedemann, 1937, fig. 6).——FIG. 161,*5b*. *A. flexuosus* BULMAN, 1950, GSC 9861, Matane, Quebec, Canada, scale bar, 10 mm (Bulman, 1950, fig. 6a).

Aorograptus WILLIAMS & STEVENS, 1991, p. 23 [**Bryograptus victoriae* HALL, 1899, p. 165; OD]. Declined to pendent, multiramous anisograptid with biradiate proximal development; distal dichotomies irregularly distributed. *Lower Ordovician* (*upper Tremadocian, Aorograptus victoriae* Biozone): Australia, New Zealand, Norway, Canada, USA, Argentina, Bolivia.——FIG. 162,*2a–b*. **A. victoriae; 2a*, holotype, NMV P 4240, scale bar, 1 mm (new); *2b,* NMV P318132A, large specimen, Victoria, Australia, scale bar, 5 mm (new).

Bryograptus LAPWORTH, 1880a, p. 164 [**B. kjerulfi;* SD GURLEY, 1896, p. 64]. Declined to pendent anisograptid with triradiate proximal development and unlimited branching capacity; bithecae alternate along the stipes; sicula elongated, commonly with long and thickened nema. *Lower Ordovician* (*upper Tremadocian, Bryograptus ramosus* Biozone): UK, Norway, Sweden, Argentina, Bolivia.——FIG. 162,*4*. **B. kjerulfi,* lectotype, PMO 71284, Vaekkero, Oslo Region, Norway, scale bar, 1 mm (Bulman, 1971b, p. 363, fig. 1a).

Chigraptus JACKSON & LENZ, 1999, p. 155 [**C. supinus;* OD]. Small quadriradiate tubarium with four, unbranched, first-order stipes disposed horizontally to slightly reclined; autothecae biform, comprising long, curved, downwardly directed, isolate autothecae proximally, grading to tubes with low angle of inclination and slightly isolate distally; sicular bitheca and bithecae present throughout the colony. *Lower Ordovician* (*Tremadocian–*?basal *Staurograptus dichotomous* Biozone): Canada.——FIG. 164,*4a–b*. **C. supinus; 4a,* holotype, GSC 117664, dorso-ventral preservation; *4b,* GSC 117666, small specimen in lateral preservation; scale bars, 1 mm (Jackson & Lenz, 1999, p. 156, fig. 4).

Choristograptus LEGRAND, 1964b, p. 52 [**C. louhai;* OD]. Biradiate anisograptid with declined tubarium; prosicula strongly reduced or lacking, with origin of th1[1] on prosicular apex; distal dichotomies irregularly spaced; short bithecae on alternate sides of stipes; slender, gradually widening thecae without rutellum; tubular sicula and typically a number of proximal thecae isolated aperturally. *Lower Ordovician* (*upper Tremadocian,* ?*Aorograptus victoriae* Biozone): Algeria, Morocco.——FIG. 163*a–d*. **C. louhai; a,* proximal end with reduced prosicula and nema; *b,* proximal fragment showing isolated thecal apertures and bitheca; *c,* distal fragment showing bitheca; *d,* apex of sicula with nema and origin of tcale bars, 0.5 mm in *a–c,* 0.1 mm in *d* (Legrand, 1964b, *pl. 3–4*).

Kiaerograptus SPJELDNAES, 1963, p. 123 [**Didymograptus kiaeri* MONSEN, 1925, p. 172; OD]. Horizontal to declined, multiramous to two-stiped, robust anisograptid; relatively long bithecae present, but typically irregularly placed; apertural

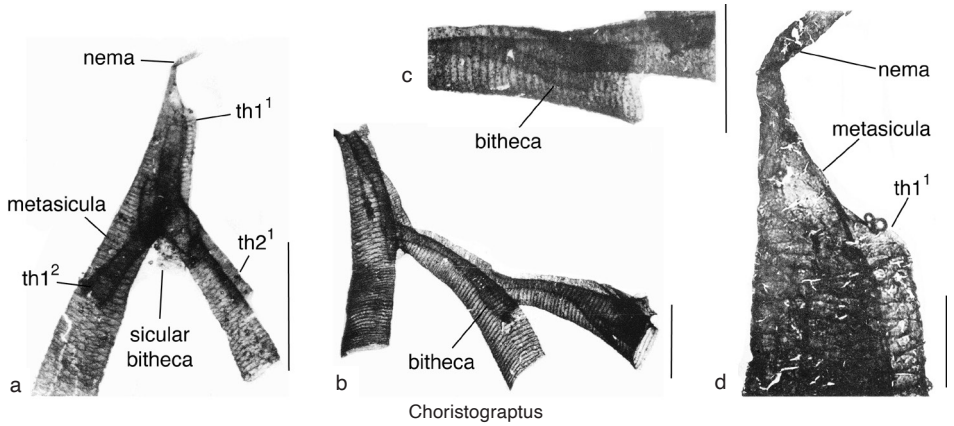


FIG. 163. Anisograptidae (p. 260).

part of sicula freely pendent; thecal apertures, at least in proximal parts, commonly isolated. *Lower Ordovician* (*upper Tremadocian, Aorograptus victoriae* Biozone): Algeria, China, Norway, Sweden, Canada, Argentina.——FIG. 164,*2a–b*. **K. kiaeri* (MONSEN); *2a,* lectotype, PMO 60212a, scale bar, 1 mm (Monsen, 1925, pl. 2,*10;* Spjeldnaes, 1963, pl. 17,*5*); *2b,* PMO 72833, fragment with bithecae, scale bar, 1 mm (Spjeldnaes, 1963, pl. 2,*1*).——FIG. 164,*2c*. *K. lauzonensis* (ERDTMANN, 1966), GSC 122714, showing distal branching, scale bar, 1 mm (Maletz & Egenhoff, 2001, fig. 4a).

Paratemnograptus WILLIAMS & STEVENS, 1991, p. 19 [**P. isolatus;* M; =*Temnograptus magnificus* PRITCHARD, 1892, p. 56, herein]. Horizontal to subhorizontal, multiramous tubarium with biradiate development and tetragraptid foundation; sicular bitheca present; stipes with plaited overlap of thecae, but without bithecae. *Lower Ordovician* (*upper Tremadocian, Aorograptus victoriae* Biozone–*Tetragraptus phyllograptoides* Biozone): Australia, Norway, Sweden, Canada, Argentina, Bolivia.——FIG. 162,*1a–e*. *T. magnificus; 1a,* holotype of *P. isolatus,* GSC 87284, scale bar, 10 mm (Williams & Stevens, 1991, fig. 10L); *1b,* holotype, NMV P34000, Lancefield, Victoria, Australia, scale bar, 10 cm (Pritchard, 1892, pl. 6); *1c,* MG1968, stipe fragment showing plaited overlap and lack of bithecae, Fezouata Lagerstätte, Morocco, scale bar, 1 mm (new; photo provided by J. C. Gutiérrez-Marco); *1d,* PMO 108.558, latex cast showing plaited overlap and lack of bithecae, Slemmestad, Norway, scale bar, 1 mm (Lindholm & Maletz, 1989, pl. 83,*7*);*1e,* lectotype of *Tetragraptus decipiens* HALL, 1899, NMV P14368, proximal end, scale bar, 1 mm (new; photo provided by F. VandenBerg).

Psigraptus JACKSON, 1967, p. 314 [**P. arcticus;* OD] [=*Yukonograptus* LIN, 1981, p. 244, English text p. 261 (type, *Psigraptus lenzi* JACKSON, 1967, p. 319, OD), syn. by RICKARDS & others, 1991, p. 249; =*Muenzhigraptus* ZHAO & ZHANG, 1985, p. 16 (type, *M. sinicus,* OD), syn. by RICKARDS & others, 1991, p. 249; =*Diphygraptus* ZHAO & ZHANG, 1985, p. 19, (type, *D. reclinatus,* OD), syn. by RICKARDS & others, 1991, p. 249; =*Hunjiangograptus* ZHAO & ZHANG, 1985, p. 20, (type, *H. typicus,* OD); =*Holopsigraptus* ZHAO & ZHANG, 1985, p. 20 (type, *H. hunjiangensis,* OD), syn. by RICKARDS & others, 1991, p. 249; =*Clonograptus* (*Neoclonograptus*) ZHAO & ZHANG, 1985, p. 21, *nom. nud.,* herein]. Reclined multiramous to pauciramous anisograptid with partly isolated metasicula and metathecae; proximal end biradiate with short, first-order stipes; bithecae present, but variably developed; autothecae tubular, without rutellum, considerably curved when aperturally isolated. *Lower Ordovician* (*upper Tremadocian, Psigraptus* Biozone): Australia, China, South Korea, Canada.——FIG. 164,*3a*. **P. arcticus,* holotype, GSC 21248, scale bar, 1 mm (new).——FIG. 164,*3b*. *P. lenzi* (JACKSON), holotype, GSC 21253, scale bar, 1 mm (new).——FIG. 164,*3c*. *P. hunjiangensis* (ZHAO & ZHANG), holotype, scale bar, 1 mm (new).——FIG. 164,*3d*. *P. reclinatus* (ZHAO & ZHANG), holotype, scale bar, 1 mm (new).——FIG. 164,*3e*. *P. typicus* (ZHAO & ZHANG), holotype, scale bar, 1 mm (new).——FIG. 164,*3f*. *P. sinicus* (ZHAO & ZHANG), holotype, scale bar, 1 mm (new).

Radiograptus BULMAN 1950, p. 89 [**R. rosieranus;* OD]. Triradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; dissepiments present. [Taxon may be synonymous to *Rhabdinopora.*] *Lower Ordovician* (*lower Tremadocian,* ?*Anisograptus matanensis* Biozone): Canada.——FIG. 161,*3*. **R. rosieranus,* holotype, GSC 9871, Cap de Rosier, Gaspe Peninsula, Quebec, Canada, scale bar, 10 mm (Bulman, 1950, pl. 6).

Sagenograptus OBUT & SOBOLEVSKAYA, 1962, p. 74 [**S. gagarini;* OD] [=*Araneograptus* ERDTMANN & VANDENBERG, 1985, p. 53 (type, *Dictyonema macgillivrayi* T. S. HALL, 1897, p. 15, OD, =*Dictyonema grande* HALL, 1892); =*Nyssenia* SOUGY, 1964, p. 187 (type, *N. zemmourensis,* OD), syn. by GUTIÉRREZ-

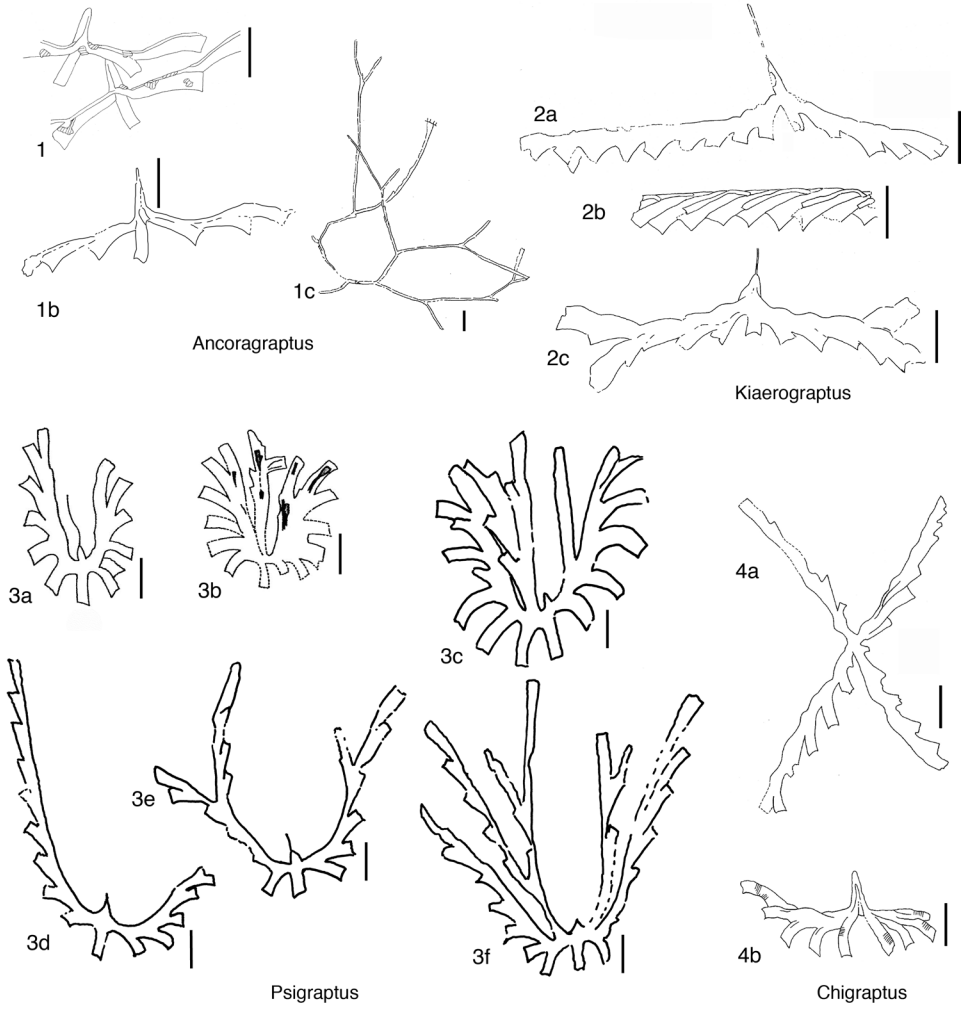


FIG. 164. Anisograptidae (p. 260–261).

MARCO & ACENOLAZA, 1987, p. 325]. Robust, possibly biradiate, multiramous tubarium with subhorizontal to pendent habit; stipes connected with dissepiments; presence of bithecae uncertain. *Lower Ordovician* (*upper Tremadocian, Sagenograptus murrayi* Biozone–*lower Floian, Tetragraptus approximatus* Biozone): Morocco, Australia, New Zealand, UK, Germany, Norway, Sweden, Canada, Russia, Bolivia, Argentina.——FIG. 165*a,c–d. S. macgillivrayi* (T. S. HALL); *a,* NMV P13126, Lancefield Quarry near Lancefield, Victoria, Australia, scale bar, 10 mm; *c,* NMV P73461, proximal end in lateral view, scale bar, 1 mm; *d,* NMV P13127, proximal end of lectotype (selected herein); (new; photos provided by A. VandenBerg).——FIG. 165*b.* **S. gagarini,* holotype, 5/8310, scale bar, 5 mm (Sobolevskaya, 2011, pl. 2,*5*).

Staurograptus EMMONS, 1855, p. 108, original spelling as *Staurograpsus* changed in ICZN, Opinion 650, 1963 [**S. dichotomus;* M] [=*Aletograptus* OBUT & SOBOLEVSKAYA, 1962, p. 76 (type, *A. hyperboreus,* OD), syn. by COOPER & others, 1998, p. 21]. Quadriradiate anisograptid with horizontal to subhorizontal, multiramous to pauciramous tubarium; distal dichotomies irregularly spaced; dissepiments rare and scattered distally in some mature and gerontic specimens of early species, otherwise lacking altogether. *Lower Ordovician* (*lower Tremadocian, Rhabdinopora proparabola* Biozone–*Rhabdinopora campanulatum* Biozone): worldwide.——FIG. 161,*2a.* **S. dichotomous,* type specimen whereabouts unknown, scale bar, 5 mm (Feng, Erdtmann, & Zhang, 2005, p. 1013).——FIG. 161,*2b. S. hyperboreus* (OBUT & SOBOLEVSKAYA,

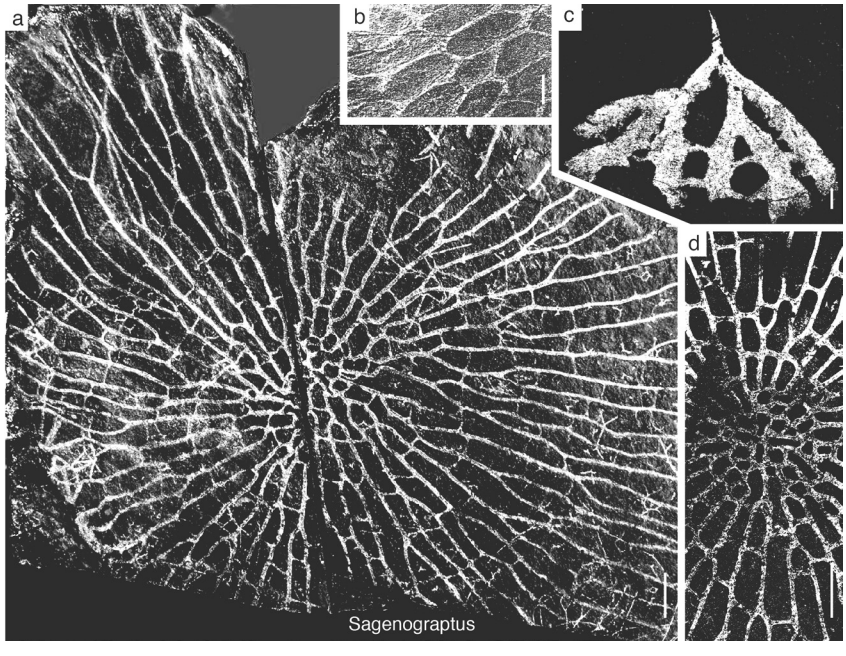


FIG. 165. Anisograptidae (p. 262).

1962), holotype, CGMSP 8310/11, scale bar, 5 mm (Feng, Erdtmann, & Zhang, 2005, fig. 11C).

Stellatograptus ERDTMANN, 1967, p. 343 [**S. stellatus;* M]. Multiramous ?anisograptid with proximally concentrated dichotomies; distal stipes long and rarely branching; proximal development and thecal style unknown; strong cortical overgrowth of proximal end. *Lower Ordovician* (*upper Tremadocian,* ?*Aorograptus victoriae* Biozone): Canada (Quebec).——FIG. 162,*3*. **S. stellatus,* holotype, 1341 at Laval University, Quebec City, material now at Geological Survey of Canada, but no GSC numbers given (personal communication, Michelle Coyne, GSC, Ottawa, March 2014), 1.2 miles downstream from the wharf at St. Michel de Bellechasse, Quebec, Canada, scale bar, 5 mm (Erdtmann, 1967, p. 344, fig. 4).

Toyenograptus LI 1984, p. 579 (English text p. 584) [**Anisograptus isolatus* BULMAN, 1954, p. 32; OD]. Triradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; thecal apertures isolated. *Lower Ordovician* (*lower Tremadocian, Anisograptus matanensis* Biozone): Norway.——FIG. 161,*6*. **T. isolatus* (BULMAN), holotype, PMO 61876, Tøyen, Oslo, Norway, scale bar, 5 mm (Bulman, 1954, fig. 13).

Triograptus MONSEN 1925, p. 169 [**T. osloensis;* OD]. Triradiate anisograptid; tubarium comprised of three horizontal, undivided stipes with distinct lateral curvature; details of thecae unknown. *Lower Ordovician* (*upper Tremadocian, Kiaerograptus kiaeri* Biozone): Norway, ?Argentina.——FIG. 161,*7*. **T. osloensis*, lectotype (selected herein), PMO 60232, scale bar, 5 mm (Monsen, 1925, pl. 4,*2*).

Triramograptus ERDTMANN in COOPER & others 1998, p. 27 [**T. atavus;* OD]. Robust, triradiate, reclined anisograptid with three stipes; mature specimens typically with long nema. *Lower Ordovician* (*lower Tremadocian, Rhabdinopora flabelliformis parabola* Biozone): Canada (western Newfoundland).——FIG. 161,*4a–b*. **T. atavus; 4a,* holotype, GSC 115854; *4b,* GSC 115857, large specimen; scale bars, 1 mm (Cooper & others, 1998, fig. 23a and 23d, respectively).

SUBORDER SINOGRAPTINA

Jörg Maletz, Yuandong Zhang, and Alfons H. M. VandenBerg

Suborder SINOGRAPTINA Mu, 1957

[Sinograptina MU, 1957, p. 387; *nom. transl.* MALETZ, ZHANG, & VANDENBERG, 2018, p. 1; *ex* Sinograptidae MU, 1957, p. 387] [=cohort Pan-Sinograpta MALETZ, CARLUCCI, & MITCHELL, 2009, p. 11]

Planktonic graptoloids with multiramous to single-stiped, horizontal to subhorizontal tubarium; sicula generally nearly parallel sided and without rutellum, oriented perpendicular to stipes; proximal development isograptid, dextral or sinistral with distinct asymmetry of the crossing canals, lost in derived forms; artus-type development in derived taxa; origin of th1[1] in middle part of prosicula in early taxa, but generally in lower part of prosicula, rarely in metasicula; thecal style varies from simple dichograptid with gradually widening thecae to forms with distinctly differentiated pro- and metathecae; thecal elaborations such as prothecal folds, lateral apertural lappets, rutella or spines common; fusellum normal to strongly reduced and possibly lacking in some (Abrograptidae). *Lower Ordovician* (*upper Tremadocian, Sagenograptus murrayi* Biozone)–*Upper Ordovician (Sandbian, Climacograptus bicornis* Biozone): worldwide.

INTRODUCTION

The maeandrograptid proximal symmetry of the Graptodendroidina (Fig. 166.4) is retained in the Sinograptina, but the orientation of the sicula is changed from an oblique position to a vertical position (Fig. 166.1–166.2). The proximal development of the early members of the Sinograptina is characterized by very slender crossing canals and slender prothecal tubes with considerably widening metathecae. It bears some similarity to the features of the Graptodendroidina, with their typical asymmetrical development of the slender crossing canals, but lacks the typical bithecae of the Graptodendroidina. In all taxa, the first crossing canal diverges from the sicula at a point distinctly higher on the metasicula than the second crossing canal. The first crossing canal grows from its origin obliquely downward and across the reverse side of the sicula. Its ventral side touches the dorsal side of the sicular aperture, where it typically bends considerably to form the horizontal stipe (Fig. 166.1). The second crossing canal grows horizontally across the metatheca of th1[1] (Fig. 166.2). Both crossing canals are slender and the thecae widen only distally, toward the apertures in *Paradelograptus*.

MALETZ, CARLUCCI, and MITCHELL (2009, p. 11) defined the subcohort Pan-Sinograpta as the group comprising the common ancestor of *Nicholsonograptus fasciculatus* (NICHOLSON, 1869)—the first species with a slender sicula and parallel-sided prosicula—and all its descendants, based on the cladistic diagram they provided. According to the authors, the cohort Pan-Sinograpta is a sister group to the cohort Pan-Reclinata, differing mainly in the development of the sicula and the shape and position of the crossing canals. The internal structure of the clade is not well resolved, but a number of distinct groups are present (MALETZ, CARLUCCI, & MITCHELL, 2009). Derived forms tend to be strongly modified and may be difficult to classify. The Sinograptidae is the only group to appear as distinct in the cladistic analysis of MALETZ, CARLUCCI, and MITCHELL (2009), however it included the genus *Maeandrograptus,* herein referred to the Sigmagraptidae (Fig. 167). The genus *Acrograptus,* which they included in the stem-reclinatids (suborder Dichograptina, herein) as a sister to *Didymograptellus* TZAJ, 1969, is now referred to the Sigmagraptidae, based on the proximal development. The genus *Perissograptus* with its four reclined stipes is considered to be a close relative to *Maeandrograptus.*

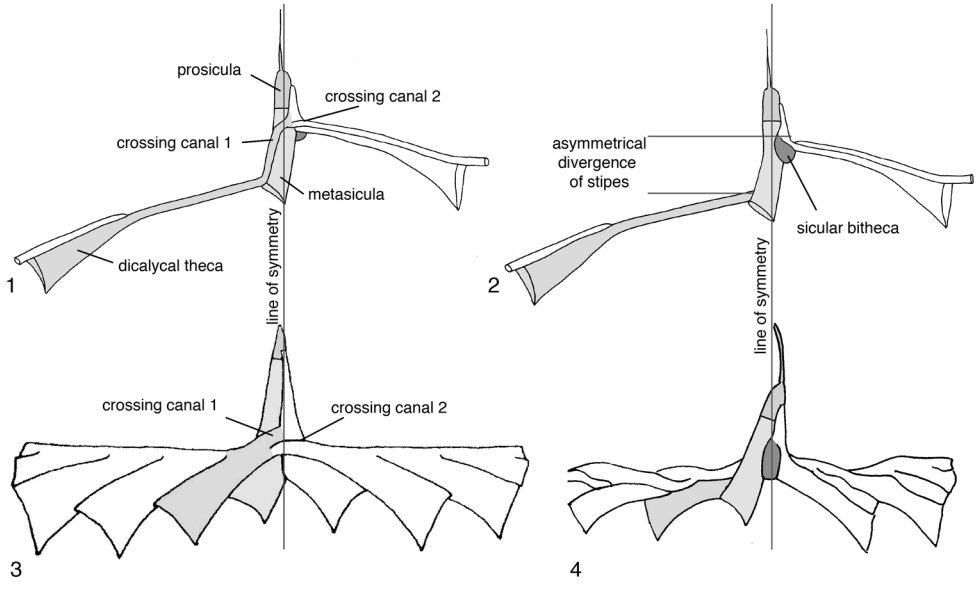


FIG. 166. Sinograptid (*1–2*) and dichograptid (*3–4*) proximal ends. *1–2, Paradelograptus onubensis* ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987; *1,* reverse view, dextral; *2,* obverse view, sinistral, showing sicular bitheca; *3, Expansograptus holmi* (TÖRNQUIST, 1901), reverse view, dextral, showing inclination of sicula; *4, Kiaerograptus*? *supremus* LINDHOLM, 1991, obverse view, sinistral, showing strong inclination of sicula (new).

TAXONOMY OF THE SINOGRAPTINA

The differentiation of the Sinograptina into families, as proposed herein, is based mainly on proximal-end features. The older (upper Tremadocian to Darriwilian) Sigmagraptidae have an asymmetrical proximal-end development with fairly simple thecal styles. The younger (largely Darriwilian) Sinograptidae possess a symmetrical development of the crossing canals and a more complex thecal style with prothecal folds, and some may even have metathecal folds. The Abrograptidae is differentiated by the reduction of the fusellum. However, whether it constitutes a monophyletic family is uncertain, because detailed tubarium structures are unknown for most members. The Thamnograptidae are referred to the Sinograptina as *incertae sedis,* as they share similarities in their thecal development. However, the proximal end of the Thamnograptidae is known only from poorly preserved specimens of *Wuninograptus* NI, 1981.

Family SIGMAGRAPTIDAE Cooper & Fortey, 1982

[Sigmagraptidae COOPER & FORTEY, 1982, p. 259] [*nom. transl.* FORTEY & COOPER, 1986, p. 652; *ex* Sigmagraptinae COOPER & FORTEY, 1982, p. 259] [incl. Goniograptidae YU & FANG, 1979, p. 441; Azygograptinae MU, 1950b, p. 176; Kinnegraptidae MU, 1974, p. 231; Prokinnegraptidae YU & FANG, 1979, p. 441]

Multiramous to one-stiped, reclined to horizontal and pendent tubaria; colony biradiate with asymmetrical placing of first-order stipes; sicula parallel sided or nearly parallel sided with parallel-sided prosicula; proximal development isograptid, dextral or sinistral, or of artus-type development in derived taxa; origin of first theca in median part of prosicula in early taxa, in lower part of prosicula in younger ones; crossing canals more slender than in Dichograptina; thecae simple or with complex and elaborate apertures, slender and sometimes elongated. *Lower Ordovician* (*upper Tremadocian, Sagenograptus murrayi* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.

COOPER and FORTEY (1982) introduced the subfamily Sigmagraptinae for gracile

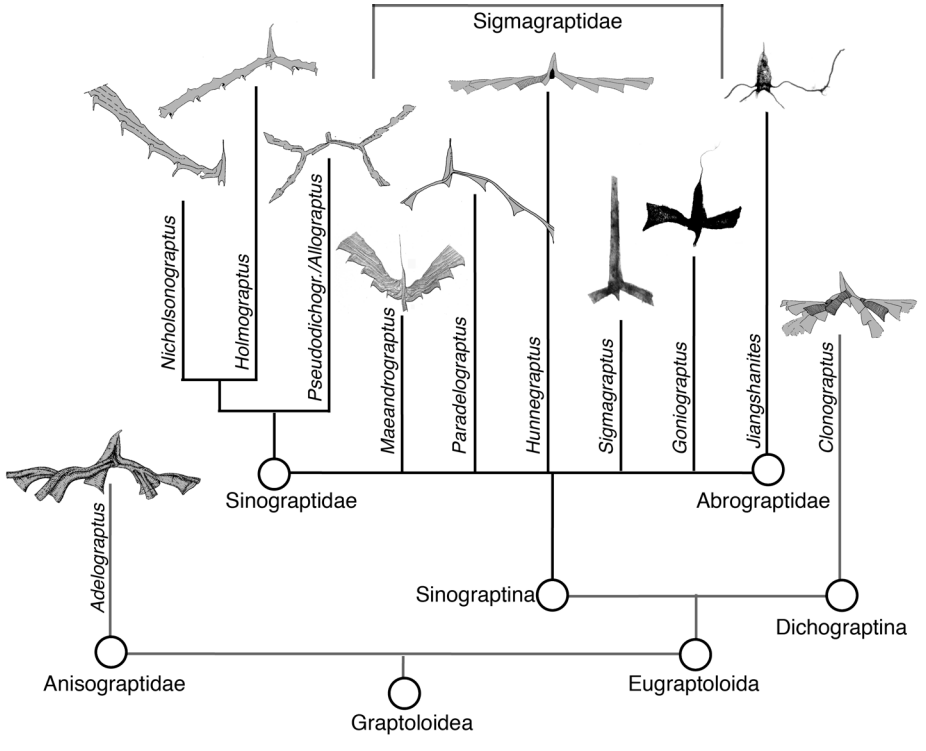


FIG. 167. The Sinograptina (new; based on diagram in MALETZ, CARLUCCI, & MITCHELL, 2009, fig. 2).

dichograptid graptolites with an asymmetrical proximal end and a long and slender sicula. The earliest sigmagraptid in the current interpretation appears to be the genus *Paradelograptus* from the upper Tremadocian *Sagenograptus murrayi* Biozone, representing the first group of graptolites in which the thecae became differentiated into distinct pro- and metathecae. The Sigmagraptidae retain the asymmetrical divergence of the stipes from their ancestors, but change the orientation of the sicula. The widening cone of the sicula of the Graptodendroidina is modified and the metasicula in the Sigmagraptidae is more or less parallel sided with little widening from the aperture of the prosicula. Rutella are lacking in early Sigmagraptidae, but elaborate rutella are present in some derived forms (i.e., *Kinnegraptus*).

MORPHOLOGY

The Sigmagraptidae includes taxa with a single stipe to taxa with numerous branching divisions. Branching appears highly irregular in early taxa, but the genera *Goniograptus* and *Sigmagraptus* possess very regular monoprogressive branching. In general, the colonies are subhorizontal to umbrella-shaped, but reclined taxa also occur, and pendent taxa are rare. All taxa with more than one stipe have th1[2] as the only proximal dicalycal theca or lack proximal dicalycal thecae. The position of later dicalycal thecae is adventitious and irregular in many species, and the position of a dicalycal theca cannot be taken as a character of higher taxonomic value.

The sicula is highly variable in the Sigmagraptidae (Fig. 168), but species with a parallel-sided pro- and metasicula prevail (Fig. 168.1). In some genera, the prosicula is relatively large, forming more than half of the length of the sicula. Considerably elongated siculae are present in some *Maeandrograptus* species and in *Sigmagraptus*. *Perissograptus* is a strongly derived genus sharing numerous tubarium characters with

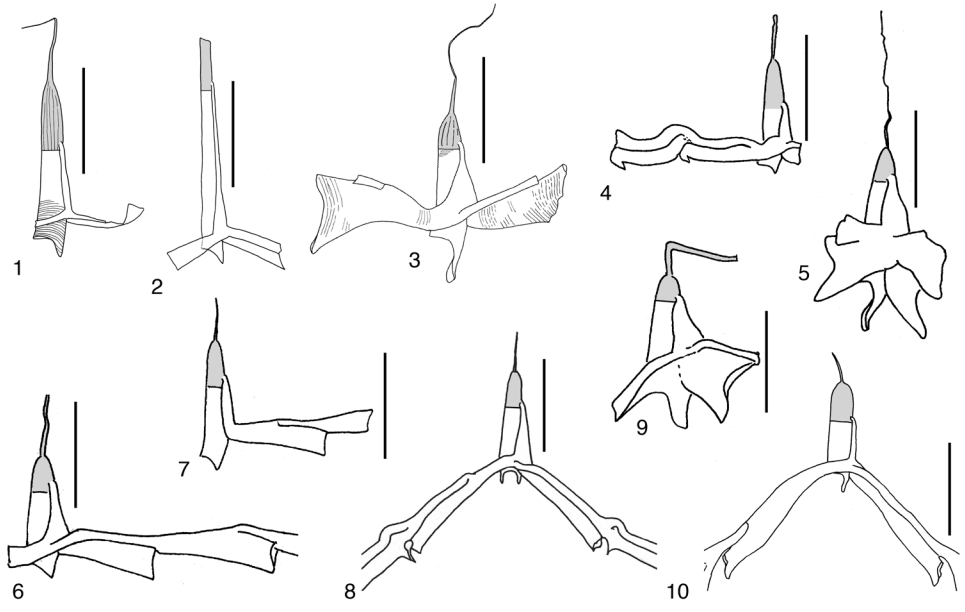


FIG. 168. Sicular and proximal development in the Sinograpta, prosicula shown in *gray. 1,* Sigmagraptine indet., GSC 81787a, showing long mitre-shaped prosicula with few longitudinal rods and isograptid, dextral development (new); *2, Sigmagraptus praecursor* RUEDEMANN, 1904, GSC 139255, CHN 11.4E, Cow Head Group, western Newfoundland (new); *3, Goniograptus thureaui* (M'COY, 1876), GSC 125786, proximal end with typical rutellate sicula and small prosicula (new); *4, Maeandrograptus sinuosus* MALETZ, 2004, holotype, GSC 125764, Sigmagraptidae (MALETZ, 2004, fig. 5I); *5,* ?*Eotetragraptus* sp. cf. *E. spinosus* (SPJELDNAES, 1953), GSC 125752, Sigmagraptidae (MALETZ, 2004, fig. 2V); *6,* GSC 125806, sigmagraptine sp. indet. (Maletz, 2004, fig. 6K); *7,* GSC 125810, sigmagraptine sp. with one single stipe (Maletz, 2004, fig. 6P); *8, Holmograptus* sp., Sinograptidae, reconstruction (new); *9, Keblograptus geminus* MALETZ, 2004, GSC 125778, Sigmagraptidae (Maletz, 2004: fig. 4C); *10, Anomalograptus reliquus* (CLARK, 1924), Sinograptidae, reconstruction (new). All scale bars, 1 mm.

Maeandrograptus but developing a reclined, four-stiped colony with an aperturally isolated, parallel-sided sicula. Siculae with strongly widening, triangular shapes develop in a number of genera (*Keblograptus, Kinnegraptus,* abrograptids) (Fig. 168.9). The prosicula has numerous longitudinal rods in many taxa, but the exact development in others is unknown. WILLIAMS and CLARKE (1999) illustrated prosiculae of *Goniograptus* sp. with few (~8–10) longitudinal ridges. There is no information on the differentiation of the conus and cauda in the prosicula of the Sigmagraptidae. The helical line is distinctive in chemically isolated specimens and in relief specimens of *Paradelograptus* in which the prosicular fusellar band is wider than the subsequent metasicular fusellar half rings (see *Adelograptus filiformis* WILLIAMS & STEVENS, 1991).

The proximal development type is isograptid, dextral in most forms (Fig. 168–Fig.169), but a sinistral development has been recognized in *Paradelograptus* (see ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987) (Fig. 169.1). SKOGLUND (1961) described chemically isolated material of the genus *Kinnegraptus* from the Dapingian of Sweden with an artus-type development and a metasicular origin of th1[1]. The proximal development is uncertain in many slender sigmagraptines so that the taxonomic interpretation may be questionable. The development in *Acrograptus affinis* (NICHOLSON, 1869) can be interpreted as of artus-type, based on a possible topotype specimen illustrated by RUSHTON (2000a). It has a distal origin of th2[2] on th2[1], thus the dicalycal theca must be th1[1].

The origin of th1[1] is in the middle part of the prosicula in some *Paradelograptus* speci-

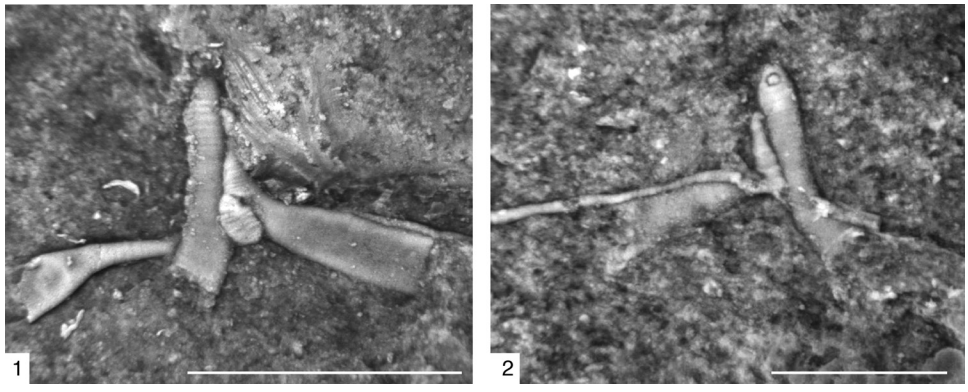


FIG. 169. Proximal development in *Paradelograptus* ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987. *1*, specimen on slab with GSC 118739, obverse view showing sicular bitheca, sinistral development (*Adelograptus antiquus* T. S. HALL, 1899 in Jackson & Lenz, 2000, fig. 7A); *2*, GSC 118750, reverse view, sinistral development, crossing canal of th1[1] broken off (*P. onubensis* ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987 in Jackson & Lenz, 2000, fig. 11A); specimens from Road River Formation, Yukon, Canada; scale bars, 1 mm (new).

mens known from relief material (Fig. 169). In most taxa, however, the origin of th1[1] is in the lower part of the prosicula (WILLIAMS & STEVENS, 1988; MALETZ, 2004). SKOGLUND (1961, fig. 5B) described and illustrated a high prosicular origin of th1[1] in *Prokinnegraptus multiramosus* (SKOGLUND, 1961), but this is based on fragmentary material and additional specimens are not available. This feature might indicate a secondarily derived condition.

The presence of bithecae is very difficult to verify in early members of the Sigmagraptidae because the stipes are extremely slender and thecal details are difficult to see. A sicular bitheca is present in some early species of the genus *Paradelograptus* (Fig. 166, Fig. 169.1), but not in derived taxa of the genus. The sicular bitheca is short and wide and opens in the crotch between the sicula and th1[1] with the aperture directed toward the reverse side of the colony. Thecal bithecae have not been recognized in *Paradelograptus* and are unlikely to be present due to the dorsal origins of the very slender prothecae.

The Sigmagraptidae are characterized by the ability to generate a variety of thecal elaborations. The thecal length may vary considerably along the stipes in a number of taxa. Because the thecae generally have a low overlap and inclination, lengthening of thecae and increase of thecal overlap provides a means of stability and rigidity for the stipes. A cross section of a distal stipe can cut through five or six thecae in mature specimens of *Maeandrograptus*. In *M. leptograptoides* (MONSEN, 1937), thecal overlap increases distally and stipes widen considerably; whereas in the robust *M. schmalenseei*, thecal length remains constant, with overlap remaining at three thecae. The changes in seen in *M. leptograptoides* occur independently in the sinograptid genera *Holmograptus* and *Nicholsonograptus*, in which thecal overlap is low in the proximal portion of the stipe but very high in the extremely robust distal portion. The thecal apertures can be simple as in *Paradelograptus*, but considerable elaborations are present in some younger forms.

Branching in the Sigmagraptidae is either progressive with regular or irregular dichotomous branching (*Paradelograptus*, *Anomalograptus*, *Allograptus*) or monoprogressive as exemplified by the genera *Goniograptus* and *Sigmagraptus*. Dichotomous lateral branching was reported in *Trichograptus,* but no cladial branching has been observed.

The genus *Azygograptus* lost all capacity for branching and bears a single, typically curved, slender stipe. MALETZ (2004) described an unusual sigmagraptine taxon without a

proximal dichotomy as sigmagraptine sp. 3. The species has a typical slender sigmagraptine sicula with low prosicular origin of th1[1]. The first dichotomy is formed as a distal dichotomy only after two successive monocalycal thecae have developed from th1[1].

The Sigmagraptidae are herein differentiated into a number of informal groups, but only for easier reference; no taxonomic implications are intended and a taxonomic differentiation of subgroups has to be left to the future when better material is known.

The following are multiramous to singlestiped genera with simple thecae.

Sigmagraptus Ruedemann, 1904, p. 701 [**S. praecursor;* OD] [=*Hemigoniograptus* Jin & Wang, 1977, p. 81 (type, *H. declinatus,* OD), syn. by Mu & others, 2002, p. 329]. Sigmagraptines with single order of progressive branching followed by monoprogressive branching, forming two main zigzag-shaped stipes and numerous lateral stipes; proximal end isograptid, dextral, with long and slender sicula; thecae simple with low thecal overlap and without apertural elaborations. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone–*Didymograptellus bifidus* Biozone): Australia, New Zealand, China, Canada, USA, Norway.——Fig. 170,*4a–c*. **S. praecursor; 4a,* lectotype, NYSM 16006, Deep Kill, New York, USA (Cooper & Fortey, 1982, fig. 60c); *4b,* holotype of *Hemigoniograptus declinatus* Jin & Wang, 1977, IV75045 (repository unknown), Qiaotingzhe Formation, central Hunan, China (Jin & Wang, 1977, fig. 7,*1*); *4c*, GSC 79889, mature specimen, Cow Head Group, western Newfoundland, Canada (Williams & Stevens, 1988, fig. 75H). All scale bars, 1 mm.

Acrograptus Tzaj 1969, p. 142 [**Didymograptus affinis* Nicholson, 1869, p. 240; OD]. Slender sigmagraptine with two horizontal to declined stipes; sicula small, triangular; proximal development artus type; thecae slender and with low thecal overlap or with distally increasing overlap. *Middle Ordovician* (*Darriwilian,* ?*Levisograptus dentatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——Fig. 171,*4a–b*. **A. affinis* (Nicholson); *4a,* lectotype (selected by Elles & Wood, 1901, p. 24), NHMUK PI Q.3108; *4b,* possible topotype, NHMUK PI Q.5858a, low relief showing th2[1] originating on distal end of th1[1] (*arrow*), indicating artus-type development; Llanvirn (Darriwilian), Tarn Moor Formation, Aik Beck, east of Ullswater, Cumbria, UK, scale bars, 1 mm (Rushton, 2000a, Atlas, Folio 1.1).

Azygograptus Nicholson & Lapworth in Nicholson, 1875, p. 269 [**A. lapworthi;* OD] [=*A.* (*Eoazygograptus*) Obut & Sennikov, 1984a, p. 100 (type, *A. coelebs* Lapworth, 1880a, p. 159, OD, syn. by Beckly & Maletz, 1991, p. 896); =*A.* (*Metazygograptus*) Obut & Sennikov, 1984a, p. 101 (type, *A. suecicus* Moberg, 1892a, p. 342, OD, syn. by Beckly & Maletz, 1991, p. 896)]. Singlestiped tubarium; th1[1] originating from metasicula, growing downward first or immediately outward from lower part of metasicula; stipe either straight or dorsally curved; sicula straight to slightly curved, moderate widening toward aperture; thecae simple, elongate, and inclined at low angle to the dorsal margin and with low thecal overlap; prothecal folds in one species. [The type material of *A. lapworthi*, from Hodgson How Quarry (1 km west of Keswick, UK), has not yet been identified]. *Lower Ordovician* (*upper Floian, Tetragraptus phyllograptoides* Biozone)–*Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone): China, Czech Republic, UK, Germany, Norway, Spain, Sweden, Canada, Argentina, Bolivia.——Fig. 171,*2a–b*. *A. suecicus; 2a,* lectotype, SGU 5247; *2b,* paratype, SGU 5248; Killeröd, Scania, Sweden, scale bars, 1 mm (Moberg, 1892a, pl. 8,*1* and 8,*2,* respectively).——Fig. 171,*2c*. **A. lapworthi,* NIGP 32222, southwest China, scale bar, 1 mm (on slab with Mu & others, 1979, pl. 38,*11*).

Catenagraptus VandenBerg, 2018b, p. 4 [**C. communalis;* OD]. Assemblages of pseudotubaria resembling those of *Azygograptus* but linked by thread-like structures (aulons) of variable length that join fallosiculae to adjacent pseudotubaria. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone): Australia.——Fig. 170,*6*. **C. communalis,* holotype, NMV P318828, Victoria, Australia, scale bar, 1 mm (VandenBerg, 2018b, fig. 2D).

Etagraptus Ruedemann, 1904, p. 644 [**Tetragraptus* (*Etagraptus*) *lentus;* M]. Four-stiped to multiramous horizontal sigmagraptines with simple thecae and low thecal inclination; proximal development isograptid, dextral; branching regular. *Lower Ordovician* (*Floian, Didymograptellus bifidus* Biozone)–*Middle Ordovician* (*Dapingian, Isograptus maximodivergens* Biozone): Australia, New Zealand, Norway, Sweden, China, Canada, USA.——Fig. 170,*2a*. **E. lentus,* syntype, NYSM 6064, scale bar, 1 mm (new).——Fig. 170,*2b–c*. *E. tenuissimus* (Harris & Thomas, 1942), holotype, NMV P32110, along with detail of thecal style (*c*), Chewtonian 2 (Lower Ordovician) Campbelltown, Allotment 41B, Victoria, Australia; scale bars, 1 mm (VandenBerg, 2008a, Atlas, Folio, 2.35). Specimen was subsequently prepared and has much longer distal stipes.

Jiangnanograptus Xiao & Chen, 1990, p. 99 [**J. undulatus;* OD]. Multiramous sigmagraptines with two declined to reclined first-order stipes and short first and second branching divisions; third- to fifth-order stipes long and slender; branching appears to be triple due to elongated metathecae; proximal development unknown. *Middle Ordovician* (*lower Dapingian, Azygograptus suecicus* Biozone): China (Jiangnan Region).——Fig. 170,*1*. **J. undulatus*, Yc77-333 (repository of material unknown), Yushan, China, scale bar, 1 mm (Xiao & Chen, 1990, fig. 9).

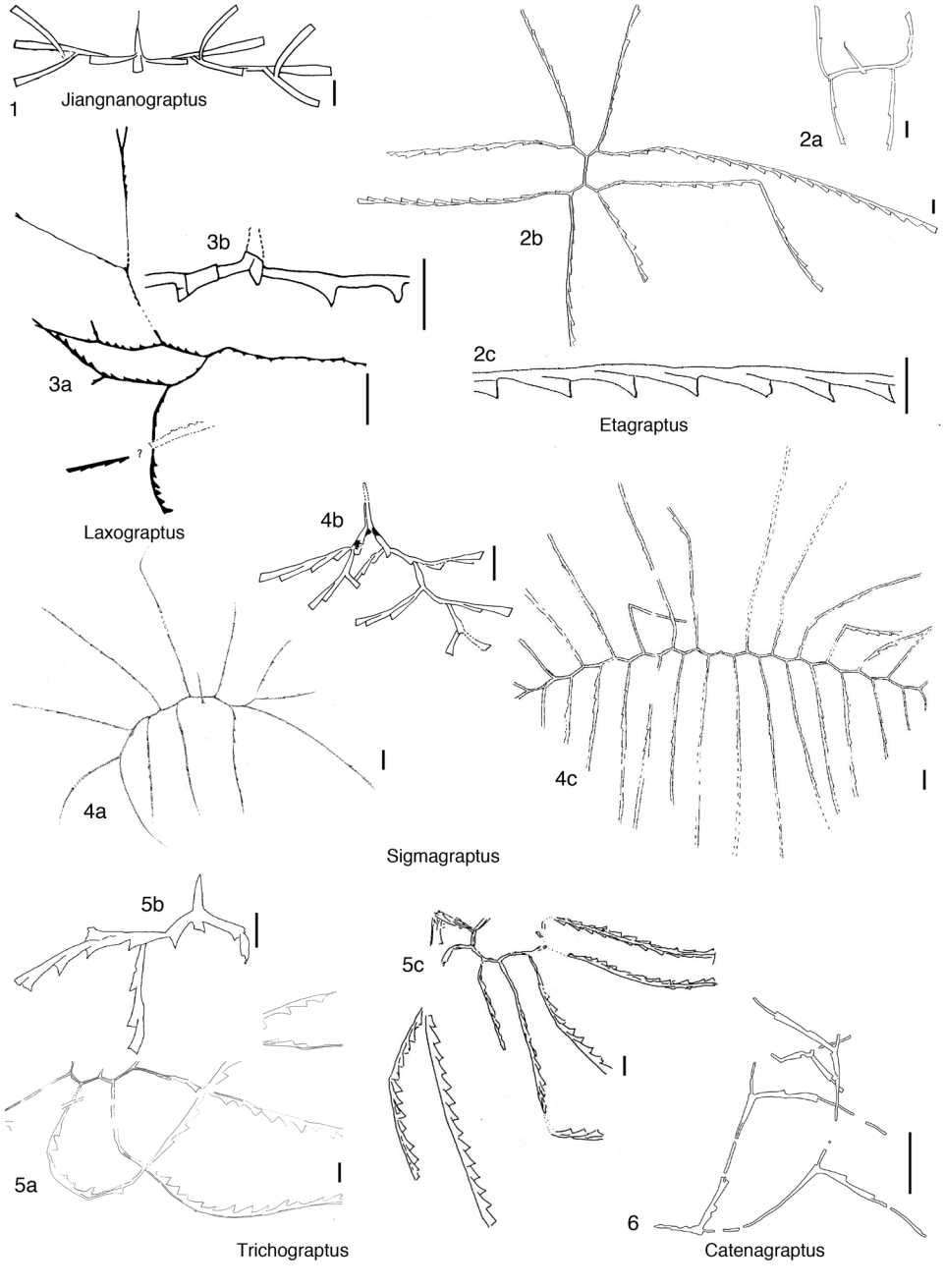


FIG. 170. Sigmagraptidae (p. 270–272).

Laxograptus COOPER & FORTEY, 1982, p. 269 [**Zygograptus irregularis* HARRIS & THOMAS, 1941, p. 310; OD]. Sigmagraptines with stipes of two or more orders in which dichotomies after the first dichotomy are delayed and placed irregularly; progressive branching; thecae simple with low overlap; indistinct rutella in some species. *Lower Ordovician* (*lower Floian, Paratetragraptus approximatus* Biozone)–?*Middle Ordovician* (*Dapingian, Isograptus maximodivergens* Biozone): worldwide.——FIG. 170,*3a–b*. **L. irregularis* (HARRIS & THOMAS), holotype, NMV P32124; *3a,* full

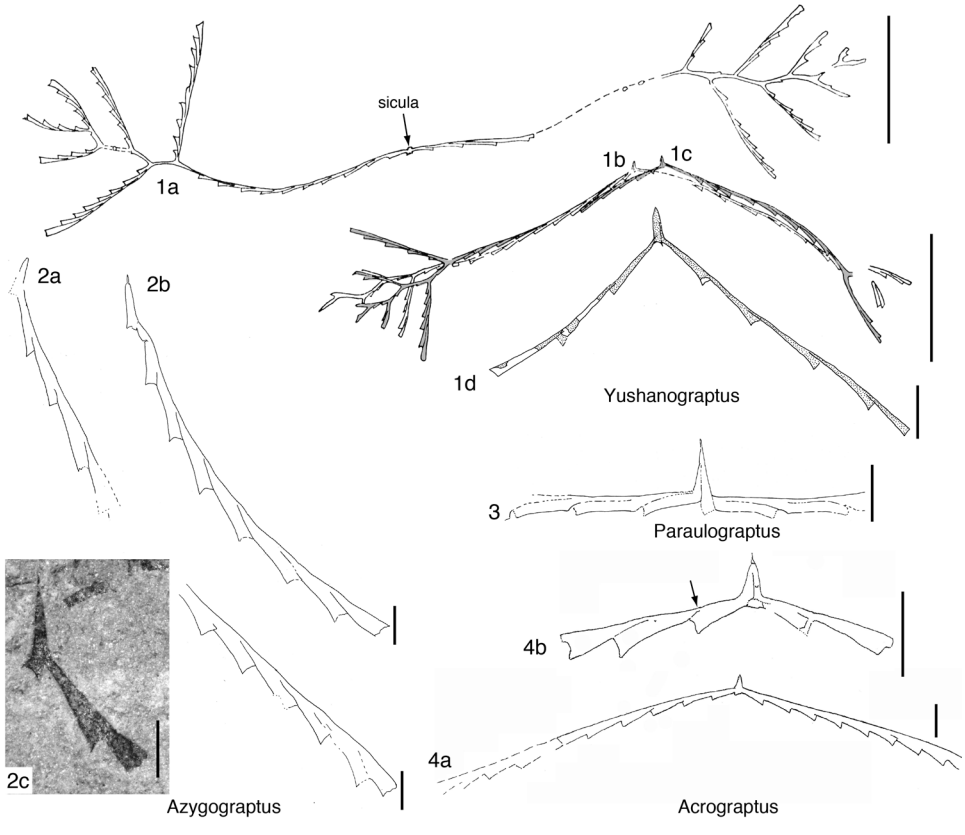


FIG. 171. Sigmagraptidae (p. 270–272).

specimen, scale bar, 5 mm; *3b,* close-up showing proximal end of holotype; Scotts Gully, Castlemaine, Victoria, Australia, scale bar, 1 mm (Rickards & Chapman, 1991, fig. 73 and 61, respectively).

Paraulograptus BOUČEK, 1973, p. 74 [**P. expectatus;* OD]. Two-stiped horizontal sigmagraptines with low-inclined, geniculate thecae and high thecal overlap distally. *Middle Ordovician* (*Darriwilian, Corymbograptus retroflexus* Biozone, *Expansograptus ferrugineus* horizon): Czech Republic.——FIG. 171,*3. *P. expectatus,* holotype, UUG-BB 85, proximal end, Šarka Formation, Krušná hora, Czech Republic, scale bar, 1 mm (adapted from Bouček, 1973, fig. 23).

Trichograptus NICHOLSON, 1876, p. 248 [**Dichograptus fragilis* NICHOLSON, 1869, p. 232; OD]. Horizontal to subhorizontal sigmagraptine with two curved main stipes; lateral second-order stipes originating on one side of main stipes through normal dichograptid, but lateral branching; proximal development isograptid, dextral, with distinct asymmetry of crossing canals; thecae simple dichograptid, low overlaping tubes. *Lower Ordovician* (*Floian, Baltograptus vacillans* Biozone)–*Middle Ordovician* (*Darriwilian, Didymograptus artus* Biozone): Australia, UK, Ireland, Norway, Argentina.——FIG. 170,*5a. *T. fragilis* (NICHOLSON), holotype, NHMUK PI Q.1, Tarn Moor Formation, Thornship Beck, Shap, Cumbria (Lake District), UK, scale bar, 1 mm (VandenBerg, 2008b, Atlas, Folio 2.26).——FIG. 170,*5b–c. T. dilaceratus* (HERRMANN, 1885), Diabasbrottet, Hunneberg, Sweden; *5b,* MB.G. DI 894/1301-2, small specimen showing sicular shape; *5c*, MB.G. DI 894/1291-1, large specimen showing lateral branching of curved main stipes; scale bars, 1 mm (new).

Yushanograptus CHEN, SUN, & HAN, 1964, p. 236 [**Y. separatus;* OD] [=*Pendeosalicograptus* JIAO, 1981, p. 65 (type, *P. zhejiangensis,* OD), syn. herein]. Multiramous sigmagraptines with long first-order stipes and monoprogressive distal branching; thecal style simple, dichograptid with low thecal overlap. *Middle Ordovician* (*Dapingian, Didymograptus abnormis* Biozone): China.——FIG. 171,*1a–d. *Y. separatus; 1a,* paratype, NIGP 14515; *1b,* paratype, NIGP 14516; *1c,* holotype, NIGP 14514; *1d*, NIGP 168219, AEP 27, proximal end in obverse view; scale bars 1 mm (*1a–1c,* Chen, Sun, & Han, 1964, fig. 1; *1d,* new).

The following are multiramous to two-stiped genera with simple thecae, differenti-

ated rutellum on sicula and typically with lateral lobes.

Eotetragraptus Bouček & Přibyl, 1952a, p. 7 [**Graptolithus quadribrachiatus* Hall, 1858, p. 125; OD]. Four-stiped sigmagraptines with simple, rutellate, commonly considerably curved thecae; stipes pendent to reclined and reflexed, rarely with dorsal spines; short and wide sicula with distinct rutellum and lateral apertural lobes; proximal development isograptid, dextral, with symmetrically placed slender crossing canals; thecal style simple, widening tubes with rutellate apertures, often with slight lateral lobes. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone–*Pterograptus elegans* Biozone): worldwide.——Fig. 172,*4a–b. E. quadribrachiatus* (Hall); *4a,* syntype, GSC 928b, specimen shows the distinct rutellum on the sicula, Lévis, Quebec, Canada, scale bar, 1 mm (new); *4b,* GSC 132327, obverse view of flattened proximal end, Bay Cove, western Newfoundland, Canada, scale bar, 1 mm (new).——Fig. 172,*4c. E. acanthonotus* (Gurley, 1896), scale bar, 1 mm (new; reconstruction based on Maletz, 1997b, fig. 7N).

Goniograptus M'Coy, 1876, p. 129 [**Didymograpsus thureaui;* M]. Sigmagraptines with two orders of progressive branching, followed by unlimited monoprogressive branching forming four zigzag main stipes; proximal end isograptid, dextral; extended rutellum on sicula; thecae dichograptid with short rutella; moderate to high thecal overlap; thecal shape variable, from low inclined and considerably widening to high overlap and strong curvature towards aperture. *Lower Ordovician* (*upper Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, Norway, Sweden, Canada, USA, Argentina.——Fig. 172,*1a–b*. **G. thureaui; 1a*, holotype, NMV P12215; *1b*, GSC 125786, proximal end; scale bars, 1 mm (new).

Harrisgraptus VandenBerg, 2019a, p. 35 [**Didymograptus eocaduceus* Harris, 1933]. Two-stiped tubaria with habit ranging from strongly reclined to horizontal; sicula and proximal thecae adorned with prominent rutella; thecae have curved ventral walls. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone): Australia, New Zealand.[VandenBerg (2019a) referred the genus to the Phyllograptidae.]——Fig. 172,*5a–c. *H. eocaduceus* (Harris), Victoria, Australia; *5a,* NMV P319254, specimen with distally overlapping stipes; *5b,* ectotype, NMV P13800 l; *5c, Didymograptus hemicyclus* Harris, 1933*,* (syn. of *H. eocaduceus*) lectotype, NMV P13797; scale bars, 1 mm (VandenBerg, 2019a, fig. 2F, 2C, and 2H, respectively).

Keblograptus Riva, 1992, p. 316 [**Didymograptus bidens* Keble, 1927, p. 157; OD]. Sigmagraptines with two slender, declined to pendent stipes; sicula short and triangular; sicular aperture with strong rutellum and often with lateral lobes; thecae curved, distinctly widening aperturally and with gentle prothecal folds in some species. *Lower Ordovician* (*upper Floian, Didymograptellus bifidus* Biozone)–*Middle Ordovician* (*lower Dapingian, Isograptus lunatus* Biozone): Australia, New Zealand, China, Norway, Canada, USA.——Fig. 172,*3a. *K. bidens* (Keble), holotype, OU 2512, Cape Providence, Chalky Inlet, Southland, New Zealand, scale bar, 1 mm (Riva, 1992, fig. 2A).——Fig. 172,*3b. K. mendicus* (Keble & Harris, 1934), GSC 81778, proximal end, western Newfoundland, Canada, scale bar, 1 mm (new).——Fig. 172,*3c. K. geminus* Maletz, 2004, holotype, GSC 125734, Martin Point south, western Newfoundland, Canada, scale bar, 1 mm (Maletz, 2004, fig. 5E).

Praegoniograptus Rickards & Chapman, 1991, p. 91 [**Goniograptus thureaui clonograptoides* Harris & Thomas, 1939, p. 55; OD]. Multiramous sigmagraptines with several orders of progressive branching followed by monoprogressive branching; thecae simple with low overlap. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone): Australia (Victoria), Canada (Newfoundland).——Fig. 172,*2*. **P. clonograptoides* (Harris & Thomas), holotype, NMV P32169, Campbelltown, Victoria, Australia, scale bar, 10 mm (new).

The following are genera with long thecal overlap and differentiated apertures, commonly with increasing overlap distally.

Jishougraptus Ge, 1988, p. 208 [**J. mui;* OD]. Sigmagraptines with a single deflexed stipe; dorsal stipe margin somewhat undulate but without pronounced prothecal folds; sicula long and slender with th1[1] origin in middle part of metasicula or close to sicular aperture; thecae long and slender with high overlap and increasing overlap distally; apertural elaborations indistinct; thecae may be geniculate. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*lower Dapingian, Azygograptus suecicus* Biozone or *Baltograptus minutus* Biozone): China, Norway, Sweden.——Fig. 173,*4a–b*. **J. mui; 4a,* juvenile, showing sicula shape; *4b,* holotype, NIGP 104481, fragment showing thecal style; scale bars, 1 mm (new).——Fig. 173,*4c. J. novus* Beckly & Maletz, 1991, paratype, PMO 118.593, latex cast, Tøyen Shale, Oslo, Norway, scale bar, 1 mm (Beckly & Maletz, 1991, pl. 1,*9*).

Maeandrograptus Moberg, 1892a, p. 344 [**M. schmalenseei;* M]. Horizontal to subhorizontal and reclined sigmagraptines with two stipes; stipes increased thecal overlap distally; thecae long and slender; sicula with long and parallel-sided prosicula and long metasicula; aperture of metasicula typically but not necessarily isolated; thecae with rutella and sometimes lateral lappets; prothecal folds and undulating thecae in some species. *Lower Ordovician* (*upper Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*lower Dapingian, Isograptus maximus* Biozone): China, Norway, Sweden, Canada.——Fig. 173*,3a. M. mobergi* (Törnquist, 1901), holotype, LO 1642T, reverse view, drawing of latex cast, Killeröd, Scania, Sweden, scale bar, 1

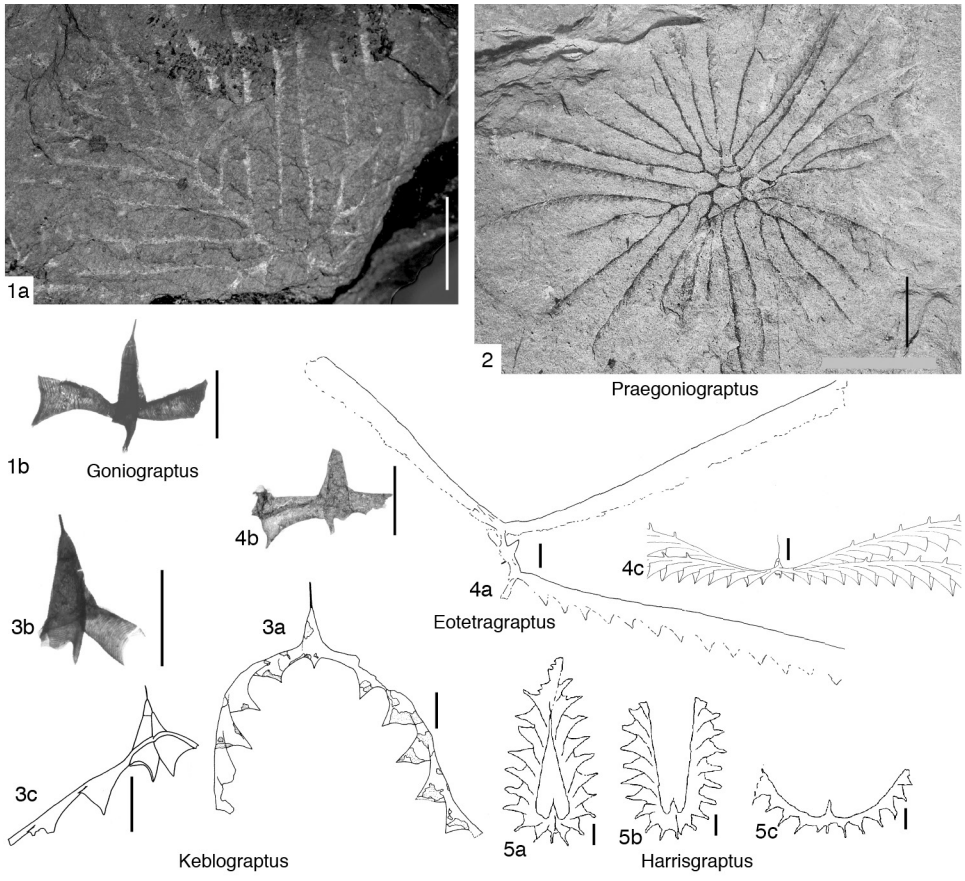


FIG. 172. Sigmagraptidae (p. 273).

mm (new).——FIG. 173,*3b–c. *M. schmalenseei; 3b,* lectotype, SGU 5255, reverse view; *3c,* paratype, SGU 5257, obverse view, showing long sicula; Killeröd, Scania, Sweden, scale bars, 1 mm (Bulman, 1932c, pl. 9).——FIG. 173,*3d. M. leptograptoides* (MONSEN, 1937), PMU 23165/2, reverse view, drawing of latex cast, Nipan, Jemtland, Sweden, scale bar, 1 mm (new).

Oslograptus JAANUSSON, 1965, p. 427 [**O. peculiaris;* M]. Sigmagraptines with a subhorizontal to pendent tubarium; thecal apertures positioned in distinct excavations formed by thecal folding. *Lower Ordovician* (*upper Floian, Didymograptellus bifidus* Biozone): Norway, Canada.——FIG. 173,*1. *O. peculiaris,* holotype, PMO 73669, drawing of latex cast, Old Quarry, Slemmestad, Norway, scale bar, 1 mm (new).

Perissograptus WILLIAMS & STEVENS, 1988, p. 88 [**Tetragraptus pygmaeus* RUEDEMANN, 1904, p. 664; M]. Sigmagraptine with four reclined stipes; proximal end with stipes diverging high on sicula, leaving apertural part of sicula free pending; thecae with distinct rutella. *Lower Ordovician* (*upper Floian, Didymograptellus bifidus* Biozone): Australia, ?China, Canada, USA.——FIG. 173,*2a–c. *P. pygmaeus* (RUEDEMANN); *2a,* lectotype (designated by WILLIAMS & STEVENS, 1988, p. 89), NYSM 6073, Deep Kill, New York, USA, (Ruedemann, 1904, pl. 12,*14*); *2b–c,* GSC 82059, obverse (*b*) and reverse (*c*) views of isolated specimen; all scale bars, 0.5 mm (infrared photos; new).

The following are multiramous to two-stiped genera with distinctly differentiated pro- and metathecae, generally with apertural elaborations (Kinnegraptidae of MU, 1974). VANDENBERG (2019b) referred these taxa to his revised subfamily Kinnegraptinae.

Kinnegraptus SKOGLUND, 1961, p. 391 [**K. kinnekullensis;* OD]. Multiramous to two-stiped sigmagraptines with horizontal to subhorizontal tubarium; proximal end isograptid or artus type, with dextral or sinistral development; origin of th1[1] in prosicula or metasicula; thecae with very slender prothecae and distinctly widening metathecae; strong rutella

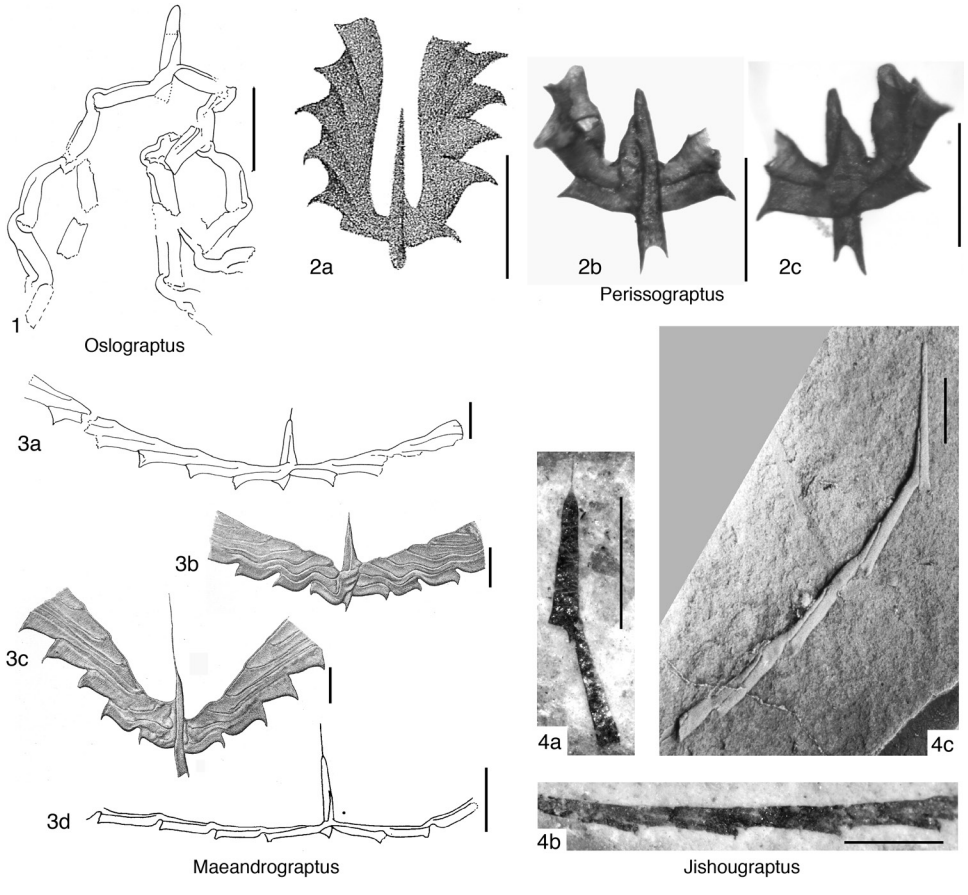


FIG. 173. Sigmagraptidae (p. 273–274).

on all thecae. *Middle Ordovician* (*lower Dapingian, Isograptus victoriae lunatus* Biozone): Norway, Sweden, Canada, Argentina.——FIG. 174,*2a–c. *K. kinnekullensis; 2a,* PMU 23633; *2b,* PMU 23634; *2c,* holotype PMU 23635; Hällekis, Västergötland, Sweden; scale bars, 0.5 mm (Skoglund, 1961, fig. 1B, 1D, and 2A, respectively).

Lignigraptus VANDENBERG, 2019b, p. 25 [**Tetragraptus chapmani* KEBLE & HARRIS, 1934; OD; =*Paradelograptus mosseboensis* ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987, syn. by VANDENBERG, 2019b, p. 27]. Proximal end with characteristic asymmetrical appearance; sicula skewed toward stipe 1; thecae long and slender; metathecal walls may be attenuated, thecal apertures bearing elongate rutellae. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone–*Didymograptellus bifidus* Biozone): Australia, Canada, USA, Sweden, Norway, China.——FIG. 174,*4a–b. *L. chapmani* (KEBLE & HARRIS); *4a,* holotype, NMV P14378, combination of counterparts, Victoria, Australia (new); *4b,* holotype of *Paradelograptus mosseboensis,* MB.G. Di 614/119; scale bars, 1 mm (new).

Paradelograptus ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987, p. 114 [**P. onubensis;* OD]. Multiramous to biramous, horizontal to subhorizontal sigmagraptines with distinct differentiation of thecae; prothecae very slender, metathecae considerably widening; thecal apertures simple and straight to bearing moderate rutellum; bithecae present in earlier species, at least on sicula. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone–*Floian, Tshallograptus fruticosus* Biozone): Australia, New Zealand, China, Sweden, Norway, Scotland, Spain, Canada, USA, Argentina, Bolivia.——FIG. 174,*1a–b. *P. onubensis;1a,* holotype, DPM 4107, scale bar, 1 mm (Erdtmann, Maletz & Gutierrez Marco, 1987, fig. 5A); *1b,* paratype, DPM 4001, large specimen, scale bar, 5 mm (Erdtmann, Maletz, & Gutierrez-Marco, 1987, fig 7C).

Prokinnegraptus MU, 1974, p. 233 [**Kinnegraptus multiramosus* SKOGLUND, 1961, p. 397; OD]. Multiramous sigmagraptines with horizontal to subhorizontal tubarium; proximal end isograptid type, with dextral or sinistral development; origin of $th1^1$ high in prosicula; thecae with very low thecal

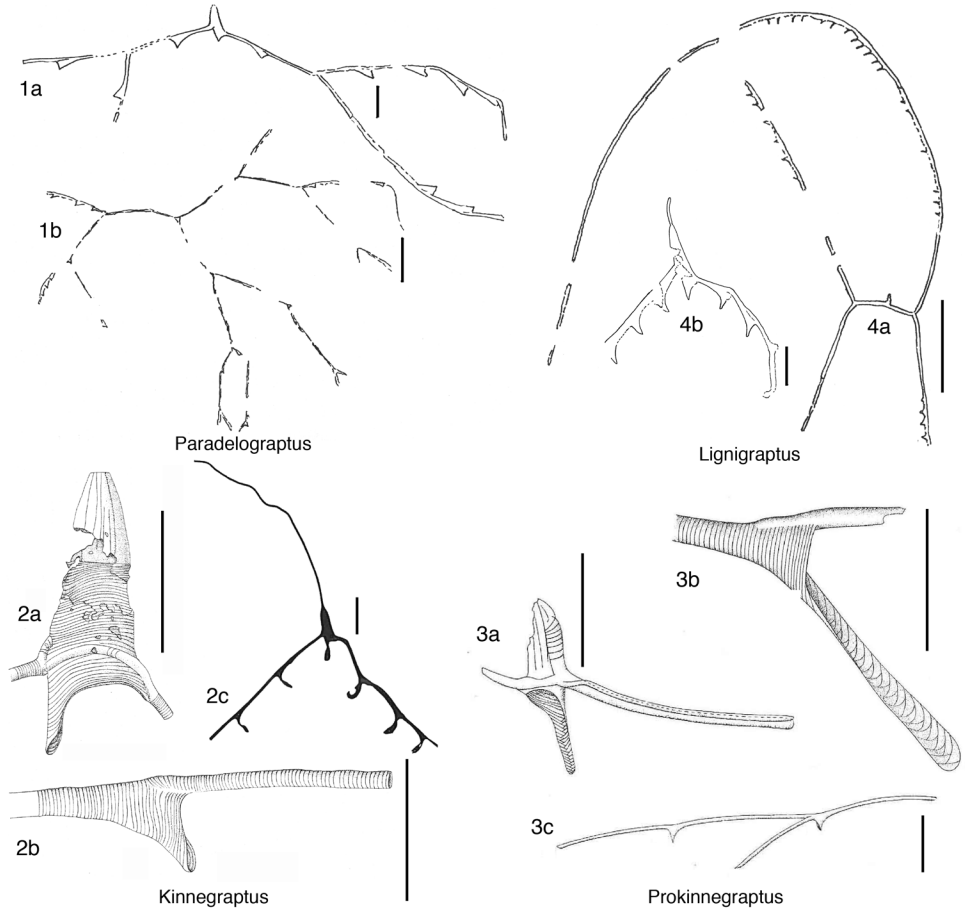


FIG. 174. Sigmagraptidae (p. 274–276).

overlap, very slender prothecae and distinctly widening metathecae; strong rutella on all thecae. *Middle Ordovician* (*lower Dapingian, Isograptus victoriae lunatus* Biozone): Norway, Sweden.——FIG.174,*3a–c*. **P. multiramosus* (SKOGLUND), Norra Skagen drill core near Hällekis, Västergötland, Sweden; *3a,* PMU 23639, Norra Skagen at 61.10 m; *3b,* PMU 23641, Norra Skagen at 62.16 m; *3c,* PMU 23642, Norra Skagen at 62.72 m; scale bars, 0.5 mm (Skoglund, 1961, fig. 5B, 6B, and 7, respectively).

Family SINOGRAPTIDAE Mu, 1957

[Sinograptidae MU, 1957, p. 387] [incl. Paradidymograptidae WANG, 1975, p. 8; Atopograptidae HARRIS, 1926, p. 59; Pseudodichograptinae HSÜ & CHAO, 1976, p. 126; Pseudotetragraptinae HSÜ & CHAO, 1976, p. 129; Holmograptinae HSÜ & CHAO, 1976, p. 132]

Planktic, graptoloid graptolites with multiramous to single-stiped, horizontal to subhorizontal tubaria; sicula parallel sided with straight aperture, perpendicular to the stipes; sicular aperture with ventral rutellum or dorsal and ventral rutellate extensions; proximal development isograptid, dextral, with symmetrically placed crossing canals close to the aperture of the sicula; origin of th1[1] in the lower part of the prosicula; thecal style typically complex with distinctly differentiated pro- and metathecae; thecal elaborations such as prothecal folds, lateral apertural lappets, rutella, or spines common. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone–*Nicholsonograptus fasciculatus* Biozone): worldwide.

The Sinograptidae includes graptolites with a symmetrical proximal development and distinctly elaborated thecal apertures

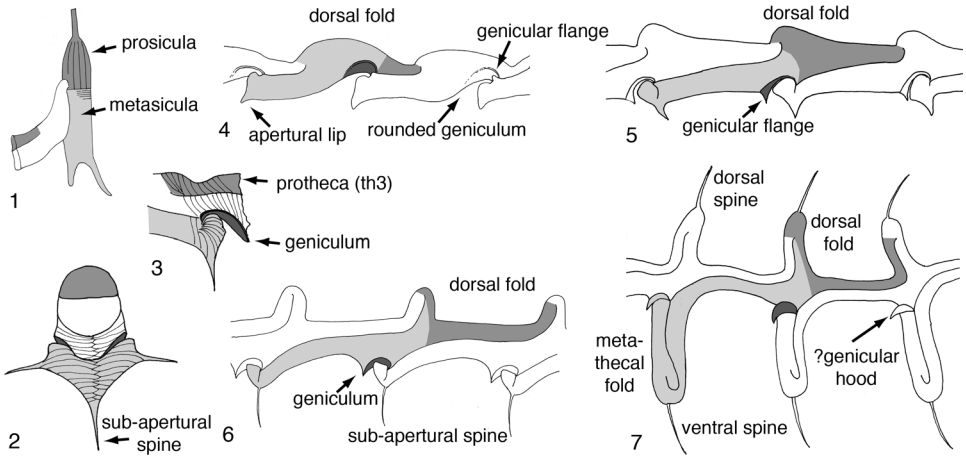


FIG. 175. Thecal development in *Holmograptus* KOZŁOWSKI, 1954 and *Sinograptus* MU, 1957. *1*, *Nicholsonograptus fasciculatus* (NICHOLSON, 1869), sicula and first theca (based on GSC 132333); *2, Holmograptus* sp., reconstruction, apertural view, showing lateral and subapertural thecal spines; *3*, *Holmograptus* sp., lateral view to show geniculum and apertural elaborations, note the lack of lateral spines; *4*, *Anomalograptus reliquus* (CLARK 1924), simple theca with median position of dorsal fold; *5*, *N. fasciculatus* with dorsal fold prior to origin of next theca and elaborated geniculum; *6*, *Holmograptus* sp. with strong dorsal fold and subapertural spine; *7*, *Sinograptus typicalis* MU, 1957 with dorsal and metathecal folds, dorsal and ventral spines (new; based in part on Kozłowski, 1954 and Zhang & Fortey, 2001).

(Fig. 175). The members of the family possess the most elaborate thecal structure known from Lower to Middle Ordovician multiramous graptolites. The thecae are fairly simple in early members, with low thecal inclination. Derived taxa may have considerable prothecal and metathecal folding, forming strongly elongated thecae. The thecal apertures may be complexly formed with introverted apertures and lateral lobes (see KOZŁOWSKI, 1954, fig. 6). Subapertural ventral spines and even paired lateral spines may be present. Dorsal spines are developed on the top of the prothecal folds in some *Holmograptus* species (MALETZ, 2009, fig. 5L–N, fig. 6H) and especially in *Sinograptus* (Fig. 175.7). The details of the thecal constructions are unknown, as fuselli are rarely preserved, even in isolated material. Therefore, the construction of the prothecal and metathecal folds is unclear. The material of KOZŁOWSKI (1954) may indicate a considerable widening of the prothecae before the insertion of a new theca (see Fig. 175.3). In this case, the dorsal prothecal folding may actually represent this widening, and the initial protheca of the succeeding theca is only part of the fold.

Sinograptus MU, 1957, p. 400 [**S. typicalis;* OD]. Two-stiped, declined sinograptids with exaggerated prothecal and metathecal folds; prothecal and ventral apertural spines present; proximal development isograptid, dextral, with symmetrically placed crossing canals. *Middle Ordovician, Darriwilian* (*upper Holmograptus lentus* Biozone): China, Canada.——FIG. 177,*2. *S. typicalis,* holotype, NIGP 8909, scale bar, 1 mm (Zhang, 2008, Atlas, Folio 2.94).

Allograptus MU, 1957, p. 388 [**A. mirus;* OD] [=*Pseudodichograptus* CHU, 1965, p. 97 (type, *P. confertus,* OD), syn. herein; =*Pseudojanograptus* HSÜ & CHAO, 1976, p. 131 (type, *?Allograptus fluitans* MU, 1957, p. 391; OD), syn. herein; =*Pseudotetragraptus* HSÜ & CHAO, 1976, p. 129 (type, *P. corniculiformis,* OD), syn. herein]. Multiramous, horizontal to subhorizontal sinograptids with as many as three orders of stipes; progressive branching, often with delayed dichotomies; thecae with variably developed prothecal folding, often possessing a geniculum and apertural elaborations. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone–*Levisograptus dentatus* Biozone): ?Australia, China, Canada, Norway.——FIG. 176,*3a*. *A. confertus* (CHU, 1965), holotype, repository unknown, scale bar, 5 mm (Chu, 1965, fig. 4).——FIG. 176,*3b*. *Allograptus* sp., GSC 102622, Lévis, Quebec, Canada, scale bar, 1 mm (Maletz, 1997b, fig.

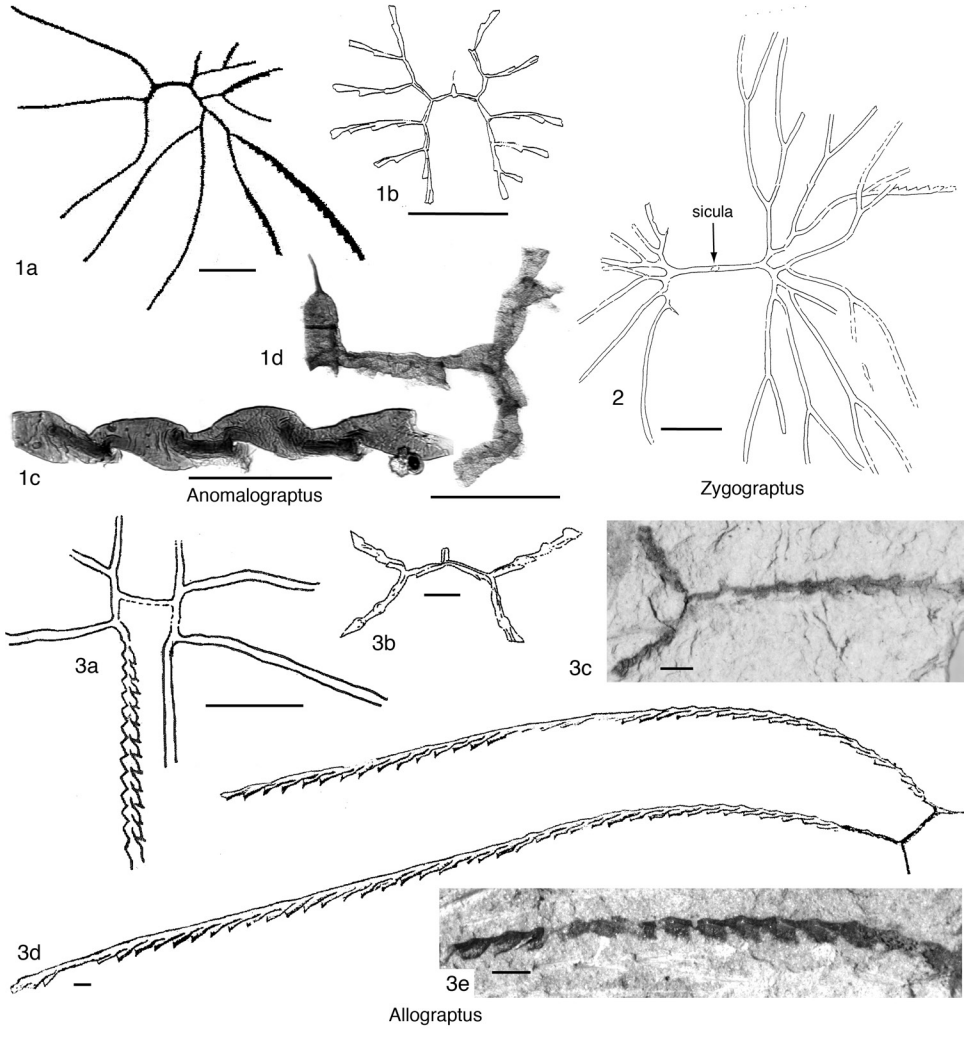


FIG. 176. Sinograptidae (p. 177–180).

8G).——FIG. 176,*3c*. **A. mirus,* holotype, NIGP 8867, internal cast, scale bar, 1 mm (new).——FIG. 176,*3d*. *A. corniculiformis* HSÜ & CHAO, 1976, holotype, No. 1575 (repository unknown), scale bar, 1 mm (Hsü & Chao, 1976, pl. 6,*3e*).——FIG. 176,*3e*. *A. fluitans* MU, 1957, holotype, NIGP 8874, scale bar, 1 mm (new).

Anomalograptus CLARK, 1924, p. 63 [**A. reliquus;* OD] [=*Brachiograptus* HARRIS & KEBLE, 1932, p. 43 (type, *B. etaformis,* OD), syn. herein; =*Pseudologanograptus* HSÜ & CHAO, 1976, p. 126 (type, *P. geniculatus*), syn. herein]. Multiramous, horizontal to subhorizontal sinograptids; first distal dichotomies usually at $th3^1$ and $th3^2$; branching crowded proximally with two to four progressive dichotomies; no distal branching; thecae with variably developed prothecal folding, sometimes possessing geniculum and apertural elaborations. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone–*Levisograptus dentatus* Biozone): Australia, New Zealand, China, Canada, USA, Argentina, Bolivia, UK.——FIG. 176,*1a, c–d*. **A. reliquus; 1a*, holotype, MCZ 101403, near Victoria Hotel, Lévis, Quebec, Canada, scale bar, 5 mm (Clark, 1924, pl. 5,*4*); *1c,* GSC 140007, stipe fragment; *1d,* GSC 139257, isolated proximal end; *Levisograptus dentatus* Biozone; *1c–d* from Western Brook Pond, bed 52, Cow Head Group, western Newfoundland, Canada; scale bars, 1 mm (new).——FIG. 176,*1b*. *A. etaformis* (HARRIS & KEBLE, 1932), paratype, NMV P24109, scale bar, 5 mm (VandenBerg, 2008c, Atlas, Folio 2.22).

Atopograptus HARRIS, 1926, p. 59 [**A. woodwardi;* OD]. Horizontal to declined, two-stiped

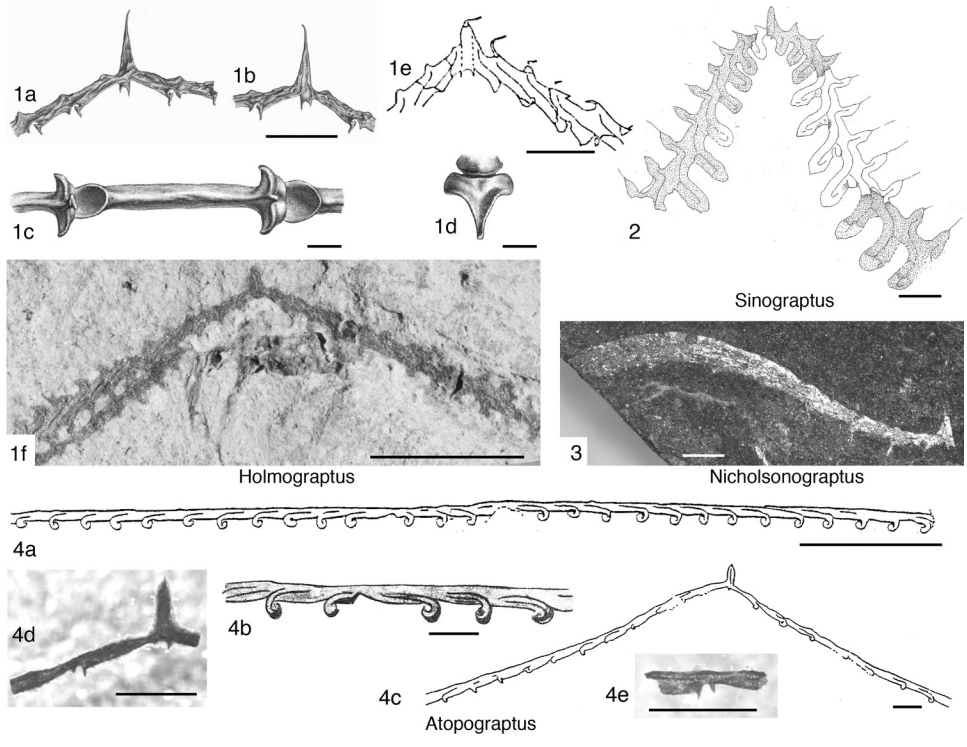


FIG. 177. Sinograptidae (p. 277–280).

sinograptid tubarium; thecae with strong geniculum and apertural hood. *Middle Ordovician*, *middle Darriwilian* (*Holmograptus lentus* Biozone–*Nicholsonograptus fasciculatus* Biozone): Australia (Victoria), China, Sweden, Canada.——FIG. 177,*4a–b*. **A. woodwardi; 4a,* holotype, NMV P 3352, janograptid specimen, Bendigo east, Victoria, Australia, scale bar 5 mm (VandenBerg, 2008d, Atlas, Folio 2.19); *4b,* enlargement of proximal end, scale bar, 1 mm (Harris, 1926, fig. 14).——FIG. 177,*4c*. *A. dubitatus* (HARRIS & THOMAS, 1935), NMV P31948, Strathfieldsaye, Bendigo, Victoria, Australia, scale bar, 1 mm (VandenBerg, 2008d, Atlas, Folio 2.19).——FIG. 177,*4d–e*. *Atopograptus* sp; *4d,* GSC 133519, proximal end; *4e,* GSC 133519, distal theca; Les Méchins, Quebec, Canada; scale bars, 1 mm (Maletz, 2009, fig. 5).

Holmograptus KOZŁOWSKI, 1954, p. 432 (French translation, p. 124) [**Didymograptus callotheca* BULMAN, 1932c, p. 16; OD] [=*Tylograptus* MU, 1957, p. 393, English translation, p. 428 (type, *T. regularis,* OD), syn. herein; =*Paradidymograptus* MU, GEH & YIN in MU & others, 1962, p. 73 (type, *P. acanthonotus,* OD), syn. herein]. Two-stiped pendent or declined to subhorizontal sinograptids; stipes with high, commonly distally increasing thecal overlap; thecal apertures elaborate, constricted with variously modified ventral and dorsal lips; prothecal folds may be present as well as spines on prothecae or thecal apertures. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone–*Holmograptus lentus* Biozone): worldwide.——FIG. 177,*1a–d*. **H. callotheca* (BULMAN); *1a–b,* holotype, NRM-PZ Cn 71835, in reverse (*a*) and obverse (*b*) views, Grå Vaginatum-kalk, Hälludden, Öland, Sweden; scale bar 1 mm (Bulman, 1936a, pl. 2,*1–2*); *1c–d,* NRM-PZ Cn 71836, stipe fragment in ventral view (*c*) showing laterally expanded thecal aperture, and geniculum and apertural view (*d*) showing apertural complexity, scale bars, 0.1 mm (Bulman, 1936a, pl. 2,*10* and 2,*13,* respectively).——FIG. 177,*1e*. *H. spinosus* (RUEDEMANN, 1904), NYSM 5916, lectotype, scale bar, 1 mm (Archer & Skevington, 1973, fig. 1a).——FIG. 177,*1f*. *H. regularis* (MU, 1957), holotype, NIGP 8892, flattened specimen, Ningkuo Shale of Tawu, Changshan, China, scale bar 5 mm (new).

Nicholsonograptus BOUČEK & PŘIBYL, 1952a, p. 14 [**Didymograpsus fasciculatus* NICHOLSON, 1869, p. 241; OD] [=*Sinazygograptus* WANG & WU in WANG & others, 1977, p. 305 (type, *S. spinatus,* OD), syn. herein; =*Hemiholmograptus* HSÜ & CHAO, 1976, p. 137 (type, *Azygograptus falciformis* EKSTRÖM, 1937, p. 32, OD), syn. herein]. Sinograptid with a single, strongly S-shaped stipe; thecae with prothecal folds and distally increasing thecal overlap; thecae with distinct geniculum and introverted apertures; thecal

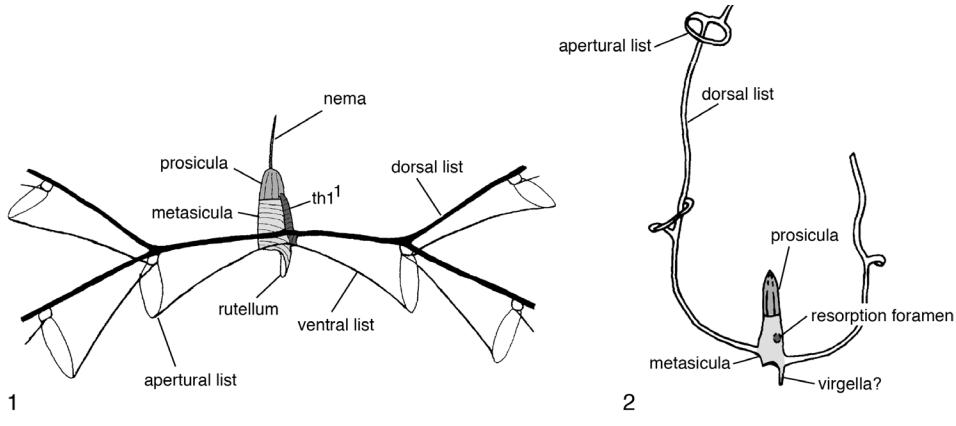


FIG. 178. Morphology of the Abrograptidae. *1, Jiangshanites* (?) *dubius* MALETZ, 1993 with prosicular origin of th1[1] and rutellate sicular aperture (adapted from Maletz, 1993, fig. 1); *2, Dinemagraptus warkae* KOZŁOWSKI, 1951, showing metasicular origin of th1[1] (resorption foramen) and possible presence of virgellar spine (adapted from Finney, 1980, fig. 11).

apertures elaborated as in *Holmograptus*, typically with long ventral spines; sicular aperture with ventral rutellum and even longer dorsal, typically curved rutellum. *Middle Ordovician* (*Darriwilian, Nicholsonograptus fasciculatus* Biozone): worldwide.——Fig. 177,*3*. **N. fasciculatus* (NICHOLSON), LO 3315T, holotype of *Azygograptus falciformis* EKSTRÖM, 1937, Röstånga, Scania, Sweden, scale bar, 1 mm (new).

Zygograptus HARRIS & THOMAS, 1941, p. 308 [**Graptolithus abnormis* HALL, 1858, p. 117; OD]. Multiramous sinograptids with strongly elongated funicle, followed by number of progressive dichotomies at close intervals of 1–3 thecae; thecae low inclined, slightly undulating, with slight apertural elaborations. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone–*Levisograptus dentatus* Biozone): ?China, Canada.——FIG. 176,*2*. **Z. abnormis* (HALL), holotype, GSC 941, Darriwilian, Lévis, Quebec, scale bar, 5 mm (new).

Family ABROGRAPTIDAE Mu, 1958

[Abrograptidae MU, 1958, p. 261]

Tubarium either multiramous or consisting of two reclined uniserial or biserial stipes, scandent and possibly dipleural; sicula completely sclerotized with strongly developed rutellum; fusellum of stipes reduced, preservable parts consisting of lists outlining thecae; thecal apertures represented by circular lists attached to ventral and dorsal lists; proximal-end development dichograptid, probably isograptid, dextral. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, UK, Poland, Canada, USA.

The Abrograptidae are herein regarded as a family closely related to the Sigmagraptidae. The inclusion is based on the shape and development of the sicula and the origin of the first theca in isolated material of *Jiangshanites* (?) *dubius* found in the *Levisograptus austrodentatus* Biozone of western Newfoundland. It is the only abrograptid for which isolated material exists, with the exception of the poorly understood *Dinemagraptus*. It has a small, cone-shaped sicula with a prosicular origin of th1[1] (Fig. 178.1), but the later proximal development is not known from the specimens, because the crossing canals are not sclerotized. The species produces a multiramous tubarium in which the first distal branching occurs after the production of the first thecal pair. *Dinemagraptus warkae* KOZŁOWSKI, 1951 is known from a single proximal end showing a sicula with a possible virgellar spine and a metasicular origin of th1[1], indicated by a resorption foramen in the middle of the metasicula (Fig. 178.2).

The recognition of the abrograptids is generally based on fragmented list structures on shale surfaces, and in many specimens,

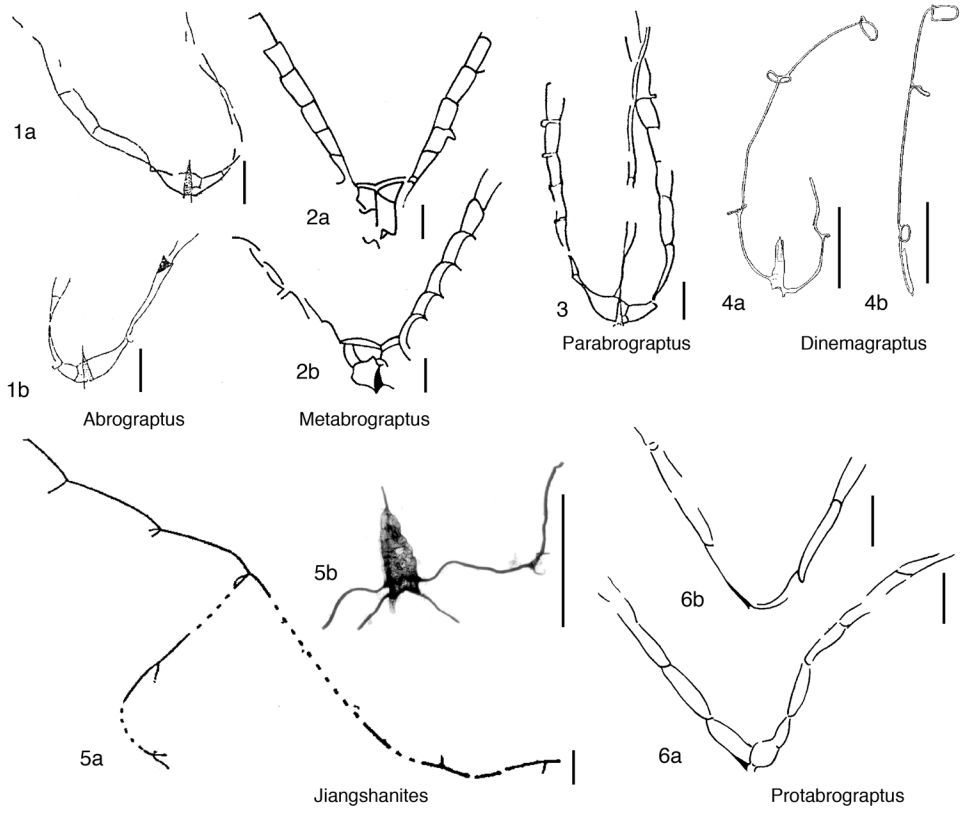


FIG. 179. Abrograptidae (p. 281–282).

the development is uncertain. For example, *Protabrographtus* is very poorly preserved and cannot be recognized as a genuine graptolite.

Abrographtus MU, 1958, p. 261 (English text, p. 264) [**A. formosus;* OD]. Reclined, two-stiped abrograptid; stipes comprised of two longitudinal filaments and apertural rings or crossbars, forming rectangular meshes; sicula with one crossing canal; development probably corresponding to *bifidus* stage of dichograptid type. *Middle Ordovician* (*upper Darriwilian, Hustedograptus teretiusculus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, Canada, USA.——FIG. 179,*1a–b*. **A. formosus; 1a,* paratype, NIGP 9402; *1b,* holotype, NIGP 9397 (type material for both missing at NIGP); *Nemagraptus gracilis* Biozone, Kiangshan, Chekiang, China; scale bars, 1 mm (Mu, 1958, pl. 1).

Dinemagraptus KOZŁOWSKI, 1951, p. 292 (French text, p. 87) [**D. warkae;* OD]. Reclined, two-stiped abrograptid; stipes reduced to dorsal and apertural lists; sicula completely sclerotized. *Middle Ordovician* (*upper Darriwilian, ?Hustedograptus teretiusculus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, Poland.——FIG. 179,*4a–b*. **D. warkae,* glacial boulder, Stara Warka, ~50 km south of Warsaw, Poland, scale bars, 1 mm (Kozłowski, 1951, fig. 1).

Jiangshanites MU & QIAO, 1962, p. 3 (English text, p. 7) [**J. ramosus;* OD]. Multiramous abrograptid; completely sclerotized sicula with sclerotized initial part of first theca; prosicular origin of th1[1]; thecae constructed of dorsal, ventral, and apertural lists. [The type material is very incomplete and a sicula is not recognizable in the specimens.] *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, Canada.——FIG. 179,*5a*. **J. ramosus,* syntype, NIGP 13240, fragment, scale bar, 1 mm (Mu & Qiao, 1962, pl. 2,*12*).——FIG. 179,*5b. J.* (?) *dubius* MALETZ, 1993, GSC 102774, sicula with incomplete first thecal pair, Western Brook Pond, south section, Newfoundland, Canada, scale bar, 1 mm (Maletz, 1993, fig. 2,1).

Metabrographtus STRACHAN, 1990, p. 934 [**M. scoticus;* OD]. Biserial-uniserial abrograptid; uniserial stipes

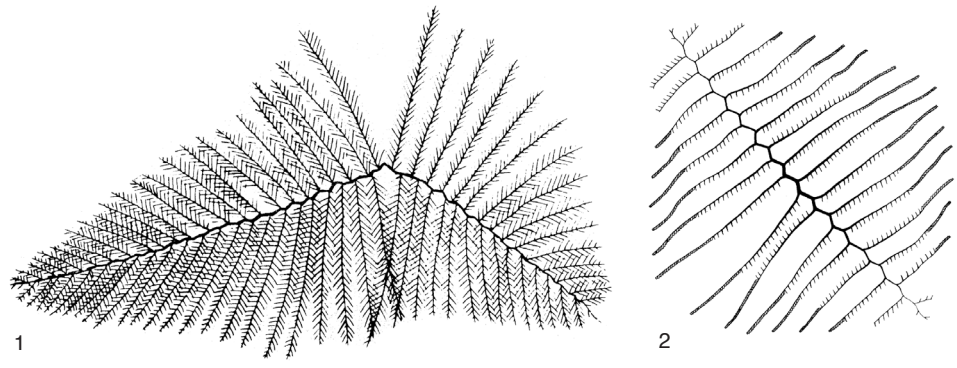


FIG. 180. *Thamnograptus capillaris* (EMMONS, 1855) reconstructions. *1,* RUEDEMANN reconstruction (1947, pl. 43, *7*); *2,* FINNEY reconstruction (1980, fig. 7).

diverge at an angle of 80° to 110°; sicula sclerotized. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): UK (Scotland), USA.——FIG. 179,*2a–b*. **M. scoticus; 2a,* holotype, BU 1336b; *2b,* paratype, BU 2150a; Glenkiln Shale, Birnock, UK, scale bars, 1 mm (Strachan, 1990, fig.1A and 1D, respectively).

Parabrograptus MU & QIAO, 1962, p. 2 [*P. tribrachiatus;* OD]. Scandent, ?biserial abrograptid; two ventrolateral lists connected with horizontal apertural lists on each side; two vertical lists in the center of the tubarium, probably connected to the sicula. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China.——FIG. 179,*3. *P. tribrachiatus,* holotype, NIGP 13236, scale bar, 1 mm (Mu & Qiao, 1962, pl. 2.*1*).

Protabrograptus NI, 1981, p. 203 [**P. sinicus;* OD]. Minute tubarium with a generally rounded base, consisting of two reclined stipes, comprised of two longitudinal filaments (ventral and dorsal) and apertural rings or crossbars; sicula fully preserved, merging into the ventral filament of second stipe [This might not be a graptolite. A sicula cannot be recognized in the type material.] *Middle Ordovician* (*upper Darriwilian, Didymograptus jiangxiensis* Biozone): China (Wuning).——FIG. 179,*6a–b*. *P. sinicus; 6a,* paratype, NIGP 57943; *6b,* holotype, NIGP 57941; Wuning, Jiangxi, China, scale bars, 1 mm (Ni, 1981, fig. 1).

Suborder UNCERTAIN

Family THAMNOGRAPTIDAE Hopkinson & Lapworth, 1875

[Thamnograptidae HOPKINSON & LAPWORTH, 1875, p. 633]

Tubarium consisting of straight or flexuous stipes (first-order branches, number unknown) with widely spaced, second-order lateral branches comprised of narrow tubular thecae bearing strongly elongated rutella or hairlike spines; thecae of lateral, second-order branches possibly abruptly changing to dichograptid thecae distally; details of proximal development unknown. *Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone)–*Upper Ordovician* (*Katian, Climacograptus bicornis* Biozone): Australia, China, Sweden, USA.

HOPKINSON and LAPWORTH (1875) established the family Thamnograptidae for the two genera *Thamnograptus* and *Buthograptus* HALL, 1861b. FINNEY (1980) revised the family Thamnograptidae and excluded the genus *Buthograptus* as unrecognizable, following BULMAN (1970, p. 139), thus, incorporating a single genus into the family. Numerous species have been included in the genus *Thamnograptus* (referenced in RUEDEMANN, 1947), but most of them consist of slender indeterminable stipe fragments. In the restricted sense, the genus is used herein for a number of multiramous Middle Ordovician, possibly planktic graptoloids with very slender thecae and unknown tubarium development. Silurian taxa are excluded and may belong to other fossil groups. The genus *Wuninograptus* is herein included in the Thamnograptidae due to a similar development of the thecae during the Middle Ordovician (late Darriwilian) age. It is the only taxon of the family from which a proximal end has been described.

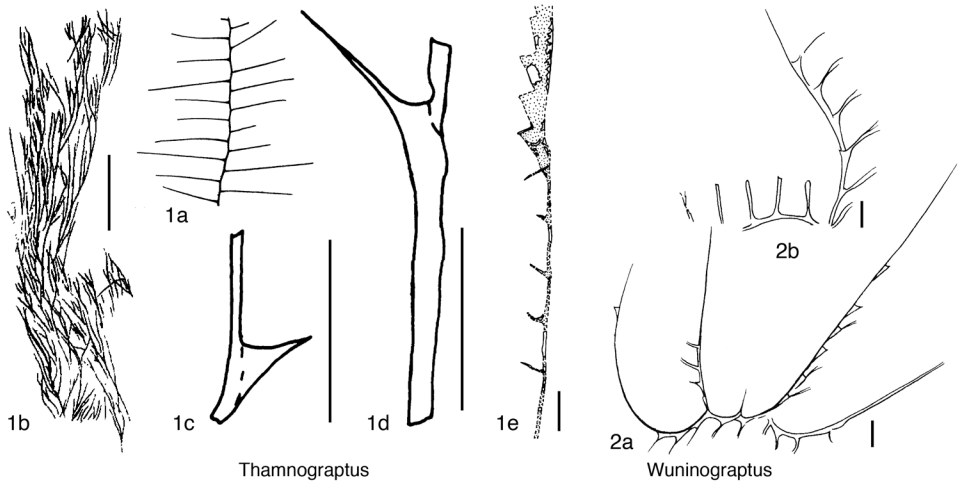


FIG. 181. Thamnograptidae Uncertain (p. 283).

Wuninograptus may otherwise be related to *Kinnegraptus*. If *Thamnograptus* is related to *Wuninograptus*, the genus could be included in the Sigmagraptidae.

MORPHOLOGY

The proximal development of the species of *Thamnograptus* is unknown as is the thecal style of most taxa. FINNEY (1980) described a few chemically isolated thecae and referred them to *T. capillaris* (EMMONS, 1855). The thecae are parallel sided through most of their length and bear a slightly widening aperture with long and slender ventral apertural spines. The thecal overlap is strongly reduced, but details of the fusellar construction are not available. According to FINNEY (1980), the thecae abruptly change to a dichograptid style in the distal parts of the second-order stipes (Fig. 180.2), but this is not confirmed from isolated material, and the illustrated shale specimens could be accidental associations of thamnograptid and acrograptid stipe fragments. The largest preserved colonies have thickened zigzag central stipes with thinner, alternating lateral stipes, similar to the tubarium construction in *Sigmagraptus*. Thus, the style of branching may be described as monoprogressive. Because all known specimens are flattened in shale, no details of the development are available.

Thamnograptus HALL, 1859b, p. 519 [**T. typus,* =*Nemagrapsus capillaris* EMMONS, 1855, p. 109, syn. by RUEDEMANN, 1908, p. 205; SD RUEDEMANN, 1908, p. 206]. Tubarium consisting of straight to slightly zigzag-shaped, flexible stipes (first-order branches, number unknown) with widely spaced, second-order lateral branches comprised of narrow tubular thecae bearing hairlike spines; thecae of lateral, second-order branches abruptly changing to dichograptid thecae distally; proximal development unknown. *Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone)–*Upper Ordovician* (*Katian, Nemagraptus gracilis* Biozone–*Climacograptus bicornis* Biozone): Australia, China, UK, Sweden, USA.——Fig. 181,*1a–e*. **T. capillaris* (EMMONS); *1a,* syntype of *T. typus* HALL, 1859b, whereabouts of specimen unknown, scale information unavailable (Hall, 1859b, fig. 2); *1b,* neotype (selected by FINNEY, 1980, p. 1190), NYSM 7368, Mount Merino, near Hudson, Columbia County, New York, USA, scale bar, 10 mm (Ruedemann, 1908, pl. 10,*5*); *1c–d,* individual thecae of neotype, scale bars, 0.5 mm (Finney, 1980, fig. 3); *1e,* OSU 32903, stipe fragment with abrupt change in thecal style, Athens Shale, Alabama, USA, scale bar, 1 mm (Finney, 1980, fig. 4F).

Wuninograptus NI, 1981, p. 204 [**W. quadribrachiatus;* OD]. Thamnograptid with three to four reclined stipes; sicula and thecae with a long, tongue-shaped apertural process and low thecal overlap; thecal apertures with thickened rim. *Middle Ordovician* (*upper Darriwilian, Didymograptus jiangxiensis* Biozone): China, Argentina.——FIG. 181,*2a–b*. **W. quadribrachiatus; 2a,* holotype, NIGP 54074; *2b,* NIGP 54077, thecal details on fragment

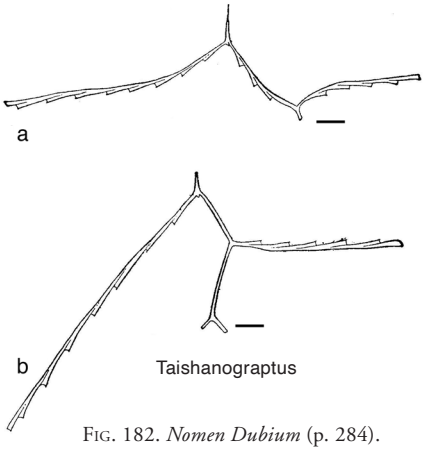


FIG. 182. *Nomen Dubium* (p. 284).

showing extended rutella; Jiangxi Province, China; scale bars, 1 mm (Ni, 1981, fig. 2,*4* and 2,*3,* respectively).

NOMEN DUBIUM

Taishanograptus LI & GE in LI, GE, & CHEN, 1987, p. 102 [**T. graciliramosus;* OD]. Sigmagraptines with slender stipes and widely spaced, irregularly placed dichotomies; thecae simple, low-inclined tubes of dichograptid type. *Middle Ordovician* (*lower Darriwilian, Cardiograptus amplus* Biozone): China. [The types are extremely poor and the presence of a sicula or proximal end is uncertain.]——FIG. 182,*a–b*. **T. graciliramosus; a,* syntype NIGP 76829; *b,* syntype, NIGP 76828; scale bars, 1 mm (Li, Ge, & Chen, 1987, fig. 2).

SUBORDER DICHOGRAPTINA

Jörg Maletz, Blanca A. Toro, Yuandong Zhang, and
Alfons H. M. VandenBerg

Suborder DICHOGRAPTINA Lapworth, 1873

[Dichograptina Lapworth, 1873b, table 1, facing p. 555; *nom. transl.* Obut, 1957, p. 19; *ex* Dichograptidae Lapworth, 1873b] [=suborder Didymograptina Lapworth, 1880f, p. 192 *nom. correct.* Jaanusson, 1960, p. 309; *ex* section Didymograpta Lapworth, 1880f]

Multiramous to two-stiped graptoloids with biradiate isograptid proximal development and maeandrograptid proximal symmetry; colony shape scandent to reclined, horizontal, and pendent; prosicula small, with widening and much larger metasicula; thecae simple, widening tubes with or without rutellum; a sicular bitheca may be present in early taxa; branching dichotomous or cladial. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone)–*Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone): worldwide.

INTRODUCTION

The Dichograptina is one of the two major groups of graptoloids originating from the earliest planktic graptolites of the family Anisograptidae (Fig. 183). According to Maletz, Carlucci, and Mitchell (2009), the Dichograptina and the Sinograpta (Sinograptina herein) can be regarded as sister groups. However, Fortey and Cooper (1986) and Lindholm (1991) suggested a polyphyletic origin of derived graptoloids (non-bithecate graptoloids) from the Anisograptidae. Thus, the sister group relationship between the Anisograptidae and the supercohort Eugraptoloida (the Graptoloidea of Bulman, 1970) as shown by Maletz, Carlucci, and Mitchell (2009) is unlikely to be correct and more research on the transition is needed.

Lapworth (1873b) understood the Dichograptidae as the group of genera that includes two-stiped to multiramous taxa with simple thecae and dichotomous bifurcation or lateral branching. He listed the genera *Didymograptus, Tetragraptus, Dichograptus, Loganograptus,* and *Clonograptus*. Obut (1957) erected the suborder Dichograptina for the families Dichograptidae, Tetragraptidae, Bryograptidae, and Didymograptidae, essentially confirming the classification of Lapworth (1873b) for multiramous to pauciramous Lower to Middle Ordovician graptoloids. However, the name Dichograptina must be credited to Lapworth under the provisions of ICZN, 1999, Article 36. Bulman (1970) used the term Didymograptina Lapworth, 1880f but included the Nemagraptidae, Dicranograptidae, and Phyllograptidae, taxa that are not closely related. The Didymograptina of Bulman (1970) thus is a polyphyletic taxon and should not be used.

Fortey and Cooper (1986) used the Dichograptina Lapworth, 1873b for the non-virgellate graptoloids and introduced the new term Virgellina for all virgellate graptoloids. They defined the Dichograptina as "graptoloids lacking bithecae and virgella" (Fortey & Cooper, 1986, p. 640) and referred the two superfamilies Dichograptacea and Glossograptacea to the taxon. Maletz, Carlucci, and Mitchell (2009) introduced the supercohort Eugraptoloida as a monophyletic taxon defining all nonbithecate graptoloids. Of these, the stem reclinatids and the Pan-Tetragrapta would be included in the Dichograptina. Maletz (2014b) referred four families to the Dichograptina: the Dichograptidae, Didymograptidae, Tetragraptidae, and the virgella-bearing Pterograptidae. He discussed the taxon as a paraphyletic unit with poor internal resolution.

MORPHOLOGY

The dichograptid sicula is known from few isolated specimens and details of its

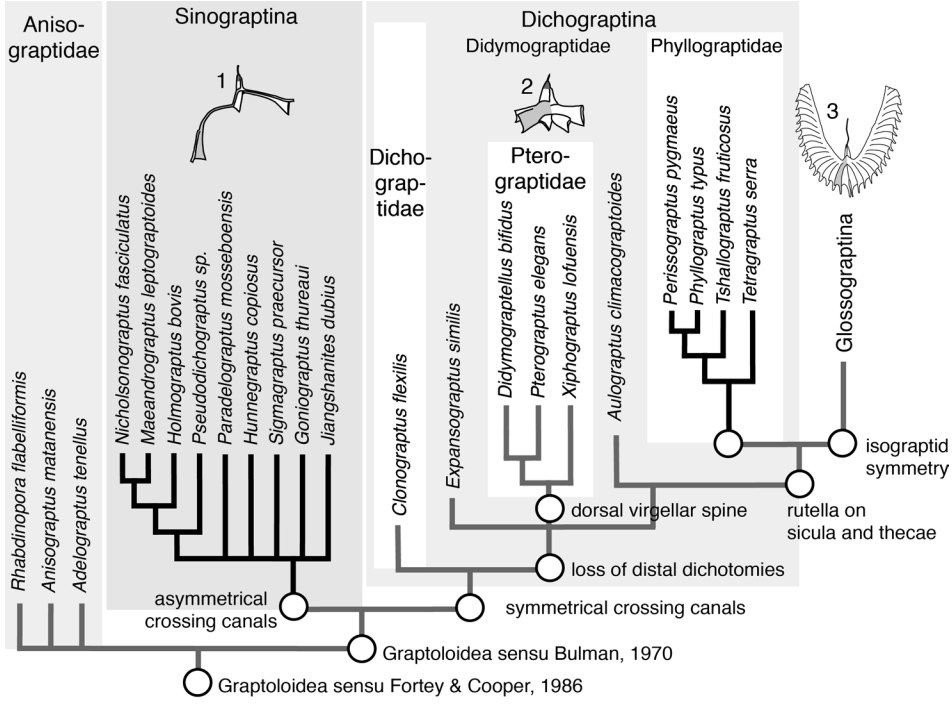


FIG. 183. Cladistic interpretation of the Dichograptina. The diagram also shows the different symmetries of the stipes in the Sinograptina (*1*), Dichograptina (*2*), and the glossograptid *Isograptus* (*3*) (adapted from Maletz, 2014b).

development are unknown for most species. However, a number of general features can be recognized (Fig. 184). It is easily differentiated from the sicula in the Sinograptina through the distinctly widening metasicula. The prosicula usually has less than one-quarter of the length of the sicula and widens gradually toward its aperture, as does the metasicula (Fig. 184.5–184.6).

The Dichograptina possess a distinct nema, which is formed as a slender rod at the tip of the prosicula. The nema is of variable length and may be quite long in some taxa but is rarely modified. It may be thickened considerably as in *Tshallograptus fruticosus* (HALL, 1858), but true nematularia, common in the Glossograptina and derived taxa, have not been described for the Dichograptina. The differentiation of the conus and cauda (Fig. 184) has rarely been discerned in the prosicula of isolated material of the Dichograptina and may not be present in many taxa. WILLIAMS and CLARKE (1999) illustrated dichograptid siculae from a variety of taxa and discussed the reduction of the cauda (not the conus—WILLIAMS and CLARKE, 1999, confused the terms conus and cauda) in early Floian taxa. These authors recognized a number of features modifying the sicula of early dichograptids, such as the differentiation of the pro- and metasicula, the diaphragm, and the development of longitudinal strengthening rods in the prosicula. The prosicula (conus) widens gradually from the apex, usually with a ratio of ~1:2, and commonly forms a long cone. In some derived taxa, however, the prosicula may be wider than long and form a wide, nearly triangular structure (e.g., *Expansograptus abditus* WILLIAMS & STEVENS, 1988). The spiral line is prominent in many specimens, and the spiral may be most dense toward the apex of the prosicula (the cauda).

Typically, the prosicula has a number of longitudinal rods secreted on the outside of the cone. In tubaria from the late Tremado-

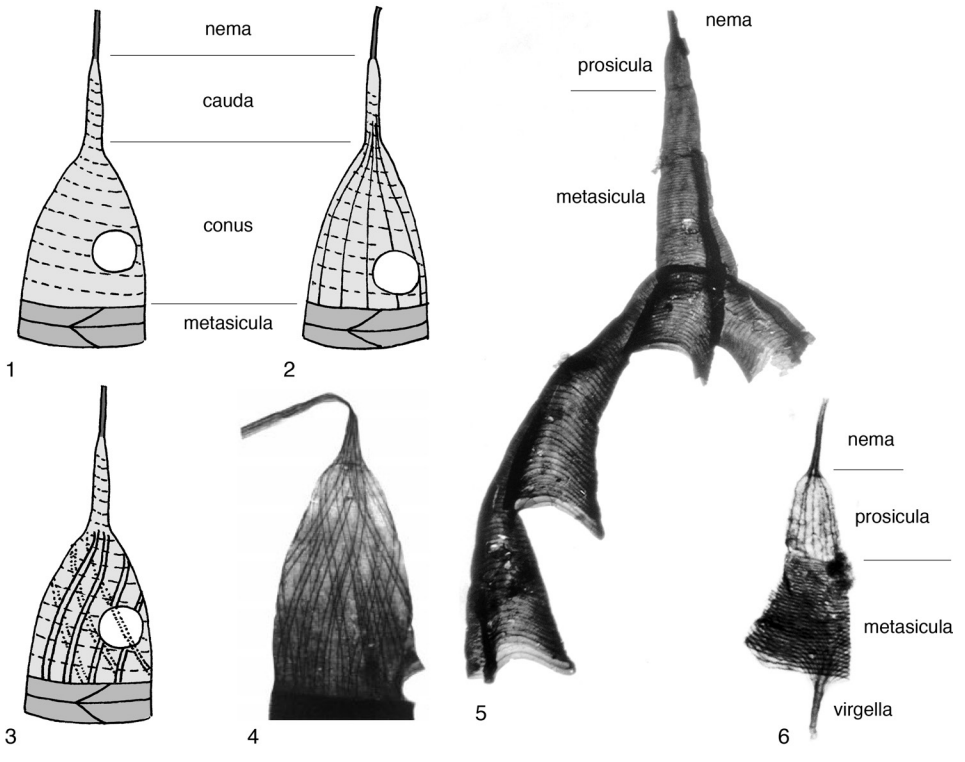


FIG. 184. Development of the sicula in Ordovician graptoloids. *1,* Anisograptidae; *2, Isograptus lunatus* HARRIS 1933; *3, Paratetragraptus approxima*tus (NICHOLSON, 1873); *4, P. approximatus* (NICHOLSON,1873), transmitted light photo; *5, Tshallograptus fruticosus* (HALL, 1858), GSC 125727, isolated proximal end showing fuselli, western Newfoundland, Canada; *6, Phyllograptus typus* HALL, 1865, GSC 125754, sicula with virgellar spine and simple longitudinal rods on prosicula, western Newfoundland, Canada (*1–4,* adapted from Williams & Clarke, 1999; *5–6,* Maletz, 2004).

cian to early Floian, the longitudinal rods are paired (Fig. 184.3–184.4) and usually run somewhat obliquely down the prosicula. This is seen in a number of phyllograptids and expansograptids illustrated by WILLIAMS and CLARKE (1999). Individual longitudinal rods are present in isograptids and may be characteristic for axonophorans, e.g., *Rectograpus gracilis* (ROEMER, 1861); see KRAFT (1926).

The metasicula is a simple, gradually widening cone formed from numerous fuselli (Fig. 184.5–184.6). It may be straight or moderately to strongly bent or curved. When present, curvature of the sicula is usually most pronounced close to the aperture and may be enhanced by the development of a rutellum. The sicula is located in the center of the tubarium, and the plane of symmetry (bilateral plane in COOPER & FORTEY, 1982, fig. 8) cuts through it—termed maeandrograptid symmetry. A distinct ventral rutellum may be developed in derived dichograptids, but other apertural modifications of the sicula are rare.

The dorsal virgellar spine developed independently from a simple rutellum in *Phyllograptus* (Fig. 184.6) and in the Pterograptidae. MALETZ (2010a) discussed in detail the origin and evolution of the dorsal virgellar spine in the genus *Xiphograptus* and related taxa. The early xiphograptid *Didymograptellus* is the only member of this group that has an origin of th1[1] in the middle part of the prosicula combined with an unusually large, parallel-sided prosicula. Both are characters present in the early planktic graptoloids of the family

Anisograptidae but have not been recognized in any other Dichograptina. Thus, it may be possible that the pterograptids have an independent origin within the Anisograptidae and are not closely related to the rest of the Dichograptina.

Maletz, Carlucci, and Mitchell (2009) regarded the symmetrical branching (bifurcation) of the two first-order stipes as the defining character of the cohort Pan-Reclinata, a character that separates its members easily from the often highly asymmetrical development in the Sinograptina (Fig. 183). Both crossing canals grow symmetrically and at the same level across the reverse side of the sicula before forming the first stipes. The proximal end symmetry is maeandrograptid, a plesiomorphic character retained from the Anisograptidae, with the plane of symmetry passing through the sicula. $Th1^1$ and $th1^2$ are symmetrically placed flanking the sicula (Fig. 185.1–185.2).

The origin of $th1^1$ is generally in the lower portion of the prosicula, but in a few taxa it may be in the middle portion (e.g., *Didymograptellus*). A metasicular origin of $th1^1$ has been demonstrated for a few taxa of *Tetragraptus* (see Skevington, 1965) and from a population of *Tshallograptus fruticosus* (Fig. 184.5) from the *Didymograptellus bifidus* Biozone of western Newfoundland (Maletz, 2004) but has not been confirmed from other species. It is common in taxa of the Didymograptidae (Fig. 185.3–185.6).

The dichograptinid tubarium is generally based on a biradiate proximal end with $th1^2$ as the first dicalycal theca. However, in a number of taxa, the development may be replaced by an independently derived condition in which the dicalycal theca is $th1^1$ (artus-type development). The change in proximal development type from isograptid (Fig. 185.3–185.4) to artus (Fig. 185.5–185.6) is best known in the genus *Baltograptus*. In the early species *Baltograptus geometricus* (Törnquist, 1901) and *Baltograptus vacillans* (Tullberg, 1880b), the proximal development is isograptid (Maletz, 1994b; Toro & Maletz, 2008), but in some later taxa, it is artus type (Maletz & Ahlberg, 2011a; Maletz & Slovacek, 2013). An isograptid proximal development is present in most expansograptids, whereas *Cymatograptus bidextro* Toro & Maletz, 2008 has an artus-type development.

The first distal dicalycal thecae in the Dichograptina are $th3^1$ and $th3^2$, forming the tetragraptid proximal end with its biradiate development (Maletz, 1992). Later dicalycal thecae are commonly placed irregularly along the stipes to form multiramous colonies and are increasingly delayed distally (Lindholm & Maletz, 1989). Thus, the branching intervals become progressively longer.

The multiramous dichograptids of the family Dichograptidae are the most distinctive graptolites of the Dichograptina. They reached colony diameters of more than 80 cm in *Hologra ptus deani* Elles & Wood, 1902 specimens, similar to the earlier anisograptid *Paratemnograptus magnificus* (Pritchard, 1892). Colony development started from the sicula with two first-order stipes (biradiate condition). Consecutive dichotomous branching led to a multiramous colony with numerous terminal branches (Fig. 186.1). During the evolution of the Dichograptina, the number of branches became reduced and two-stiped Didymograptidae appeared early in the Floian.

Dichograptina encompasses the full range of colony shapes, ranging from scandent (*Phyllograptus*) through reclined (*Tetragraptus*), horizontal, declined, and deflexed to pendent forms (*Didymograptus*). Pendent and deflexed forms are most common in pauciramous taxa. *Tshallograptus fruticosus* is a typical example of a deflexed two- to four-stiped species. Branching in the Dichograptina in general is dichotomous, through a bifurcation, with the stipe divisions typically Y-shaped. With rare exceptions, it only occurs at the growing tips of stipes. Lateral branching is present in some multiramous taxa (e.g. *Schizograptus*), but the precise method of branching in these has not been determined as no relief material or isolated specimens are available. The

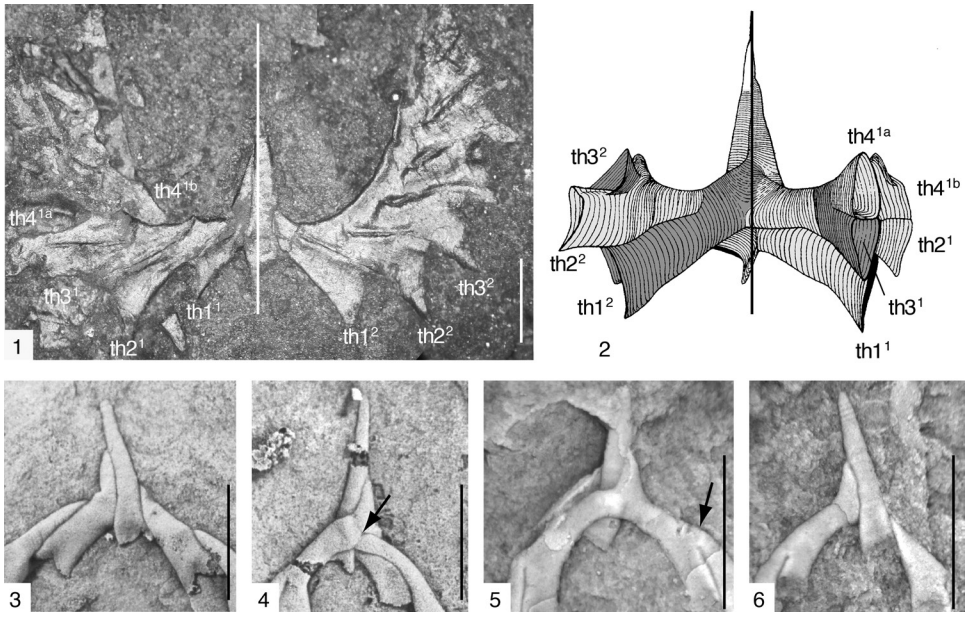


FIG. 185. Proximal development of the Dichograptina. *1, Tetragraptus reclinatus* ELLES & WOOD, 1902, LO 10598t, obverse view, *vertical line* shows line of symmetry, Lerhamn drill core, Sweden (new); *2, Tetragraptus* sp., reconstruction of proximal end in reverse view, *vertical line* shows line of symmetry, dicalycal thecae ($th1^2$, $th3^1$, $th3^2$) in *darker gray* (adapted from Bulman, 1970, fig. 53); *3–4, Baltograptus vacillans* (TULLBERG, 1880b), PMU 23157, isograptid development in obverse (*3*) and reverse (*4*) views; *5–6, Baltograptus minutus* (TÖRNQUIST 1879), artus-type development in reverse (*5*) and obverse (*6*) views, PMU 23165, Nipan, Jemtland, Sweden, *arrows* in *4–5* indicate origin of $th2^1$; all scale bars, 1 mm (*3–6,* adapted from Maletz, 1994a).

number of terminal stipes has been regarded as important and was used to differentiate genera and species in the past. It is now generally accepted, however, that the number might be variable and a species of *Dichograptus* does not invariably bear eight stipes. A certain intraspecific variation is to be expected, but additional complications may have been introduced by accidental loss of stipes and damage to the colonies during their lifetime.

Lateral branching is typical in *Pterograptus* species, but here the branching occurs in the form of cladial branching (SKWARKO, 1974; MALETZ, 1994a). The origin of the new stipe is from the aperture of the parent theca. Branching in this case is not at the growing tip of the stipe but can occur at later stages in the growth of the colony.

The thecae of the Dichograptina are simple, aperturally widening tubes (Fig. 186.2–186.3). They range from straight to strongly ventrally curved. Apertural modifications are rare and include extended rutella in some taxa. A few taxa (e.g., *Aulograptus*) develop more complex thecal apertures with genicular flanges and thickened apertural rims. Prothecal folding is present in some taxa. The most pronounced prothecal folding is in the genus *Cymatograptus*, but the details of this thecal development are unknown.

In many species with low thecal inclination, the stipes are largely parallel sided and the thecal overlap is low. In other taxa, thecae are larger distally, and the initial parts of the stipes have considerable widening (Fig. 186.3). In some, this widening decreases markedly after the first few thecae, when the zooids apparently reached their maximum size. In others, thecal size increases distally, both in length and apertural width and inclination. This may be due to continued

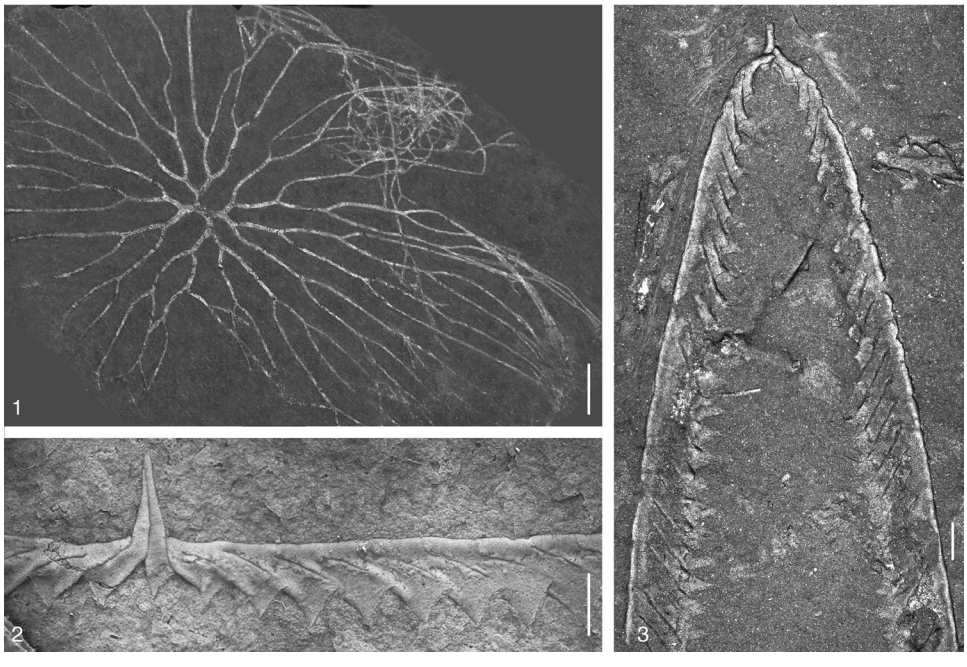


FIG. 186. Main tubarium features of the Dichograptina. *1. Clonograptus flexilis* (HALL, 1865). NMV P309374, large multiramous colony showing dichotomous branching, Lancefield Quarry, Victoria, Australia, specimen originally illustrated in Morris (1988, Ph.D. thesis), scale bar, 10 mm (new); *2, Expansograptus holmi* (TÖRNQUIST, 1904), PMU 23166, latex, obverse view, Diabasbrottet, Västergötland, Sweden, scale bar, 1 mm (new); *3, Didymograptus artus* (ELLES & WOOD, 1901), PMU 31742, reverse view, showing increase of thecal overlap and curvature, Fågelsångsdalen drill core at 22.9 m, Scania, Sweden, scale bar, 1 mm (new).

thecal growth after the growing stipe tip has passed them. Thus, thecae may have reached extreme lengths, as in robust specimens of the *Didymograptus murchisoni* (BECK in MURCHISON, 1839) type (e.g., *Didymograptus clavulus* PERNER, 1895; see BOUČEK, 1973; *Didymograptus obesus* WANG, 1974) or in *Didymograptellus bifidus* (HALL, 1865) and related taxa (WILLIAMS & STEVENS, 1988; MALETZ, 1994b).

Family DICHOGRAPTIDAE Lapworth, 1873

[Dichograptidae LAPWORTH, 1873b, table 1, facing p. 555] [incl. Schizograptinae GE in MU & others, 2002, p. 201; Mimograptinae GE in MU & others, 2002, p. 316]

Biramous to multiramous graptoloids with biradiate isograptid proximal development, symmetrically placed crossing canals and maeandrograptid proximal symmetry; prosicula small, with widening and much larger conical metasicula; sicular bitheca may be present in early taxa; thecae simple, widening tubes with or without rutellum; branching dichotomous to lateral. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone)–*Middle Ordovician* (*Dapingian, Expansograptu hirundo* Biozone).

Characters present in all Dichograptidae are a biradiate proximal end, a multiramous or pauciramous colony, simple thecae, and the absence of bithecae. Important details of the proximal development of many genera of the Dichograptidae are not clear. Thus, the family and the included taxa are largely based on inference and indirect evidence.

The Dichograptidae must be regarded as a paraphyletic taxon because the relationships to the Didymograptidae and Pterograptidae remain unclear. The roots of the Didymograptidae have not been explored due to the lack of sufficient material. The development of the prosicula and proximal development in the

early Pterograptidae (e.g., *Didymograptellus*) similarly suggests that this family may have its roots independently in the Anisograptidae.

Dichograptus Salter, 1863a, p. 136, original spelling as *Dichograpsus* changed in ICZN, Opinion 650, 1963 [**Dichograpsus sedgwickii;* SD Gurley, 1896, p. 64]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive bifurcations starting from a tetragraptid proximal end and without distal dichotomies; central disk in some species but not in others; thecae simple with moderate overlap. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Dapingian, Isograptus maximodivergens* Biozone): worldwide.——Fig. 187,*1a*. **D. sedgwickii,* lectotype (selected by Elles & Wood, 1902, explanation on pl. 10), BGS GSM 7650, Middle Skiddaw Slates, Braithwaite, Cumbria, UK, *arrow* indicates position of sicula, scale bar, 10 mm (Elles & Wood, 1902, pl. 10,*3a*).——Fig. 187,*1b*. *D. octobrachiatus* (Hall, 1858), lectotype (selected by Williams & Stevens, 1988, p. 24), GSC 931i, Lévis, Quebec, Canada, scale bar, 10 mm (Hall, 1865, pl. 7,*1*).

Clonograptus Hall & Nicholson in Nicholson, 1873, p. 138, original spelling as *Clonograpsus* changed in ICZN, Opinion 650, 1963 [**Graptolithus rigidus* Hall, 1858, p. 121, SD Miller, 1889, p. 179] [=*Temnograptus* Nicholson, 1876, p. 248 (type, *Dichograpsus multiplex* Nicholson, 1868d, p. 129, OD), syn. by Lindholm & Maletz, 1989, p. 718; =*Anthograptus* Törnquist, 1904, p. 22 (type, *A. nidus,* M), syn. by Lindholm & Maletz, 1989, p. 718]. Multiramous, horizontal to subhorizontal dichograptid with increasing distances of numerous distal, more irregularly placed dichotomies; thecae simple, widening tubes with moderate overlap and without extended rutella; proximal development isograptid, dextral, or sinistral. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone–*Floian, Tshallograptus fruticosus* Biozone): worldwide.——Fig. 187,*3a*. **C. rigidus* (Hall), lectotype, GSC 935b, *arrow* indicates position of sicula, scale bar, 10 mm (Lindholm & Maletz, 1989, p. 719, fig. 2D).——Fig. 187,*3b*. *C. flexilis* (Hall, 1858), lectotype, GSC 965c, *arrow* indicates position of sicula, scale bar, 10 mm (Lindholm & Maletz, 1989, p. 724, fig. 3A).——Fig. 187,*3c–e*. *C. multiplex* (Nicholson, 1868d); *3c,* lectotype, NHMUK PM Q31, *arrow* indicates position of sicula, scale bar, 10 mm (Lindholm & Maletz, 1989, fig. 7); *3d,* LO 1748T, holotype of *Anthograptus nidus* Törnquist, 1901, scale bar, 10 mm (Lindholm & Maletz, 1989, fig. 11c); *3e,* reconstruction from latex cast of juvenile, dicalycal theca striped, scale bar, 1 mm (Maletz, 1992, fig. 1e).

Herrmannograptus Monsen, 1937, p. 186 [**Graptolithus milesi* Hall in Hager, 1861a, p. 372; OD]. Multiramous dichograptid with a funicle formed by two first-order stipes comprised of two thecae each; up to seven or more orders of dichotomy with second and later dichotomies delayed; proximal end with sicular bitheca; bithecae lacking along stipes; thecae simple with slight rutellum. *Lower Ordovician* (*Floian,* ?*Paratetragraptus approximatus* Biozone): USA.——Fig. 188,*1a–e*. **H. milesi* (Hall in Hager); *1a,* lectotype, AMNH 433/1, scale bar, 10 mm; *1b–e,* juvenile specimens from type slab, showing astogeny, sicular bitheca visible in *1e,* float, Monkton, Vermont, USA; scale bars, 1 mm (Lindholm & Maletz, 1989, fig. 4).

Holograptus Holm, 1881b, p. 45 [**H. expansus;* M] [=*Rouvilligraptus* Barrois, 1893, p. 109 (type, *Graptolithus richardsoni* Hall, 1865, p. 107, OD), syn. by Bulman, 1970, p. 114]. Multiramous colony based on tetragraptid proximal end; lateral stipes of third and later orders originate at irregular intervals on either side of parent stipes, which follow the growth direction of second-order stipes; lateral stipes can themselves produce further lateral stipes; central web may be present; commonly long second-order stipes before insertion of first lateral stipes. *Lower Ordovician* (*Floian, Paratetragraptus approximatus/Tetragraptus phyllograptoides* Biozone–*Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone): Sweden, UK, France, Canada, Bolivia.——Fig. 190,*1a*. **H. expansus,* holotype, NRM-PZ Cn 1500, *Tetragraptus phyllograptoides* Biozone, Diabasbrottet, Hunneberg, Sweden, *arrow* indicates position of sicula, scale bar, 10 mm (Holm, 1881b, pl. 13,*1*).——Fig. 190,*1b. H. deani* Elles & Wood, 1902, holotype, BU 1374, *arrow* indicates position of sicula, Skiddaw Slates, Buttermere, Newlands Valley, Cumbria, UK, scale bar, 10 mm (Elles & Wood, 1902, pl. 8,*2a*).——Fig. 190.*1c. H. richardsoni* (Hall, 1865), syntype, GSC 937a, Lévis, Quebec, Canada, scale bar, 10 mm (Hall, 1865, pl. 12,*1*).

Hunnegraptus Lindholm, 1991, p. 298 [**H. copiosus;* OD]. Multiramous dichograptids with long first-order stipes of uneven length; thecae slender, dichograptid with moderate overlap; proximal end isograptid, dextral or sinistral with sicular bitheca; sicula parallel sided, obliquely placed between the stipes; thecae along stipes with dorsal origins, lacking bithecae. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone): Australia, ?China, Bulgaria, Norway, Sweden, Canada, USA, Argentina, Bolivia.——Fig. 188,*2a–d*. **H. copiosus; 2a,* holotype, PMO 58969, Galgeberg, Oslo, Norway; *2b,* LO 5978t, Slemmestad, Norway; *2c–d,* LO 5976 and counterpart, Storeklev, Hunneberg, Sweden; scale bars, 5 mm (*2a–b*); 1 mm (*2c–d*) (Lindholm, 1991, fig. 8).

Loganograptus Hall, 1868, p. 237 [**Graptolithus logani* Hall, 1858, p. 115; OD]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive distal bifurcations starting from a tetragraptid proximal end and without distal dichotomies; central disc present; thecae simple with moderate inclination and overlap. *Lower Ordovician* (*Floian, Baltograptus vacillans* Biozone)–*Middle Ordovician* (*Dapingian, Expansograptus*

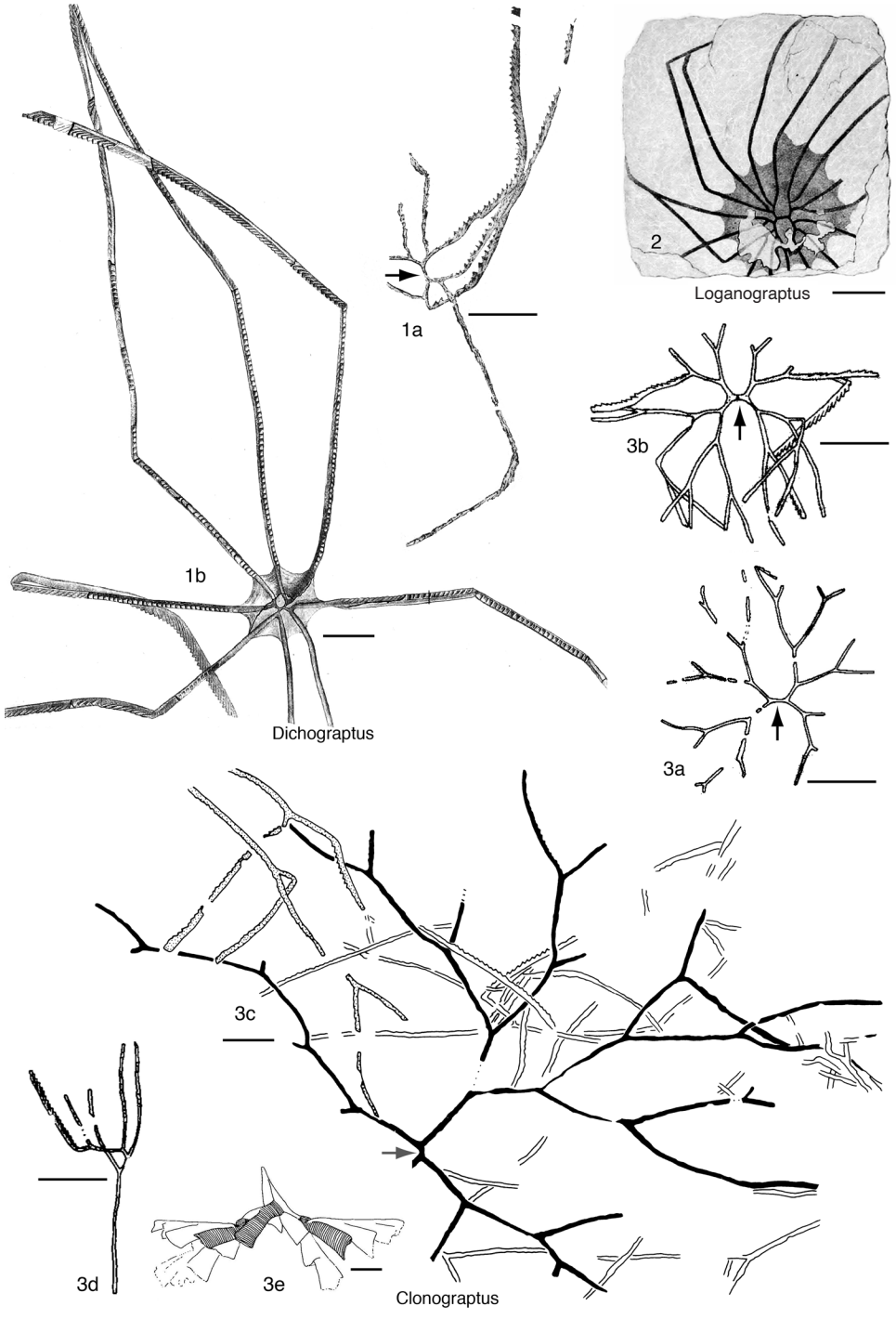


FIG. 187. Dichograptidae (p. 291–293).

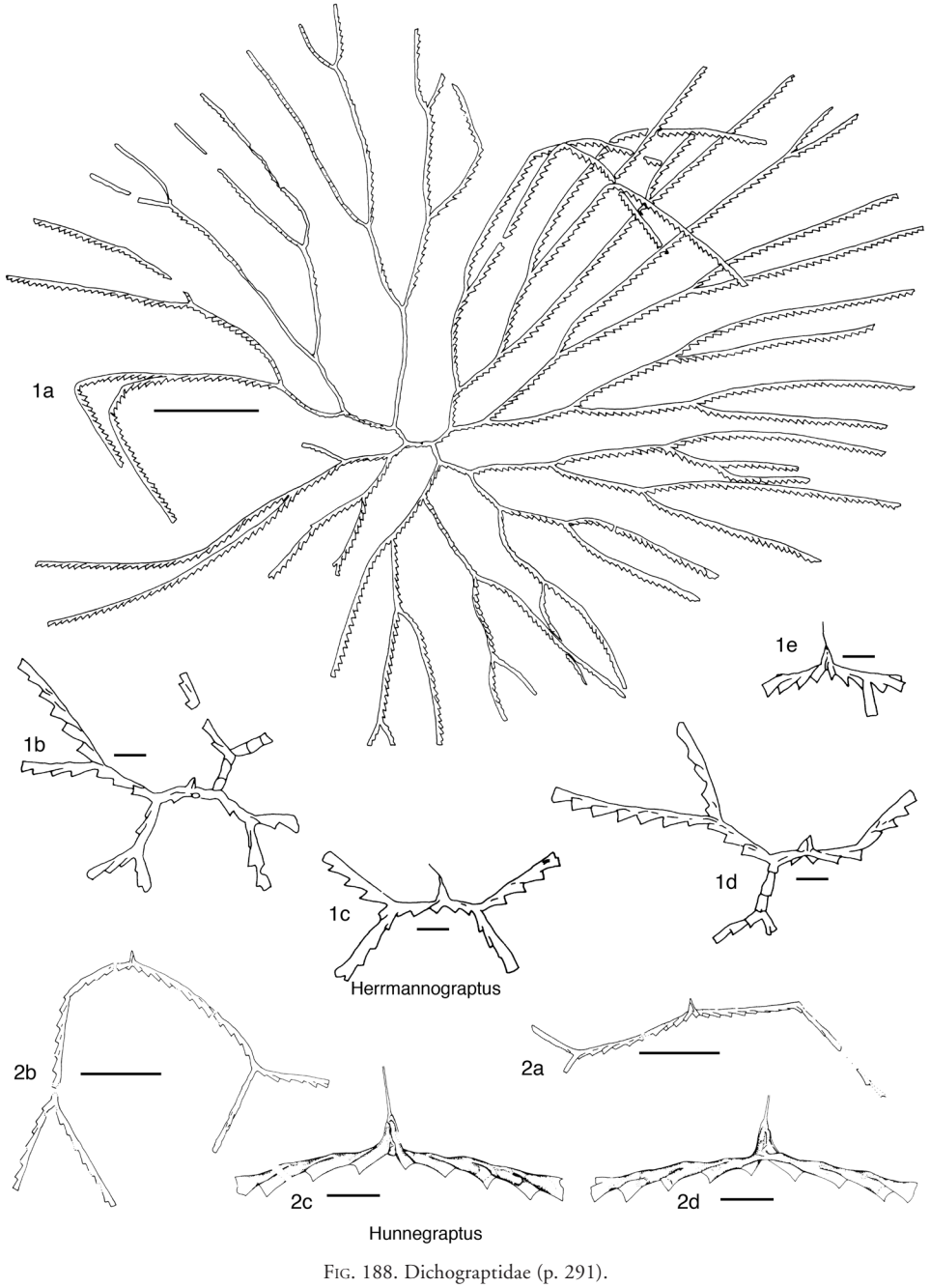
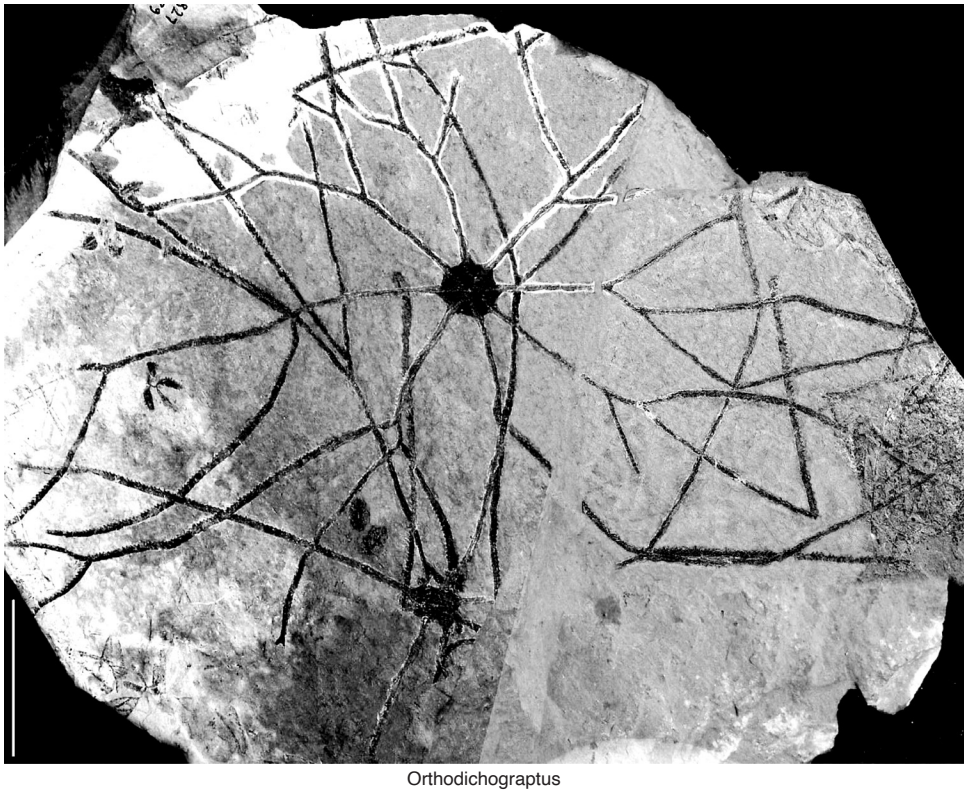


FIG. 188. Dichograptidae (p. 291).

hirundo Biozone): worldwide.——FIG. 187,*2*. **L. logani* (HALL), GSC 932a, Lévis, Quebec, Canada, scale bar, 10 mm (Hall, 1865, pl. 9,*2*).

Mimograptus HARRIS & THOMAS, 1940, p. 197 [**M. mutabilis;* M] [=*Kstaugraptus* TZAJ, 1973, p. 5 (type, *K. obuti,* OD), syn. herein]. Dichograptid based on two subhorizontal to declined main stipes and irregularly placed lateral stipes on both sides of main stipes; proximal end details unknown. *Lower Ordovician* (*upper Floian, Didymograptellus bifidus* Biozone)–?*Middle Ordovician* (*Darriwilian*, ?*Levisograptus austrodentatus* Biozone): China,



Orthodichograptus

FIG. 189. Dichograptidae (p. 294). Color image available in *Treatise Online* 108.

Kazakhstan, Australia.——FIG. 191,*2a–2c*. **M. mutabilis; 2a,* NMV P34927B, holotype, Allotment 41B, Parish of Campbelltown, Victoria, Australia, *arrows* indicates position of sicula, scale bar, 10 mm (new); *2b–c,* NMV P318805, specimen showing sicula, Victoria, Australia, *arrow* (*2b*) indicates position of sicula, scale bars, 10 mm (*2b*), 1 mm (*2c*) (new).——FIG. 191,*2d, M. obuti* (TZAJ, 1973), holotype, GM 1226/360, *arrow* indicates position of sicula, Chu-Iliy Mountains, southern Kazakhstan, interval is of Darriwilian age as it includes biserials, scale bar, 10 mm (Tzaj, 1973, fig. a).

Orthodichograptus D. E. THOMAS, 1972, p. 529, [**O. robbinsi;* OD]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive distal bifurcations starting from a tetragraptid proximal end followed by one or more orders of delayed dichotomy; central disc present; thecae simple with moderate overlap. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone): Australia.——FIG. 189. **O. robbinsi,* holotype, NMV P73827 (upper specimen) and paratype, NMV P83089 (lower specimen), Victoria, Australia, scale bar, 50 mm (new).

Schizograptus NICHOLSON, 1876, p. 248 [**Dichograpsus reticulatus* NICHOLSON, 1868d, p. 143; OD] [=*Kellamograptus* RICKARDS & CHAPMAN, 1991, p. 45, (type, *Trochograptus australis* HARRIS & THOMAS, 1938a, OD), syn. herein; =*Trochograptus* HOLM, 1881b, p. 48 (type, *T. diffusus,* M), syn. herein; =*Ctenograptus* NICHOLSON, 1876, p. 248 (type, *Dichograpsus* (?) *annulatus* NICHOLSON, 1869, p. 233, OD), syn. herein]. Multiramous tubarium with two dichotomous bifurcations producing a tetragraptid proximal end, followed by three or more orders of lateral branching produced on one side of parent stipe, which follows the growth direction of second-order stipes; thecal style poorly known. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Dapingian, Expansograptus hirundo* Biozone): worldwide.——FIG. 190,*2a*. **S. reticulatus* (NICHOLSON), lectotype (selected by NICHOLSON, 1876, p. 248), NHMUK PM Q29, *arrow* indicates position of sicula, Skiddaw Slates, Scale Hill, Loweswater Cottages, Cumbria, UK, scale bar, 10 mm (Elles & Wood, 1902, pl. 7).——FIG. 190,*2b*. *S. australis* (HARRIS & THOMAS, 1938a), holotype, NMV P32081, Allotment 25B, northern boundary, section III, Sandon, Victoria, Australia, *arrow* indicates position of sicula, scale bar, 50 mm (Rickards & Chapman, 1991, fig. 82).

Triaenograptus T. S. HALL, 1914, p. 115 [**T. neglectus;* M] [?=*Tridensigraptus* ZHAO, 1964, p. 638 (type,

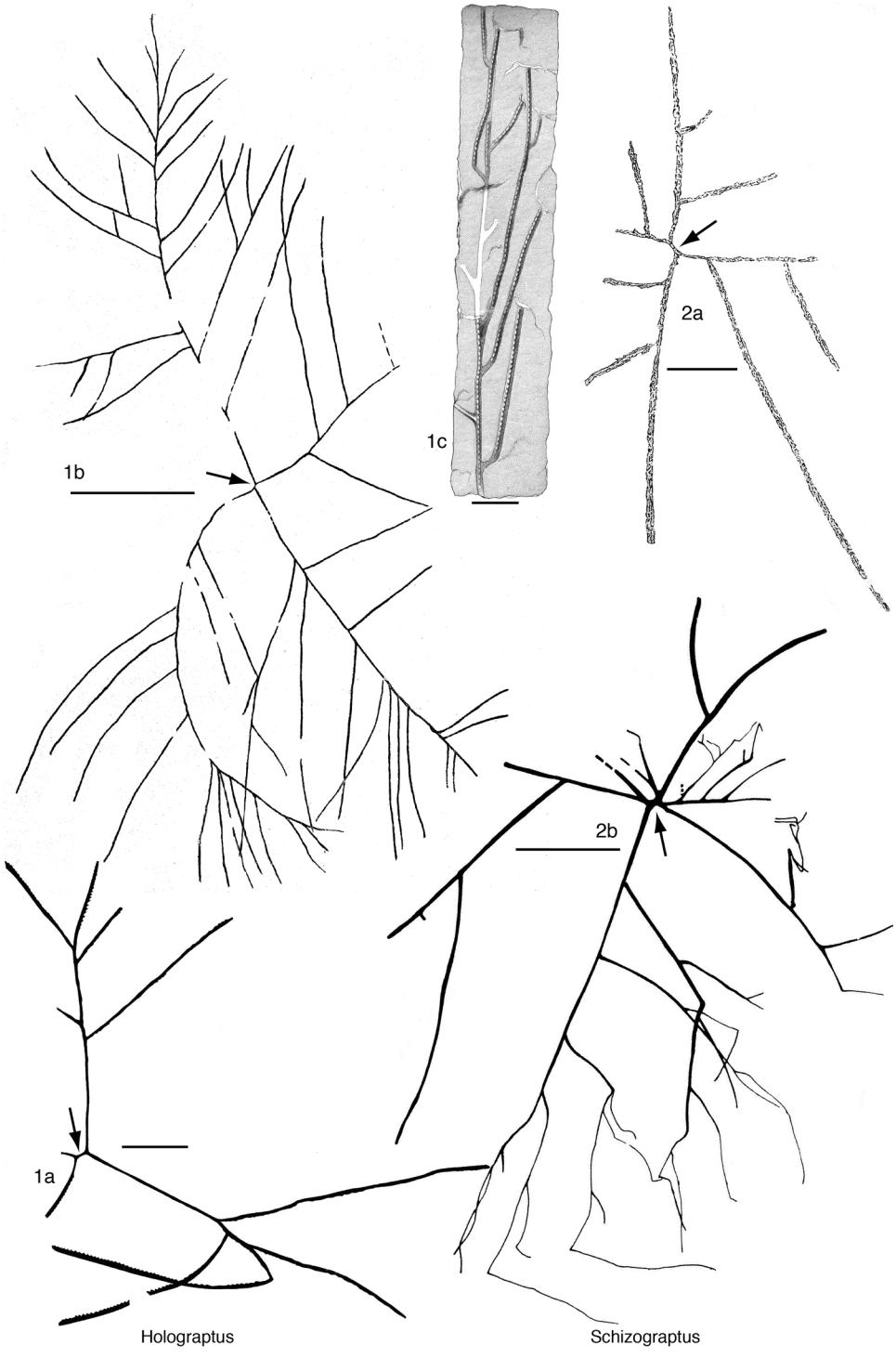


Fig. 190. Dichograptidae (p. 291–294).

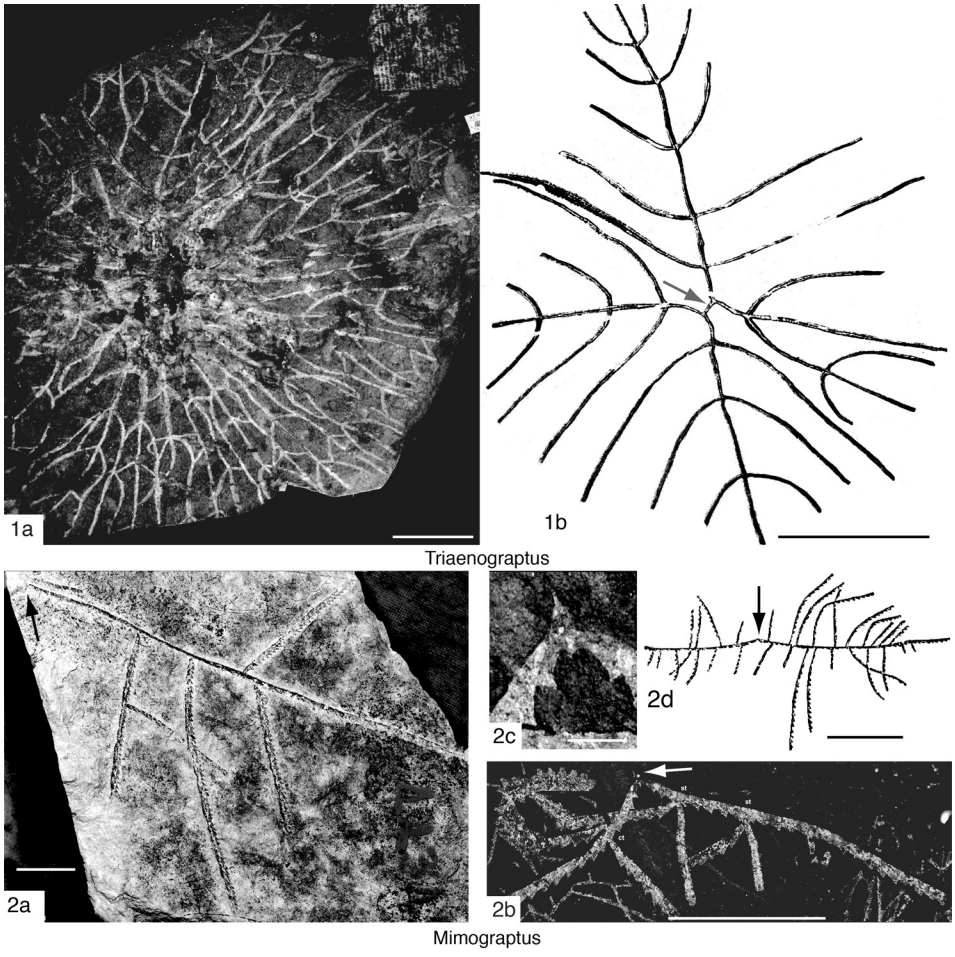


FIG. 191. Dichograptidae (p. 293–296). Color images of specimens available in *Treatise Online* 108.

Tridensigraptus zhejiangensis, OD), syn. herein]. Large umbrella-shaped dichograptid with tetragraptid proximal end; paired lateral branches (tridents) of third and later orders anastomose with adjacent branches in larger specimens; details of proximal end not known. *Lower Ordovician* (*upper Floian, Isograptus lunatus* Biozone)–*Middle Ordovician* (*Dapingian, Expansograptus hirundo* Biozone): Australia, China.——FIG. 191,*1a*. **T. neglectus,* holotype, NMV P132125, Barkers Creek Slate Quarry, north of Castlemaine, Victoria, Australia, scale bar, 50 mm (new).——FIG. 191,*1b*. *T. zhejiangensis* (ZHAO, 1964), holotype, GMCH 1836, Duze, western Zhejiang, China; *arrow* indicates position of sicula, scale bar, 50 mm (Zhao, 1964, pl. 3,*1*).

Family PHYLLOGRAPTIDAE Lapworth, 1873

[Phyllograptidae LAPWORTH, 1873b, table 1, facing p. 555] [=Tetragraptidae FRECH, 1897, p. 593 (*ex* subfamily Tetragraptini FRECH, 1897, p. 593); =Tetragraptidae MU, 1950b, p. 180; =Tetragrapta in MALETZ, CARLUCCI, & MITCHELL, 2009, p. 12; =Pseudotrigonograptidae OBUT & SENNIKOV, 1984a, p. 80]

Four- to two-stiped, pendent to horizontal, reclined, reflexed, and scandent, biradiate graptoloids produced by one proximal dichotomy and with th3[1] and th3[2] as only distal dicalycal theca; sicula conical, widening distinctly toward the aperture, with rutellum and small prosicula; thecae simple, widening tubes commonly with distinct rutellum; proximal end development isograptid, dextral. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone): worldwide.

The Phyllograptidae LAPWORTH, 1873b originally included only the scandent quad-

riserial dichograptids. It is used herein for the paraphyletic clade identified as the family Tetragraptidae Frech, 1897 by Maletz (2014b). Maletz, Carlucci, and Mitchell (2009, p. 12) defined their crown-clade Tetragrapta as "the common ancestor of *Tetragraptus serra* (Brongniart, 1828)and the first taxon to have distal dicalycal thecae limited to th3[1] and th3[2], forming a quadriramous rhabdosome." They referred to it as the superorder Pan-Tetragrapta but essentially accepted the clade as a monophyletic grouping. Cooper and Fortey (1982) emended Phyllograptidae Lapworth, 1873b to include the genera *Phyllograptus* and *Xiphograptus,* based on the interpretation of the virgellar spine as a synapomorphy of the group. However, Maletz (2010a) considered the origin of the dorsal virgellar spine to be independent in *Phyllograptus* and *Xiphograptus*, based on chemically isolated material.

The members of the Phyllograptidae can be characterized by the presence of only two distal dichotomies, those at th3[1] and th3[2] (see Maletz, 1992, fig. 1e). Stipe reduction by suppression of distal dichotomies is present in some species, such as the two- to four-stiped members of *Tshallograptus fruticosus* (see Harris & Thomas, 1938b; Thomas, 1960). Stipe attitude is quite variable, whereas the proximal development with its compact crossing canals appears to be largely constant. Cooper and Fortey (1982) studied details of the proximal development of *Phyllograptus* and *Pseudophyllograptus* from isolated material and serial sectioning and compared it with the development in *Tetragraptus*. The proximal development of *Pseudotrigonograptus* is known from the investigation of Fortey (1971), who demonstrated that the construction of its tubarium is identical to that of other phyllograptids. The sicula develops a dorsal virgellar spine in the genus *Phyllograptus* (see Cooper & Fortey, 1982; Maletz, 2010a), but the precise evolutionary origin of this feature has not been traced.

The evolutionary relationships of the genera *Tetragraptus* and the scandent phyllograptids were evaluated by Strandmark (1902) and Cooper and Lindholm (1985), among others; and it is clear that taxa such as *Tetragraptus phyllograptoides* Strandmark, 1902 and *Tetragraptus cor* (Strandmark, 1902) can be regarded as good indicators of this transition, even though the precise evolutionary relationships are not known. The appearance of partly scandent *Tetragraptus* species at several levels in the Lower to Middle Ordovician may indicate a complex repetitive evolution of phyllograptid-like species. Cooper and Lindholm (1985) suggested the existence of at least three independent lineages leading to phyllograptoid colonies, interpreted as an example of convergent evolution in graptolites.

Phyllograptus Hall, 1858, p. 137 [**P. typus;* OD] [=*Phyllograpsus* Hall in Nicholson, 1872a, 1872b; non *Phyllograpsus* Angelin in Salter, 1858 (=*Rhabdinopora* Eichwald, 1855)]. Phyllograptid with four stipes united along dorsal margins, producing cruciform cross section; median septa reduced to framework of fornices and central columella with open foramen between thecae of adjacent series; sicula with dorsal virgellar spine, often strongly elongated and thickened, proximal development isograptid, dextral; thecae continuing to grow and elongate as tubarium itself continues to grow. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Dapingian, Isograptus victoriae* Biozone): Canada, USA, Australia, New Zealand, Argentina, China.——Fig. 192,*1a–e*. **P. typus; 1a,* lectotype, GSC 942b, ?G-locality, Lévis, Quebec, Canada; *1b–c,* PMO NF 3312, PMO NF 3314, isolated material in obverse (*b*) and reverse (*c*) views; *1d,* PMO NF3314, distal view of isolated fragment showing interthecal foramina; *1e,* reconstruction to show central columella; *1b–d,* Spitsbergen, Norway; scale bars, 1 mm (Cooper & Fortey, 1982, fig. 67a–b, 71, 71k, and 74, respectively).

Corymbograptus Obut & Sobolevskaya, 1964, p. 27 [**Didymograpsus v-fractus* Salter, 1863a, p. 138; OD]. Deflexed, two-stiped phyllograptid with distally distinctly widening stipes; proximal development isograptid, dextral; low prosicular origin of th1[1]; crossing canals low on sicula; sicula long and slender as in *Tshallograptus* with mitre-shaped prosicula. *Lower Ordovician* (*Floian, Cymatograptus protobalticus* Biozone)–*Middle Ordovician* (*Darriwilian, Corymbograptus retroflexus* Biozone): China, UK, Czech Republic, Norway, Sweden, Canada, USA, Argentina, ?Bolivia.——Fig. 193,*3a–b*. **C. v-fractus* (Salter); *3a,* neotype, BU 1005a, *Baltograptus jacksoni* Biozone, Buttermere, Skiddaw Slates, Cumbria, UK (Rushton, 2011, fig. 1A); *3b,* BU 1005b, proximal end of larger specimen, scale bars, 1 mm (Rushton, 2011, fig. 1D).——Fig. 193,*3c–d. C. v-fractus tullbergi* (Monsen, 1937);

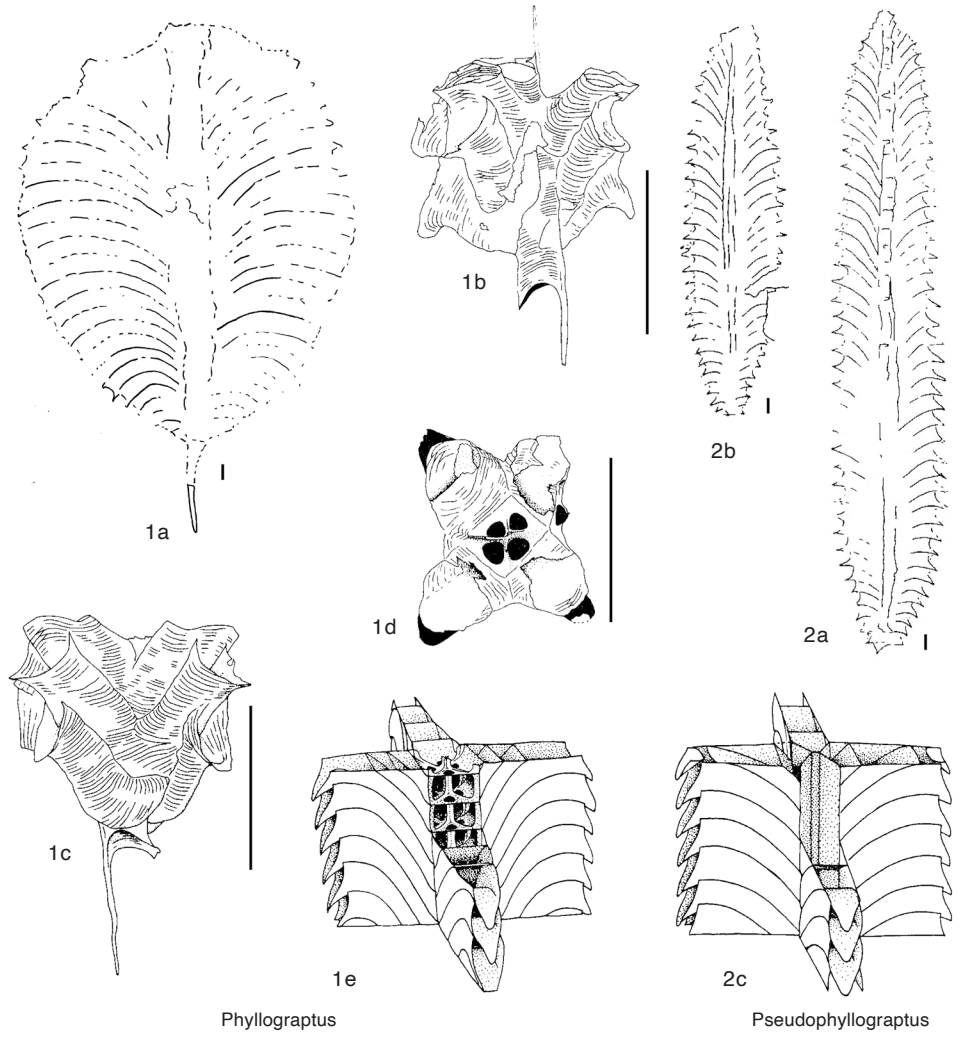


FIG. 192. Phyllograptidae (p. 297–299).

drawings from latex cast, counterpart of holotype, PMO K0484, reverse view (*c*) and PMO 59957 obverse view (*d*); Oslo Region, Norway, scale bars 1 mm (new).——FIG. 193,*3e. C. retroflexus* (PERNER, 1895), OMR 54919, proximal end in reverse view, Drahouš, Czech Republic, scale bar, 1 mm (new).

Paratetragraptus OBUT, 1957, p. 38 [**Tetragraptus approximatus* NICHOLSON, 1873, p. 136; OD]. Phyllograptid with nearly horizontal tubarium; proximal end with slightly deflexed funicle; paired, parallel-oriented second-order stipes; proximal development isograptid, dextral, with robust and wide crossing canals. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone–*Tshallograptus fruticosus* Biozone): worldwide.——FIG. 195,1. **P. approximatus* (NICHOLSON), lectotype, NHMUK PM 1996, Lévis, Quebec, Canada (G-locality, see Maletz, 1997b), scale bar, 1 mm (Nicholson, 1873, fig. 2a).

Pendeograptus BOUČEK & PŘÍBYL, 1952a, p. 12 [**Tetragraptus pendens* ELLES, 1898, p. 491; OD]. Pendent phyllograptid with four stipes; proximal development isograptid, dextral; low prosicular origin of th1[1]; sicula long and slender. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone): worldwide.——FIG. 193,*1. *P. pendens* (ELLES), lectotype (selected by WILLIAMS & STEVENS, 1988, p. 38), NHMUK PM Q37, Barf, Loweswater Formation, Skiddaw Slates, Cumbria, UK, scale bar, 1 mm (adapted from Elles, 1898, fig. 13).

Pseudophyllograptus COOPER & FORTEY, 1982, p. 241 [**Phyllograptus angustifolius angustifolius* HALL, 1858; OD]. Phyllograptid with four stipes united along dorsal margins, producing cruciform

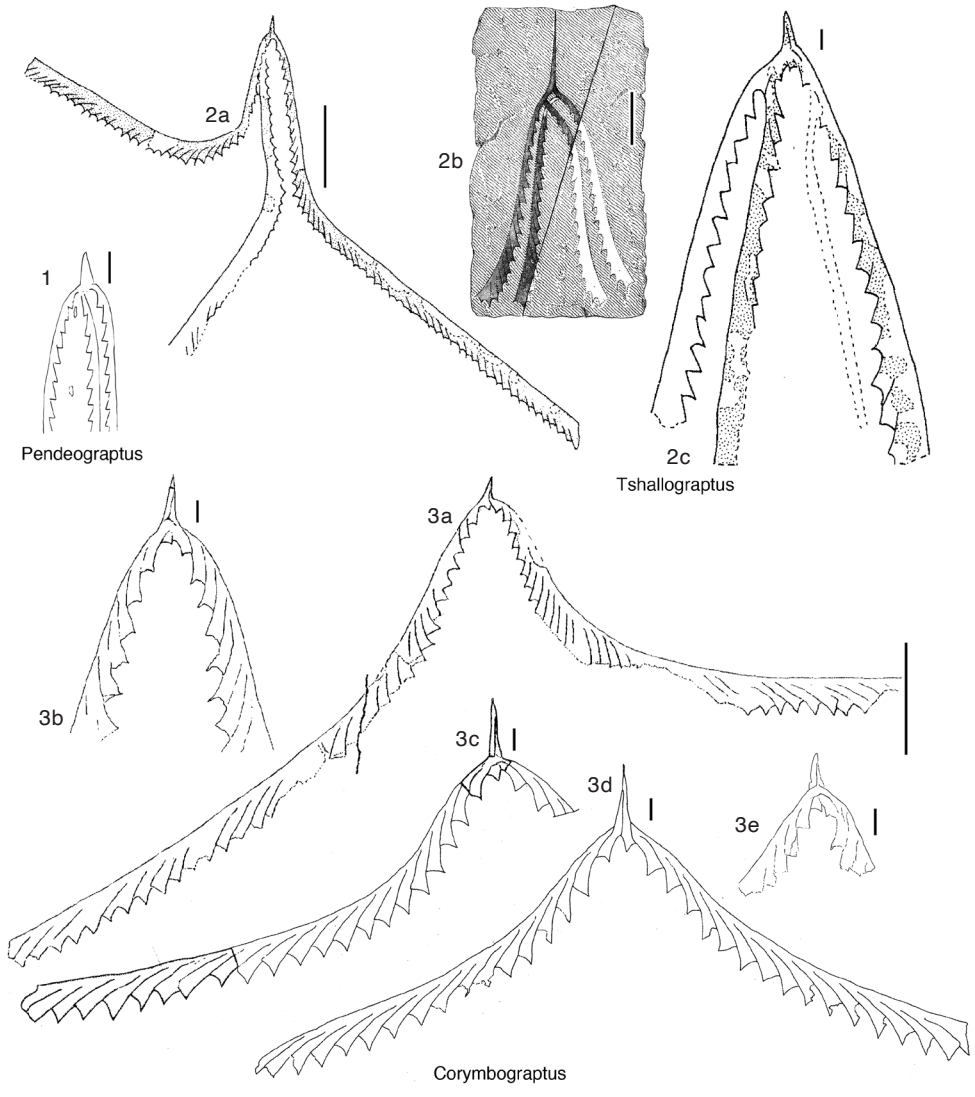


FIG. 193. Phyllograptidae (297–300).

cross section; median septa cruciform, imperforate; proximal development isograptid, dextral. *Lower Ordovician* (*Floian, Tetragraptus akzharensis* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone): worldwide.——FIG. 192,*2a–c*. **P. angustifolius* (HALL)*; 2a,* lectotype, GSC 939b; *2b,* paratype, GSC 939; *2c,* reconstruction to show median septum; *Levisograptus dentatus* Biozone Lévis, Quebec, Canada; *2a–b,* scale bars, 1 mm (Cooper & Fortey, 1982, fig. 48f, 48e, and 51, respectively).

Pseudotrigonograptus MU & LEE, 1958, p. 397 (p. 416, English text) [**P. uniformis;* OD] [=*Tristichograptus* JACKSON & BULMAN, 1970, p. 108 (type, *Graptolithus ensiformis* HALL, 1858, p. 133, OD), syn by FORTEY, 1971, p. 192]. Quadriserial or rarely triserial, scandent phyllograptid with stipes not only united along their dorsal margins, but also in lateral contact, elliptical in cross section; median septa cruciform, imperforate; proximal development isograptid, dextral; thecae may have continued growth. *Middle Ordovician* (*Dapingian, Isograptus lunatus* Biozone–*Darriwilian*, *Holmograptus spinosus* or *Nicholsonograptus fasciculatus* Biozone): worldwide.——FIG. 194,*a–b*. **P. ensiformis* (HALL, 1858); *a,* lectotype (selected by RICKARDS, 1973b, p. 598), GSC 949g, Cote Frechette section, Lévis, Quebec, Canada, scale bar, 1 mm (Hall, 1865, pl. 14,*4*); *b,* cross section diagram Cooper & Fortey, 1982, fig. 53).——FIG.194,*c–d, P. minor* MU & LEE, 1958,

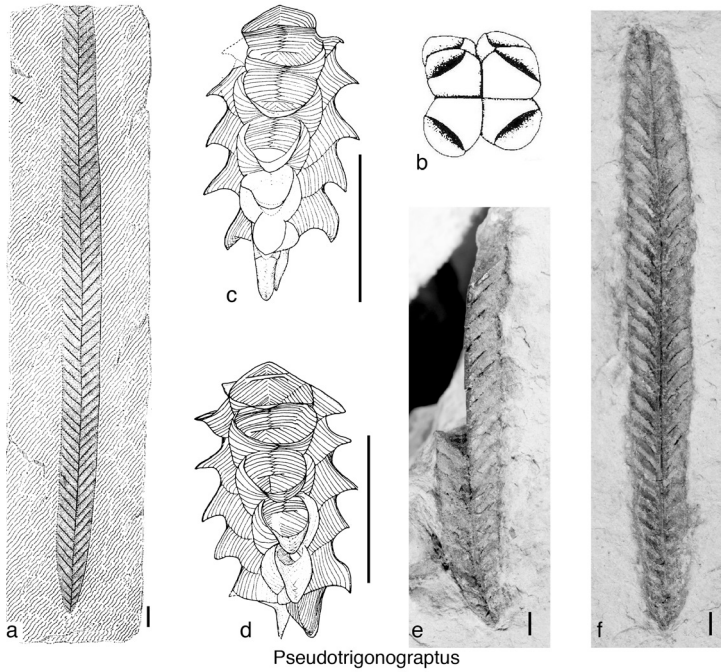


FIG. 194. Phyllograptidae (p. 299–300).

three-stiped taxon in different views (not preserved, see SM A70588 for a similar specimen), Spitsbergen, Norway; scale bars, 1 mm (Fortey, 1971, fig. 3).——FIG.194,*e–f* (on one slab); **P. uniformis; e,* holotype, NIGP 9719, *Exigraptus clavus* Biozone, Ningkuo Shale, Huangnikang, Kiangshan, China (new); *f,* paratype, NIGP 9718; scale bars, 1 mm (new).

Tetragraptus SALTER, 1863a, p. 140, original spelling as *Tetragrapsus* changed in ICZN, Opinion 650, 1963 [**Graptolithus bryonoides* HALL, 1858, p. 126; OD (=*Tetragraptus serra* BRONGNIART, 1828, p. 71, see ELLES & WOOD, 1902, p. 66)] [*non Tetragrapsus* RATHBUN, 1918, p. 273 (Decapoda)]. Phyllograptid with four horizontal to reclined, reflexed, and scandent stipes; proximal end isograptid, dextral, with wide crossing canals and tetragraptid proximal end; thecae with considerable overlap and moderate development of rutellum. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone): worldwide.——FIG. 195,*2a*. **T. serra,* lectotype, NHMUK PM 26995, Lévis, Quebec, Canada, scale bar, 1 mm (Cooper & Fortey, 1982, fig. 14).——FIG. 195,*2b*. *T. bryonoides* (HALL), lectotype, GSC 978, scale bar, 1 mm (Cooper & Fortey, 1982, fig. 16).——FIG. 195,*2c. T. cor* (STRANDMARK, 1902), SGU 3844, 1-2 preservation, scale bar, 1 mm (Cooper & Lindholm, 1985, fig. 3g).——FIG. 195,*2d–e*. *T. phyllograptoides* STRANDMARK, 1902; *2d,* LO 5377t, specimen in 1-2 preservation; *2e,* LO 5372t, specimen in a-b preservation; scale bars, 1 mm (Cooper & Lindholm, 1985, fig. 1m and 1c).——FIG. 195,*2f–g*. *T. phyllograptoides triumphans* COOPER & FORTEY, 1982; *2f,* PMO NF3303, juvenile in obverse view; *2g,* PMO NF 3181, proximal end in reverse view showing massive crossing canals; scale bars, 1 mm (Cooper & Fortey, 1982, fig. 22c and 22g, respectively).

Tshallograptus VANDENBERG, 2017, p. 54 [**Graptolithus fruticosus* HALL, 1858, p. 128; OD]. Pendent to deflexed phyllograptid; proximal development isograptid, dextral; low prosicular origin of th1[1]; crossing canals low on sicula; sicula long and slender, with mitre-shaped prosicula. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone–*Didymograptellus kremastus* Biozone): worldwide.——FIG. 193,*2a–c*. **T. fruticosus* (HALL); *2a,* GSC 79584, large, three-stiped specimen, Cow Head Group, western Newfoundland, Canada, scale bar, 10 mm (Williams & Stevens, 1988, fig. 27s); *2b,* paratype, GSC 925, showing deflexed stipe ends, sicula merges into thickened nema, scale bar, 5 mm (Hall, 1865, pl. 6,*1*); *2c,* lectotype, GSC 926, Isle d'Orleans, Quebec, Canada; scale bar, 1 mm (Williams & Stevens, 1988, fig. 27G).

Family DIDYMOGRAPTIDAE Mu, 1950

[Didymograptidae MU, 1950b, p. 180 (*emend.* MU & others, 2002, p. 228)] [incl. Aulograptinae HSÜ & CHAO, 1976, p. 137]

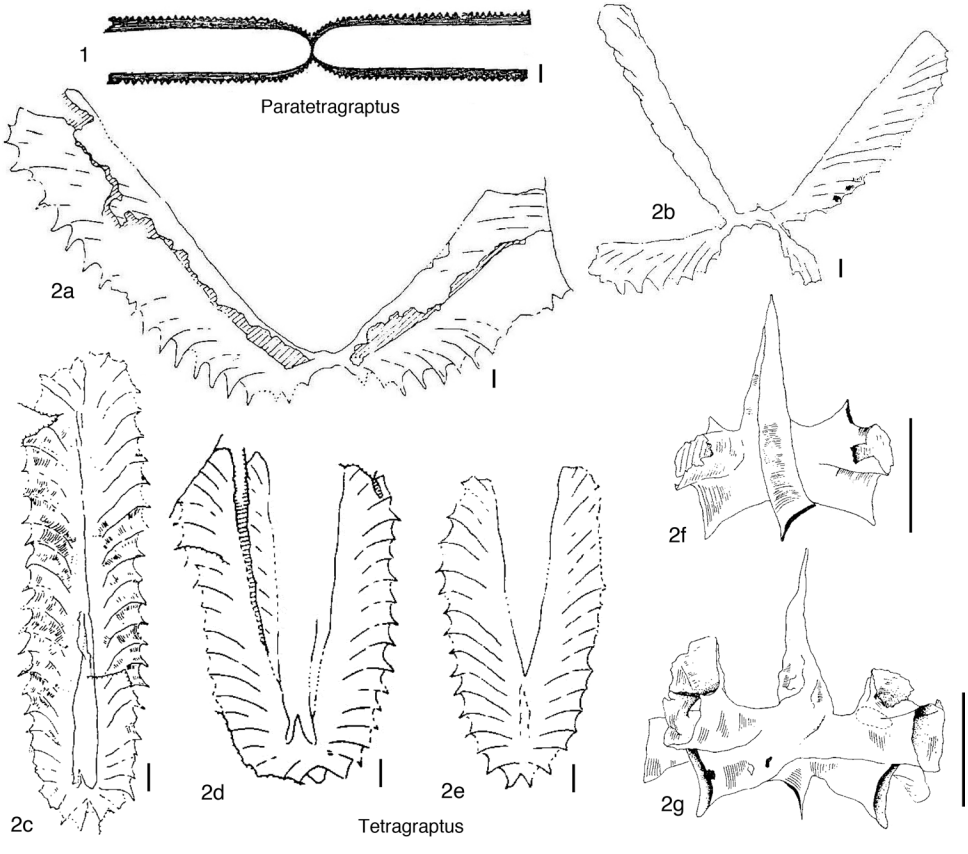


FIG. 195. Phyllograptidae (298–300).

Two-stiped, pendent to horizontal, reclined, reflexed, and deflexed graptoloids; sicula conical, widening distinctly toward aperture, with small prosicula; thecae simple, widening tubes; rutellum present in derived taxa; thecae rarely complex or with prothecal folding; proximal development isograptid, dextral or derived artus type. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone): worldwide.

The Didymograptidae is a poorly defined group of two-stiped taxa with a highly variable tubarium shape, ranging from pendent to reclined. The taxa are united by a conical sicula with a relatively small prosicula. The proximal development is of the isograptid dextral type or the derived artus type with the crossing canals symmetrically placed but typically having distinct differences in width. The position of the foramen for th1[1] is in the lower part of the prosicula in early taxa (Fig. 196.1) but may be in the middle part of the metasicula (Fig. 196.2) and even in its lower part in derived forms. GUTIÉRREZ-MARCO (1986) considered the separation of genera or subgenera based on the presence of an isograptid- or artus-type proximal development in the genus *Didymograptus.* He differentiated the subgenus *Jenkinsograptus* with an isograptid-type development from *Didymograptus* with an artus-type development. MALETZ (1994b) and MALETZ and SLOVACEK (2013), however, preferred to keep species with isograptid- and artus-type developments in the genus *Baltograptus,* indicating that the position of the dicalycal theca might be of lesser importance for taxonomic interpretations.

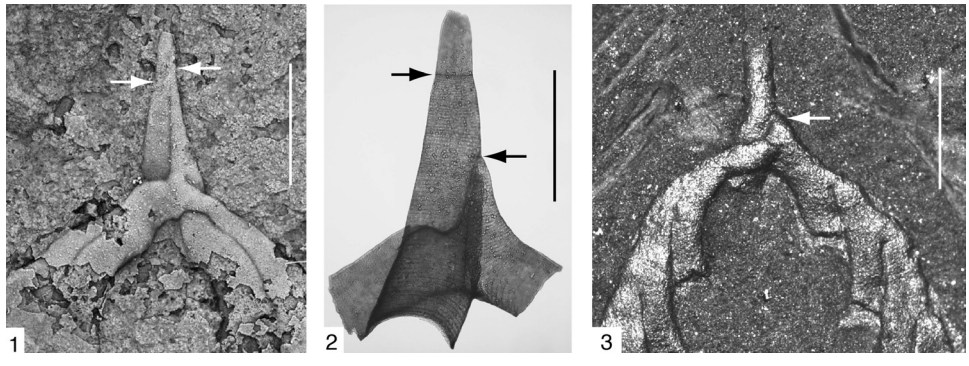


FIG. 196. The proximal development of the Didymograptidae. *1, Expansograptus* sp., PMU 23168, latex cast, low prosicular origin of th1[1], Hunneberg, Västergötland, Sweden (new); *2, Baltograptus kurcki* (TÖRNQUIST, 1901), SGU 9615, isolated specimen showing fuselli, metasicular origin of th1[1], artus-type development, Talubäcken, Dalarna, Sweden (new); *3, Didymograptus artus* (ELLES & WOOD, 1901), PMU 31742, reverse view, Fågelsångsdalen drill core, 22.9m, Scania, Sweden (new). All scale bars, 1 mm.

The distinction of *Norvegiograptus* LI & others, 2014 based on the proximal development is unclear. The authors state an artus-type development with a dicalycal th1[2] in the English translation of the text and show an isograptid, sinistral development (LI & others, 2014, fig. 2B). Further specimens identified as *Norvegiograptus liber* (MONSEN, 1937) have an artus-type development (LI & others, 2014, fig. 4) in dextral and sinistral specimens.

Numerous taxa have been referred to the genus *Didymograptus* in the past (MU & others, 2002), and many have been reassigned to other genera in recent decades due to the recognition of constructional differences in the proximal development and thecal style. The sigmagraptine genus *Acrograptus* TZAJ, 1969 largely includes species with a sigmagraptine parallel-sided sicula and slender, asymmetrically placed stipes. Species with a dorsal virgellar spine are now included in *Didymograptellus*, *Yutagraptus*, and *Xiphograptus*, as revised by MALETZ (2010a), and are referred to the Pterograptidae. Most horizontal and some reclined and declined forms are now referred to *Expansograptus*.

Didymograptus M'COY, 1851 in SEDGWICK & M'COY, 1851–1854, p. 9, original spelling as *Didymograpsus* changed in ICZN Opinion 650, 1963 [**Graptolithus murchisoni* BECK in MURCHISON, 1839, p. 694; SD MILLER, 1889, p. 185] [=*Cladograpsus* GEINITZ, 1852, p. 29 (type, *Graptolithus murchisoni* BECK in MURCHISON, 1839, p. 694, SD BULMAN, 1929, p. 169), obj.; =*Parazygograptus* KOZŁOWSKI, 1954, p. 439 (type, *P. erraticus,* OD), syn. by MALETZ, 1994b, p. 30; =*Trigonograpsus* NICHOLSON, 1869, p. 231 (type, *T. lanceolatus*, M), syn. by JACKSON & BULMAN, 1970, p. 108]. Pendent didymograptid with low metasicular origin of th1[1] and artus-type proximal development; stipes slender or distinctly widening distally; proximal end usually covered by cortical overgrowth in gerontic specimens. *Middle Ordovician* (*Darriwilian, Didymograptus artus* Biozone–*Pseudamplexograptus distichus* Biozone): Belgium, UK, Czech Republic, France, Germany, Norway, Spain, Sweden, China, North Africa, Saudi Arabia, western Australia, Bolivia, Colombia, Peru.——FIG. 197,*1a. D. murchisoni* (BECK in MURCHISON), lectotype (selected by ELLES & WOOD, 1901, p. 40), BGS GSM 6820b, Gelli, near Llandrindod, Wales, UK, scale bar, 1 mm (Strachan & Kashogji, 1984, fig. 7).——FIG.197, *1b–d. D. artus* (ELLES & WOOD, 1901); *1b,* CPC 7010, isolated proximal fragment showing artus-type development, Canning Basin, Willara 1 drill core, Australia, scale bar, 0.5 mm (Skwarko, 1968, fig. 2); *1c–d, D. erraticus*, holotype, ZPAL G./III, complete specimen (*d*) and proximal end (c) showing fuselli, Poland, scale bars 1 mm (*1c*), 0.5 mm (*1d*) (Kozłowski, 1954, fig. 9).——FIG. 197,*1e. Didymograptus* sp., NHMUK PM Q49, holotype of *Trigonograpsus lanceolatus*, scale bar, 1 mm (Jackson & Bulman, 1970, fig. 1).

Aulograptus SKEVINGTON, 1965, p. 25 [**Didymograptus cucullus* BULMAN, 1932c, p. 15; OD (=*Didymograptus climacograptoides* BULMAN, 1931, p. 41, syn. by MALETZ, 1997a, p. 29)]. Pendent didymograptid with metasicular origin of th1[1]; stipes subparallel, gradually widening distally; proximal development of isograptid type; thecae with strongly modified, geniculate thecal apertures. *Middle Ordovician* (*lower Darriwilian, Undulograptus austro-*

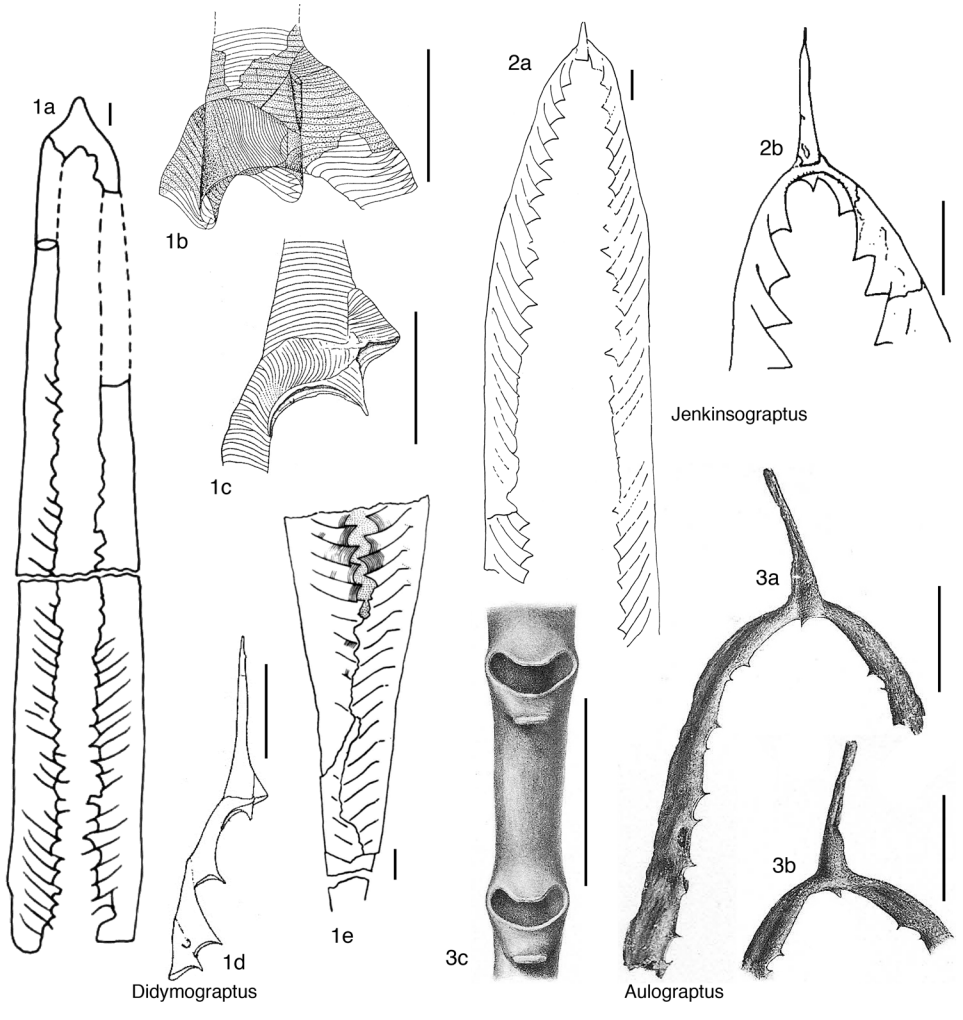


FIG. 197. Didymograptidae (p. 302–305).

dentatus Biozone–*Nicholsonograptus fasciculatus* Biozone): Belgium, UK, Czech Republic, Norway, Spain, Sweden, Canada, Argentina, Bolivia, Peru, China.——FIG. 197,*3a–c*. *A. climacograptoides* (BULMAN, 1931); *3a–3b,* originally described as the holotype of *A. cucullus,* NRM-PZ Cn 1261, obverse (*a*) and reverse (*b*) views, Hälludden, Öland, Sweden, scale bars, 1 mm (Bulman, 1932**c**, pl. 1,*3–4*); *3c,* fragment showing thecal apertures, reconstruction, scale bar, 1 mm (Bulman, 1932**c**, pl. 1,*5*).

Baltograptus MALETZ, 1994b, p. 36 [**Didymograptus vacillans* TULLBERG, 1880b, p. 42; OD] [=*Norvegiograptus* LI & others, 2014, p. 173 (type, *Didymograptus liber* MONSEN, 1937, p. 122, OD, =*D. kurcki* TÖRNQUIST, 1901), syn. herein]. Horizontal to deflexed, declined and pendent didymograptids; sicula slender, with long supradorsal portion; proximal development of isograptid or artus type with moderately low origin of th1[1] from metasicula and comparably long ventral free apertural length of sicula; isograptid suture very short or missing. *Lower Ordovician* (*Floian, Cymatograptus protobalticus* Biozone–*Baltograptus minutus* Biozone): UK, Czech Republic, France, Norway, Sweden, Turkey, Argentina, Bolivia, China.——FIG. 198,*2a–c*. **B. vacillans* (TULLBERG); *2a,* lectotype, LO 345t, Kiviks Esperöd, Scania, Sweden (new); *2b–c,* PMU 23157, reverse (*b*), and obverse view (*c*) drawing of latex cast, Diabasbrottet, Hunneberg, Sweden (new). All scale bars, 1 mm.——FIG. 198,*2d–e*. *B. kurcki* (TÖRNQUIST, 1901), *2d*, LO 1633t, proximal end, obverse view; *2e,* lectotype, LO 1632T, reverse view of molds; Tøyen Shale

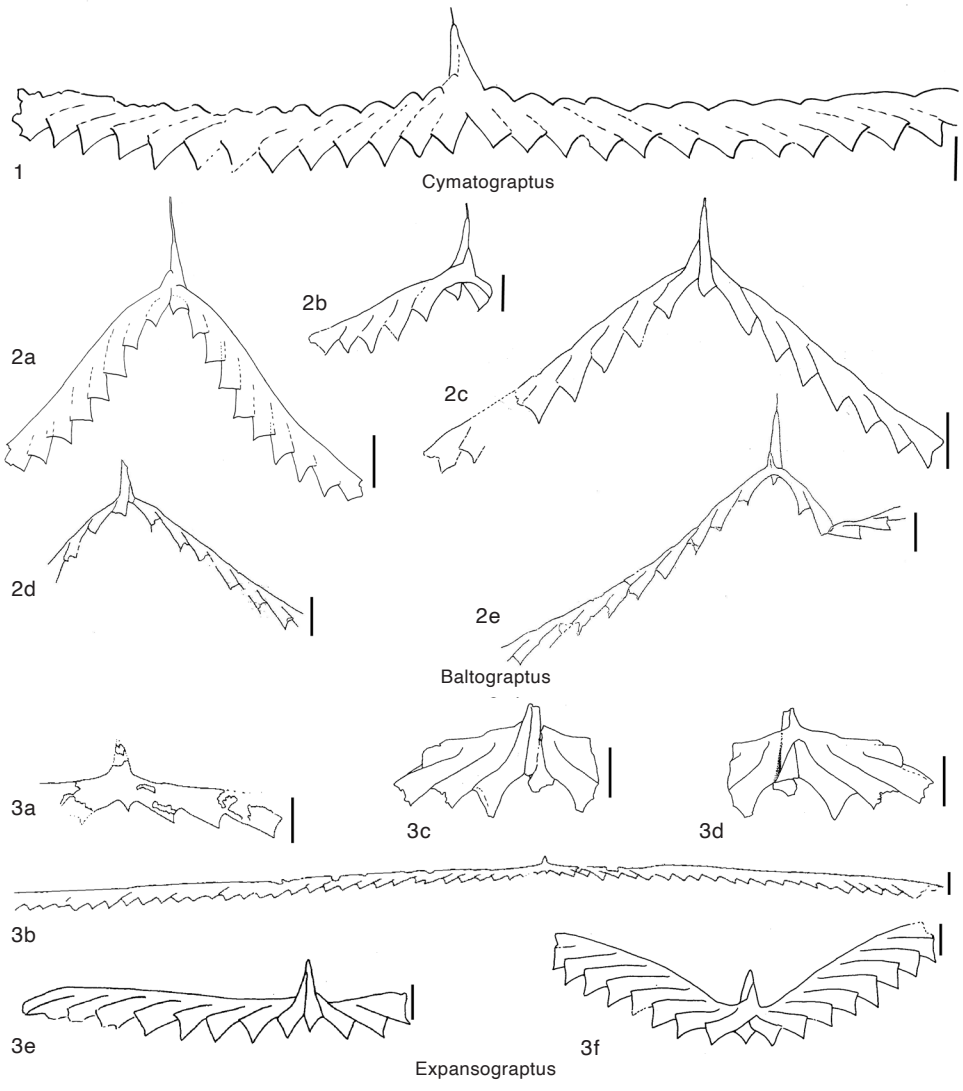


FIG. 198. Didymograptidae (p. 303–305).

Formation, Jerrestad, Scania, Sweden, scale bars, 1 mm (Rushton, 2008, Atlas, Folio 2.51).

Cymatograptus JAANUSSON, 1965, p. 424 [**Didymograptus undulatus* TÖRNQUIST, 1901, p. 10; OD]. Slender, horizontal to subhorizontal or declined tubarium; thecae simple with moderate inclination and some species with prothecal folds; sicula relatively long and slender, with small (less than one-fourth of sicular length) prosicula; supradorsal portion of sicula prominent and with long free ventral side of the aperture; proximal development type isograptid, dextral to artus type, dextral or sinistral; low prosicular origin of th1[1]. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone–*Baltograptus jacksoni* Biozone): Norway, Sweden, Argentina, Australia (New South Wales), Bolivia, China, Canada.——FIG. 198,*1*. **C. undulatus* (TÖRNQUIST), lectotype, LO 1574T, *Tetragraptus phyllograptoides* Biozone, Diabasbrottet, Hunneberg, scale bar, 1 mm (new).

Expansograptus BOUČEK & PŘÍBYL, 1952a, p. 13 [**Graptolithus extensus* HALL, 1858, p. 132; OD] [=*Extensograptus* BOUČEK & PŘÍBYL, 1952a (English abstract), p. 1, misspelling of *Expansograptus*]. More or less horizontal didymograptids with isograptid, dextral proximal development; proximal portion of sicula perpendicular to stipes; sicular and thecal apertures straight, without elaborations; origin

of th1[1] low on prosicula; stipe width variable; crossing canals more or less symmetrically placed on sicula; crossing canal 1 is initially much wider than crossing canal 2; length of isograptid suture variable. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Darriwilian, Undulograptus austrodentatus* Biozone): worldwide.——Fig. 198,*3a–b*. **E. extensus* (Hall), lectotype, GSC 976, proximal end (*a*) and complete specimen (*b*), scale bars, 1 mm (Cooper & Fortey 1982, fig. 40d–e).——Fig. 198,*3c–d*. *E. hirundo* (Salter, 1863a), obverse (*c*) and reverse (*d*) view, Tøyen Shale, Slemmestad, Oslo, Norway; scale bars, 1 mm (new).——Fig. 198,*3e*. *E. suecicus* (Tullberg, 1880*b*), T226, Tøyen section, Oslo, Norway, scale bar, 1 mm (new).——Fig. 198,*3f*. *E. urbanus* (Monsen, 1937), PMU 23152B, drawing of latex cast in reverse view, Diabasbrottet, Hunneberg, Sweden, scale bar, 1 mm (new).

Jenkinsograptus Gutiérrez-Marco, 1986, p. 199 [**Didymograptus spinulosus* Perner, 1895, p. 22; OD]. Pendent didymograptid with low metasicular origin of th1[1] and isograptid-type proximal development; stipes slender or distinctly widening distally. *Middle Ordovician* (*Darriwilian, Didymograptus artus* Biozone–*Nicholsonograptus fasciculatus* Biozone): Belgium, UK, Czech Republic, France, Germany, Norway, Spain, Sweden, China, Saudi Arabia.——Fig. 197,*2a–b*. *J. spinulosus* (Perner); *2a,* holotype, NMP L7564, *Corymbograptus retroflexus* Biozone, Šarka Formation, Osek near Rokycany, scale bar, 1 mm (adapted from Bouček, 1973, fig. 27a); *2b,* NHMUK PM Q5161, proximal end in reverse view, Llanfallteg Formation, South Wales, UK; scale bar, 1 mm (Fortey & Owens, 1987, fig. 112a).

Family PTEROGRAPTIDAE Mu, 1950

[Pterograptidae Mu, 1950b, p. 180] [*nom. emend.* Mu, 1974, p. 231, *ex* Pterograptinae Mu, 1950, p. 180]

Two-stiped, pendent to deflexed, and horizontal graptoloids; cladial branching in some taxa form secondarily multiramous tubaria; sicula conical, widening distinctly toward aperture and with small prosicula, or parallel-sided with wide prosicula; sicula with distinct dorsal virgellar spine and antivirgellar origin of th1[1]; thecae simple, widening tubes with moderate development of rutella; proximal development isograptid or artus type, dextral. *Lower Ordovician* (*Floian, Paratetragraptus akzharensis* Biozone)–*Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone): worldwide.

All taxa of the Pterograptidae possess a dorsal virgellar spine on the sicula. This spine is regarded as the defining synapomorphy. The family may be monophyletic, but no cladistic analysis of the group has yet been carried out. Maletz, Carlucci, and Mitchell (2009) included a group of virgellate taxa among the stem reclinatids. The Pterograptidae incorporates the virgellate dichograptids, except for the four-stiped, scandent members of the genus *Phyllograptus* in which the virgellar spine evolved independently (Maletz, 2010a). The proximal part is quite variable with the dimension of the prosicula changing considerably from a comparably large prosicula in the early taxa (Fig. 199.1, Fig. 199. 3) to a small one in later taxa (Fig. 199.4, Fig. 199.7, Fig. 199.10–11). The proximal development is of the isograptid type, but derived species possess an artus-type development (Fig. 199.10). All taxa have two main stipes with an orientation ranging from pendent to deflexed and horizontal, and, in a few cases, slightly reflexed proximally. The genera *Pterograptus* and *Pseudobryograptus* have a multiramous, pendent colony shape through the addition of thecal cladia.

The Pterograptidae originated during the Floian with the genus *Didymograptellus* bearing primitive, symplesiomorphic characters, such as the origin of th1[1] in the middle part of the prosicula and simple thecae (Fig. 199.1–199.3). The earliest known species *Didymograptellus primus* Maletz, 2010a from the *Tetragraptus akzharensis* to *Tshallograptus fruticosus* biozones already had a fully developed dorsal virgellar spine. The evolutionary origin of the dorsal virgellar spine is unknown as no morphologically intermediate taxa are available showing its formation. The development of the sicula with the large, parallel-sided prosicula, however, may indicate a close connection to the Anisograptidae, as in this group, the pro- and metasicula generally appear to be parallel sided and do not have a widening from the aperture of the prosicula onward.

Pterograptus Holm, 1881a, p. 74 [**P. elegans;* M]. Pterograptid with long slender sicula, prosicula expanded, origin of th1[1] on metasicula, th1[1]

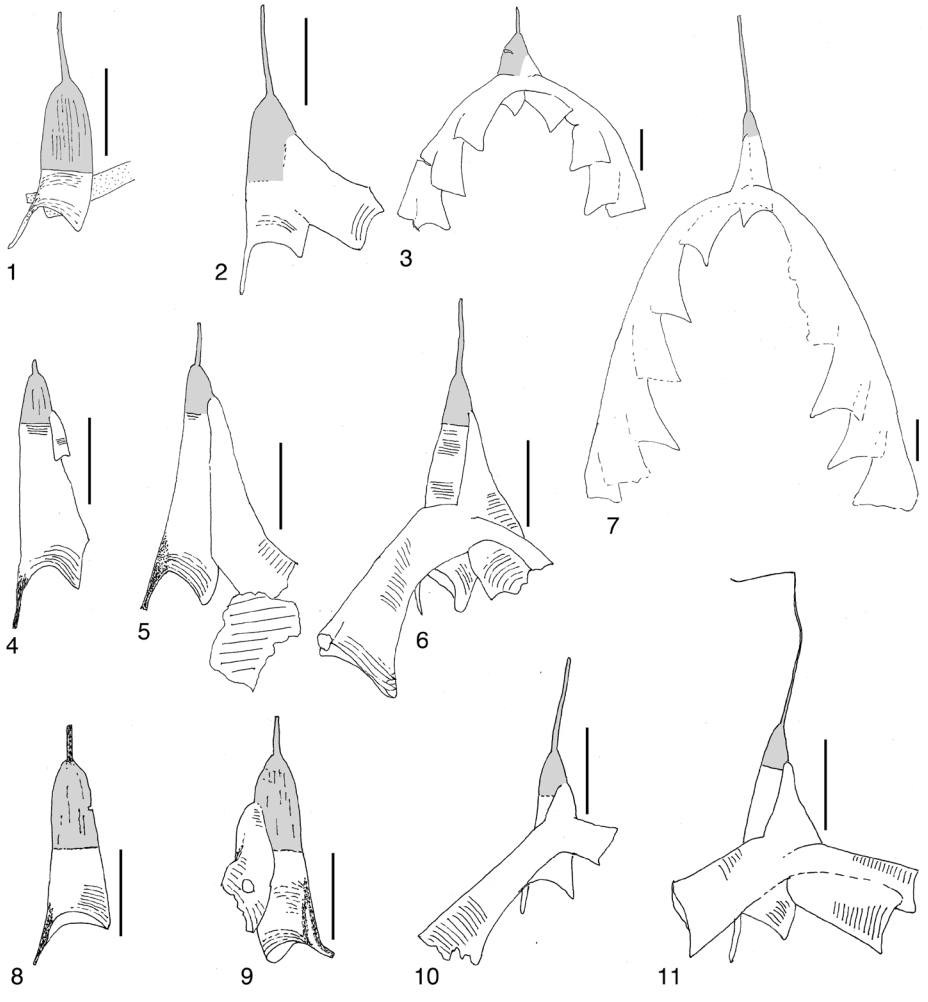


FIG. 199. Proximal ends of isolated pterograptids. *1–3, Didymograptellus bifidus* (HALL, 1865). *1,* Growing sicula, metasicula incomplete; *2,* complete sicula with th1[1]; *3,* proximal end of larger specimen; *4–7, Yutagraptus mantuanus* RIVA, 1994; *4,* sicula with initial part of th1[1]; *5,* sicula with incomplete th1[1]; *6,* proximal end in reverse view, showing virgellar spine; *7,* complete proximal end; *8–9, Didymograptellus primus* MALETZ, 2010a; *8,* incomplete sicula with prominent virgellar spine; *9,* juvenile with incomplete th1[1]; *10, Xiphograptus artus* MALETZ, 2010a, proximal end showing artus-type development; *11, X. lofuensis* (LEE, 1961), proximal end with isograptid development; prosicula in *gray;* all scale bars, 0.5 mm (specimens adapted from Maletz, 2010a).

dicalycal (artus-type development); alternating cladial branches on each theca of the two main stipes; main stipes declined to deflexed. *Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone): UK, France, Germany, Portugal, Sweden, Norway, Canada, USA, Argentina, China, Australia, New Zealand.——FIG. 200,*1a–c. *P. elegans; 1a–1b,* holotype, PMO 2697, Oslo Region, Norway, scale bars, 10 mm (Holm, 1881a, fig. 2–3); *1c,* GSC 102784, flattened and bleached proximal end showing artus-type development, scale bar, 0.5 mm (Maletz, 1994a, fig. 1).——FIG. 200,*1d. P. lyricus* KEBLE & HARRIS, 1934, paratype, NMV P13755, showing zigzag pattern of main stipe, Victoria, Australia, scale bar, 1 mm (new).——FIG. 200,*1e. P. scanicus* HOLM, 1881a, reconstruction, scale bar, 10 mm (Bulman, 1970, fig. 77).

Didymograptellus COOPER & FORTEY, 1982, p. 220 [**Graptolithus bifidus* HALL, 1865, p. 73; OD]. Simple, parallel-sided sicula with a nearly straight aperture and prominent dorsal virgellar spine; prosicula large, at least one-third to one-half of sicular length; proximal development isograptid type, dextral, with high origin of th1[1] in prosicula;

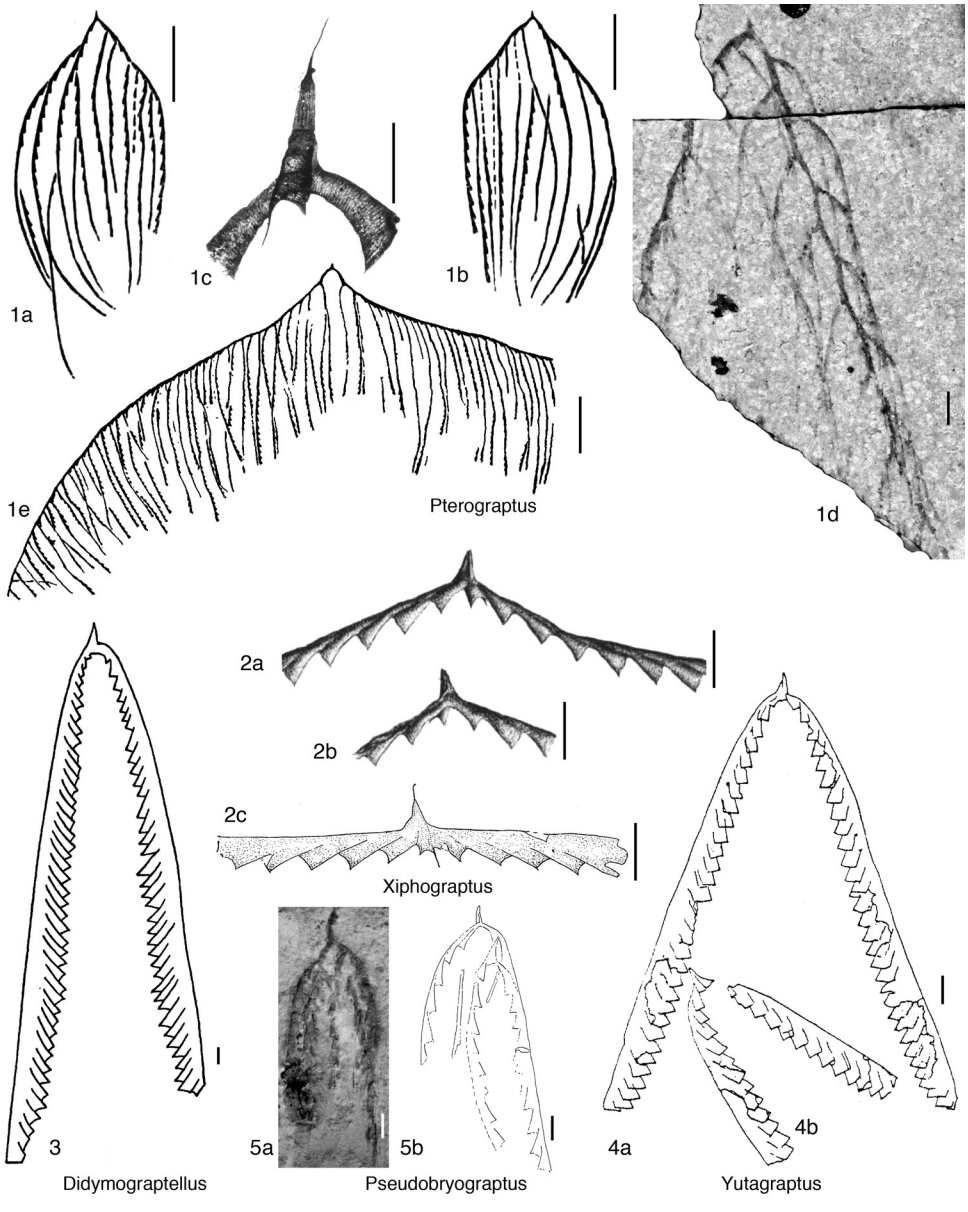


FIG. 200. Pterograptidae (p. 305–308).

crossing canals low on sicula; thecae simple dichograptid with straight apertures; tubarium form pendent. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Dapingian, Arienigraptus gracilis* Biozone): Canada, USA, Argentina, Bolivia, China, Australia, New Zealand.——FIG. 200,*3. *D. bifidus* (HALL), lectotype, GSC 910a, Lévis, Quebec (possibly Begin's Hill section), scale bar, 1 mm (Berry, 1962b, fig. 2a).

Pseudobryograptus MU, 1957, p. 385 (p. 421, English translation) [**P. parallelus;* OD]. Small, pendent tubarium with five to eight stipes; thecae simple with low inclination and overlap; branching after the initial dichotomy possibly by cladia generation; proximal development likely artus type. *Middle Ordovician* (*Darriwilian,* ?*Holmograptus lentus* Biozone): China, Argentina, Australia, ?Canada.——FIG. 200,*5a–b. *P. parallelus; 5a,* holotype, NIGP 8863; *5b,* paratype, NIGP 8864;

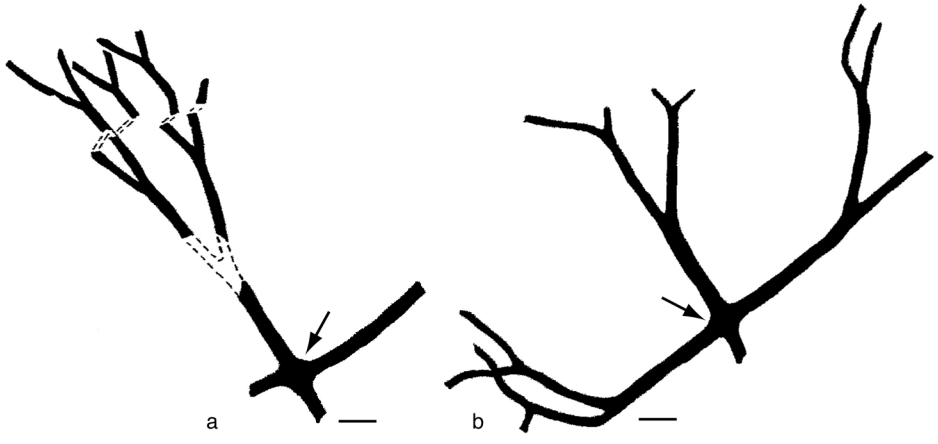


FIG. 201. Suborder Uncertain (p. 308).

possibly *Holmograptus lentus* Biozone (originally cited as *Didymograptus hirundo* Biozone); Changshan, western Chekiang, China, scale bars, 1 mm (new).

Xiphograptus COOPER & FORTEY, 1982, p. 289 [**Didymograptus formosus* BULMAN, 1936a, p. 24; OD]. Simple conical, considerably widening sicula with straight aperture and prominent dorsal virgellar spine (antivirgellar origin of th1[1]); prosicula small, less than one-fourth of sicular length; proximal development isograptid or artus type, th1[1] dextral and originating low in prosicula; crossing canals low on sicula, isograptid suture absent on reverse side; thecae simple dichograptid with straight apertures; tubarium form horizontal, declined, or less commonly, deflexed, with no or little distal widening of the stipes. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone and possibly to *Dicellograptus vagus* Biozone): worldwide.——FIG. 200,*2a–b. *X. formosus* (BULMAN), lectotype, NRM-PZ Cn1264, obverse (*a*) and reverse (*b*) views, Hälludden, Öland, Sweden, scale bars, 1 mm (Bulman, 1936**a**, pl. 1,*5–6*).——FIG. 200,*2c*. *X. lofuensis* (LEE, 1961), holotype, NIGP 10541, Dawan Formation, Majiang, Guizhou Province China, scale bar, 1 mm (Ni, 1988, fig. 1a).

Yutagraptus RIVA, 1994, p. 4 [**Y. mantuanus;* OD]. Simple conical, considerably widening sicula with straight aperture and prominent dorsal virgellar spine; prosicula small, less than one-fourth of sicular length; proximal development isograptid type, dextral, with low origin of th1[1] in prosicula; crossing canals low on sicula, isograptid suture lacking on reverse side; thecae simple dichograptid with straight apertures; tubarium form pendent with no or little distal widening of the stipes. *Middle Ordovician* (*Dapingian, Didymograptellus bifidus* Biozone–*Darriwilian, Levisograptus austrodentatus* or *Levisograptus primus* Biozone): Australia, Canada, USA, ?Iran.——FIG. 200,*4a–b*. **Y. mantuanus,* RPM 13677, holotype (*a*) and paratype (*b*) as associated on slab, Mantua, Utah, scale bar, 1 mm (Riva, 1994, fig. 3M–N).

Suborder UNCERTAIN

Calamograptus CLARK, 1924, p. 61 [**C. porrectus;* OD]. Multiramous dichograptid with tetragraptid proximal end and long second-order stipes; distal stipe division intervals decreasing in length; thecal style and proximal development unknown. *Lower Ordovician* (*upper Tremadocian*, *Clonograptus* Biozone): Canada. [The taxon is based on two very poor specimens, possibly a senior synonym of *Paratemnograptus.*]——FIG. 201,*a–b*. *C. porrectus* CLARK, 1924; *a,* holotype, MCZ IP 101402; *b,* paratype, MCZ IP 10140; North Ridge, Lévis, Quebec, Canada; scale bars, 10 mm (Clark, 1924, pl. 5,*2* and 5,*1,* respectively).

SUBORDER GLOSSOGRAPTINA

Jörg Maletz and Yuandong Zhang

Suborder GLOSSOGRAPTINA Jaanusson, 1960

[Glossograptina Jaanusson, 1960, p. 319] [=Pan-Glossograpta Maletz, Carlucci, & Mitchell, 2009, p. 14] =Pan-Bireclinata Maletz, Carlucci, & Mitchell, 2009, p. 13, *partim*]

Two-stiped, reclined to scandent graptoloids with isograptid symmetry; scandent taxa monopleural or dipleural; sicula tubular, commonly elongated, slightly widening toward Faperture, with small prosicula less than one-third of sicular length; proximal development type isograptid, dextral, with prosicular origin of th1[1] or, in a few cases, a derived pattern; thecae simple, gradually widening tubes, typically with distinct rutella; apertural thecal spines and lacinia present in derived taxa; attenuation of fusellum common. *Middle Ordovician* (*Dapingian*)–*Upper Ordovician* (*Katian*): worldwide.

The paraphyletic taxon Glossograptina includes the partial clade identified by the isograptid symmetry of the colony as the defining synapomorphy (see Maletz & Mitchell, 1996, fig. 8; Maletz, Carlucci, & Mitchell, 2009, fig. 2). However, it excludes the Axonophora (biserial, dipleural graptoloids).

INTRODUCTION

Numerous, well-preserved relief specimens and even chemically isolated specimens of the Glossograptina provide the basis for a detailed understanding of colony construction. The main uniting synapomorphic character of the Isograptidae as the basal Glossograptina is the isograptid symmetry, in which the line of symmetry passes between the sicula and th1[1] (Fig. 202.2–202.3). This differs considerably from the maeandrograptid symmetry in earlier dichograptids (Fig. 202.1). In the maeandrograptid symmetry, the line of symmetry passes through the sicula, with th1[1] and th1[2] positioned symmetrically on both sides of the sicula. The maeandrograptid symmetry occurs in early Tremadocian anisograptids, and variations may be due to the orientation of the sicula, which can be vertical or inclined.

Jaanusson (1960) originally included only the family Glossograptidae in the Glossograptina because the phylogenetic relationships with the ancestral Isograptidae were unknown. Maletz and Mitchell (1996, p. 651) expanded the family to include the isograptids and the glossograptids, to acknowledge their close phylogenetic relationships, stating that it is not possible to define a taxon as a monophyletic unit without including both the traditional glossograptids and the isograptids. In contrast, in the taxonomy adopted herein, the Glossograptina are not monophyletic but represent a paraphyletic unit from which the Axonophora originated through the manubriate isograptids (Mitchell, Maletz, & Zhang, 1995; Fortey, Zhang, & Mellish, 2005; Maletz, 2010a). The suborder Glossograptina includes the suborder Pan-Glossograpta and the stem isograptids of the superorder Pan-Bireclinata of Maletz, Carlucci, and Mitchell (2009).

EVOLUTION

The Isograptidae, as the basal Glossograptina, differ from the derived, monopleural Glossograptina, mainly in that the stipes do not have monopleural arrangement. Differences in thecal style and proximal development are minor. Cooper (1973) suggested a reclined didymograptid, similar to *Didymograptus eocaduceus* Harris, 1933, as the ancestor to the Isograptidae. However, Maletz and Mitchell (1996); Maletz, Carlucci, and Mitchell (2009); and Maletz (2010a) identified the Tetragraptidae as ancestral to the Isograptidae. The abundant three- and two-stiped reclined

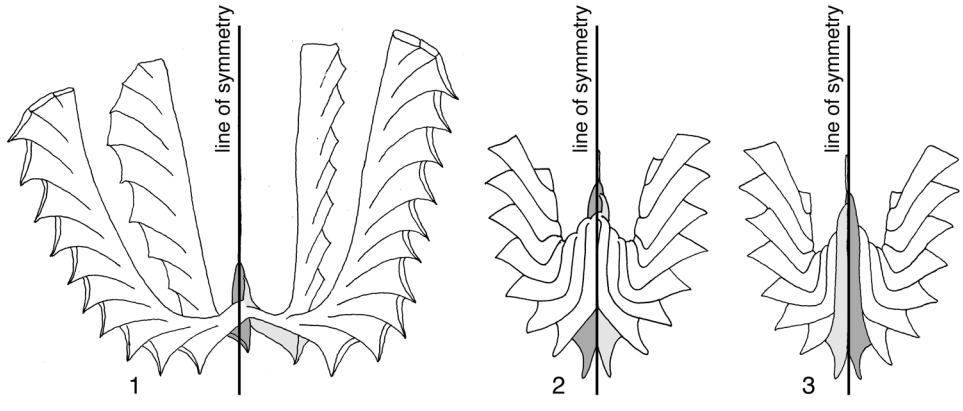


FIG. 202. The proximal symmetry of the Glossograptina. *1, Tetragraptus askerensis* (MONSEN, 1937), maeandrograptid proximal symmetry of a dichograptid in reverse view (adapted from MALETZ, 2011a, fig. 2); 2–3, *Arienigraptus dumosus* (HARRIS, 1933), isograptid symmetry in reverse (*2*) and obverse (*3*) views; sicula in *dark gray,* th1[1] in *light gray* (new).

tetragraptids of the upper Floian (Lower Ordovician) would have required only the loss of the distal dicalycal thecae, followed by a change to isograptid symmetry, to be transformed into an isograptid without an intermediate didymograptid or expansograptid ancestor. MALETZ (2011a) illustrated a number of three- and two-stiped reclined tetragraptids that may represent the transitional forms in the transformation of the reclined tetragraptids to the isograptids.

Cladistic analyses (MALETZ & MITCHELL, 1996; MALETZ, CARLUCCI, & MITCHELL, 2009) have provided insights into the evolutionary relationships of the Glossograptina that indicate that the Glossograptidae and the Axonophora evolved independently from the Isograptidae (Fig. 203). The Isograptidae lead to the scandent, monopleural Glossograptidae through the partial monopleural genera *Skiagraptus* and *Bergstroemograptus* (MALETZ & MITCHELL, 1996), but the differentiation of the two groups is difficult as the new synapomorphies are not recognizable in flattened material. A second independent lineage leads from the derived arienigraptids to the axonophoran graptolites (e.g., *Apiograptus,* COOPER & MCLAURIN, 1974) (Fig. 203). The members of the family Isograptidae provide a number of important biostratigraphic marker species for the Dapingian to Darriwilian (Ordovician) time interval (HARRIS, 1933; COOPER, 1973).

Family ISOGRAPTIDAE Harris, 1933

[Family Isograptidae HARRIS, 1933, p. 85] [incl. Cardiograptidae MU & ZHAN, 1966, p. 96]

Two-stiped, reclined to scandent or proximally scandent (dipleural) Glossograptina with isograptid or derived maeandrograptid symmetry, with or without manubrium; sicula conical, commonly elongated, widening gradually toward aperture, with small prosicula; origin of th1[1] in lower part of prosicula; proximal development type isograptid, dextral; thecae simple, widening tubes, typically with distinct rutella. *Middle Ordovician* (*Dapingian–Darriwilian*): worldwide.

The family Isograptidae is the paraphyletic partial clade based on the reclined, two-stiped colony with the isograptid symmetry as defining synapomorphy (MALETZ & MITCHELL, 1996). As discussed earlier, it excludes the monophyletic Glossograptidae with the monopleural colony shape and the virgellate Axonophora with the biserial, dipleural development of the colonies (Fig. 203). The Axonophora and the Glossograptidae originated independently from the Isograptidae, but the details of the transformations are not yet clear.

HARRIS (1933) established the Isograptidae as a separate family from the Dichograp-

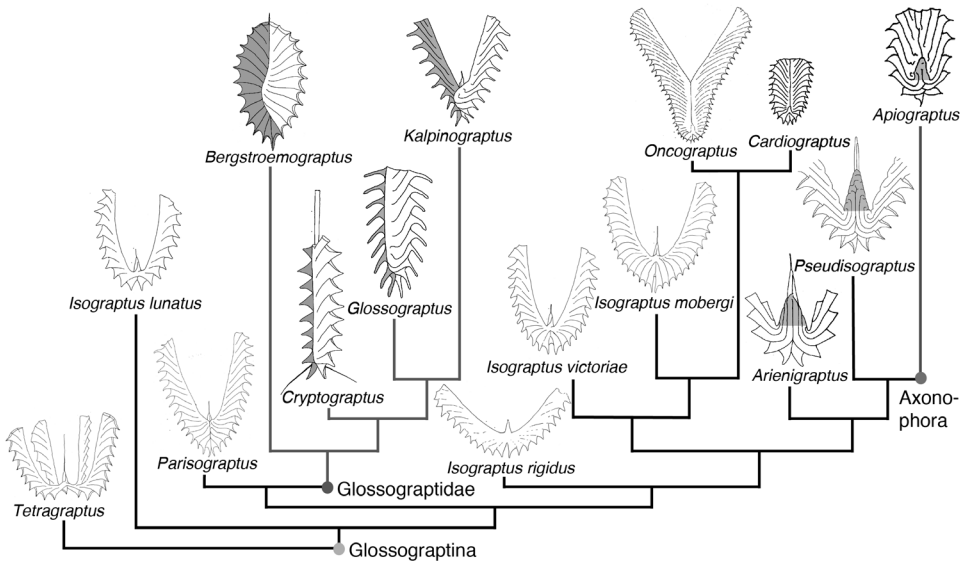


FIG. 203. Evolutionary relationships of the Glossograptina (new).

tidae, which is distinguished by having a two-stiped tubarium with reclined stipes. He included the genus *Maeandrograptus* MOBERG, 1892a, but this genus is now transferred to the Sigmagraptidae, though some species included in *Maeandrograptus* by HARRIS (1933) are now placed in the genus *Pseudisograptus* (COOPER, 1973; COOPER & NI, 1986). COOPER (1973) recognized isograptid symmetry as a more important character, and the definition of the family is now based upon this symmetry and the reclined arrangement of the two stipes. Isograptids are generally easily recognized and useful for biostratigraphic and paleogeographic purposes. They evolved quickly during the Dapingian to early Darriwilian into a number of short-lived species that are regarded as important biostratigraphic index species (HARRIS, 1933; COOPER, 1973). The Isograptidae represent the stem group of the superorder Pan-Bireclinata MALETZ, CARLUCCI, and MITCHELL, 2009.

The family Isograptidae includes several other family group taxa. MU and ZHAN (1966) established the Cardiograptidae for biserial, dipleural taxa and included *Cardiograptus, Paracardiograptus,* and *Skiagraptus,* of which *Skiagraptus* is now referred to the Glossograptidae, due to its partly monopleural arrangement of the stipes. YU and FANG (1981a) originally defined the Arienigraptinae as a subfamily of the Kalpinograptidae JIAO, 1977 (listed as QIAO, 1977 in MU & others, 2002, p. 369). MALETZ and MITCHELL (1996) elevated the subfamily to family rank and recognized the genus *Arienigraptus* as a pseudisograptid, but *Kalpinograptus* is now regarded as a secondarily two-stiped glossograptid (MALETZ & MITCHELL, 1996). Following HARRIS (1933), the arienigraptid genera *Arienigraptus* and *Pseudisograptus* are included in the Isograptidae herein and interpreted as a paraphyletic group from which the Axonophora (the biserial, dipleural graptolites) originated (MITCHELL, MALETZ, & ZHANG, 1995; FORTEY, ZHANG, & MELLISH, 2005; MALETZ, 2010a).

Defining the precise boundary between the Isograptidae and the Axonophora has been problematic. Because of the scarcity of well-preserved and isolated specimens, it is difficult to observe the important synapomorphic characters in this transition. The taxonomy adopted in this revision places the biserial, dipleural taxa with a distinct

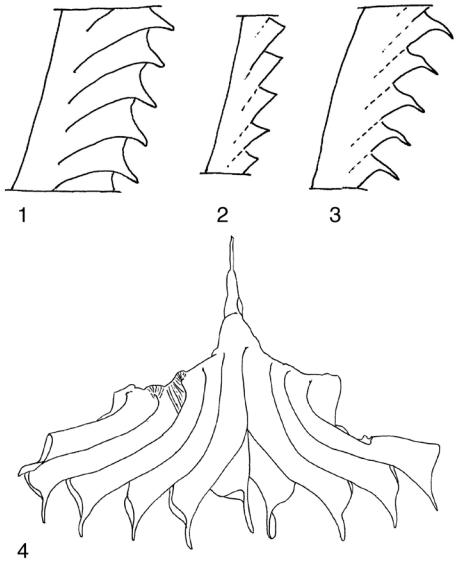


FIG. 204. Thecal style in the Isograptidae. *1,* Isograptid thecal style; *2,* simple manubriate thecal style; *3,* advanced manubriate thecal style (*1–3,* adapted from Cooper & Ni, 1986, fig. 3); *4, Arienigraptus geniculatus* (SKEVINGTON, 1965), PMU ÖI 1209, holotype showing advanced manubriate thecal style with lateral lappets on all thecae (adapted from Skevington, 1965, fig. 54D).

manubrium (*Apiograptus*) and derived from the genus *Pseudisograptus* in the Axonophora (MALETZ, 2014b). This serves as a simple distinction of the latter group from the Isograptidae.

MORPHOLOGY

The tubaria and thecal styles of the Isograptidae are fairly simple and show little morphological variation. In addition to their characteristic isograptid symmetry, the species of the Isograptidae generally possess a dextral mode of growth (Fig. 202). Very few specimens with a sinistral development have been discovered, even though this development is common in earlier graptoloids (HUTT, 1974a). COOPER and FORTEY (1982, fig. 54C–D) illustrated a single sinistral specimen of *Isograptus imitatus* HARRIS, 1933. A sinistral proximal development is also present in a number of specimens of *I. spjeldnaesi* MALETZ, 2011a from Norway (MALETZ, 2011a, fig. 6A).

The thecae of the Isograptidae are simple tubes, slender and widening slowly towards the aperture in most taxa. Apertures have a pronounced ventral rutellum in most isograptids but possess no additional elaboration (Fig. 204.1). In contrast, the manubriate taxa *Arienigraptus* and *Pseudisograptus* possess more variation in their thecal style. The thecae are simple tubes, slowly widening towards the aperture and without a rutellum in early taxa. COOPER and NI (1986) termed this thecal style the simple manubriate thecal style (Fig. 204.2). In derived taxa, the distal thecae commonly have long and strongly differentiated rutella of the advanced manubriate thecal style (Fig. 204.3). These thecal apertures are more similar to the lamelliform rutellum of the monopleural glossograptids (see MALETZ, 2010a). Paired lateral lappets appear frequently on the thecal apertures of the arienigraptids and have been illustrated from chemically isolated material in *Arienigraptus geniculatus* (SKEVINGTON, 1965) (Fig. 204.4).

In the Isograptidae, the proximal development is of the isograptid type (COOPER & FORTEY, 1983), and its basic construction is identical to the development in the Anisograptidae (MALETZ, 1994b). The development essentially describes the presence of two crossing canals and a dicalycal $th1^2$ on the reverse side of the tubarium. The thecal origins of $th1^2$ and $th2^1$ are seen in close succession as nearly vertical openings (Fig. 205.1). The crossing canals are subhorizontally oriented, growing in opposite directions, and have different dimensions, with crossing canal 1 wider than crossing canal 2 (Fig. 205.1). This branching also reveals the origins of the two daughters of the dicalycal theca $th1^2$ at different positions along the mother theca.

In a number of derived isograptids, the development of the proximal end is modified: the two asymmetrical crossing canals are replaced by a much more symmetrical construction without changing the position of the dicalycal theca (Fig. 205.2). In these taxa, the ventral wall of $th1^1$ grows

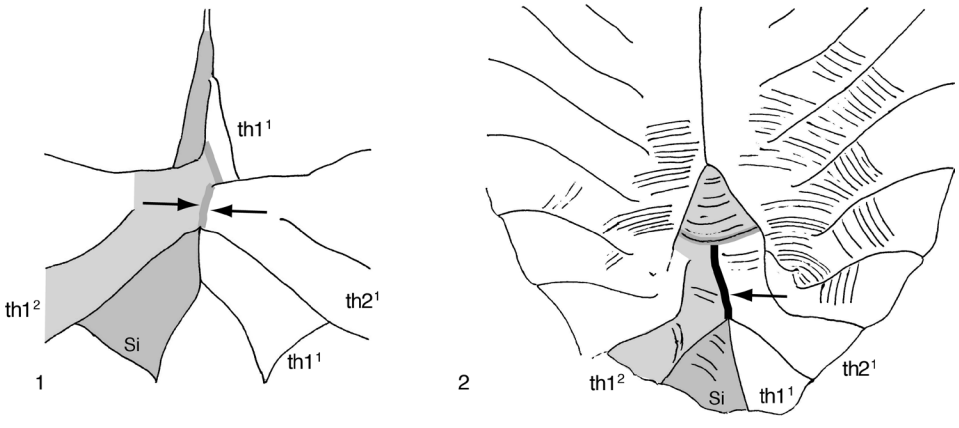


FIG. 205. Isograptid development in the Isograptidae, with thecal notation. *1, Isograptus rigidus* MALETZ, 2011a, showing successive origins of th1² and th2¹ (*gray lines*) in a normal isograptid-type proximal development; *2, Cardiograptus amplus* HSÜ, 1947, showing paired origin of th1² and th2¹ (*gray line*) from a downward growing flange and suture between th1² and th2¹ (*black line*); *Si,* sicula (new; adapted from photograph in Fortey, Zhang, & Mellish, 2005, fig. 10a).

vertically downward as a widening flange along the sicula for some distance before it begins to produce a small lip, from which a strip of fusellar material is formed, dividing the temporary opening of the downward-growing thecal tube into two large, lateral openings. From there, the tubes of th1² and th2¹ grow as a symmetrical pair. Later thecae are formed in the normal way. This development produces a feature that recalls the arienigraptid suture in relief specimens (Fig. 205.2), but it does not include the parallel downward growth of th2¹ and th2². This feature is present in a number of *Isograptus* species (e.g., *I. maximodivergens* and *I. mobergi*) and is present in *Oncograptus* and *Cardiograptus*.

The reclined arrangement of the stipes in the Glossograptina is the result of a shortening of the distance between thecal origins and the increase in width of the thecal foramina in the early thecae of the isograptids of the *I. victoriae* lineage. A number of proximal thecae produce this arrangement, whereas the distal thecae all possess approximately equal origination distances. The complex proximal development of the genus *Parisograptus* is known from only a few specimens (MALETZ & ZHANG, 2003). It includes an upward stacking of thecal origins in the proximal end and an initially biserial, dipleural stipe arrangement (Fig. 206).

The arienigraptids increase the complexity of the proximal development by the formation of a manubrium and the insertion of intrathecal folds in most taxa. In these, the thecal overlap may be more complex with the second thecal pair (th1² and th2²) covering most of the sicula and th1¹ on the reverse side (Fig. 206). Due to this development, the obverse and reverse sides of the tubaria look quite different: on the obverse side, the sicula and th1¹ are freely visible along their full lengths (e.g., *Pseudisograptus manubriatus janus* COOPER & NI, 1986).

The manubrium, a massive and complex structure, dominates the proximal end of the isograptids of the genera *Arienigraptus* and *Pseudisograptus* (Fig. 207). The second thecal pair (th1² and th2¹) formed the crossing canals but instantly grew downward along the sicula and th1¹ on the reverse side of the tubarium, forming the characteristic arienigraptid suture. The paired sicula and th1¹ are completely exposed on the obverse side of the colony (Fig. 207.3), but they are covered on the reverse side for most of their length by the second thecal pair (Fig. 207.2). In *Pseudisograptus*, the more complex overlap of the proximal thecae covers the arienigraptid suture (Fig. 207.1).

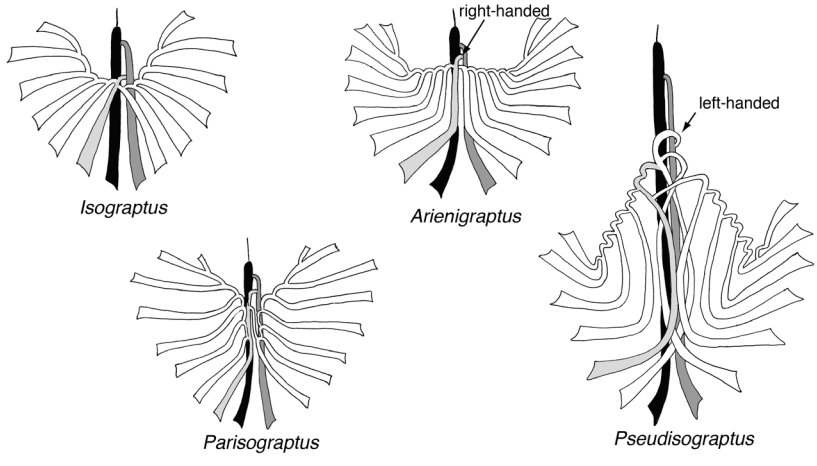


FIG. 206. Growth directions of proximal thecae in the Isograptidae. Sicula in *black,* th1[1] in *dark gray,* dicalycal theca in *light gray;* all diagrams in reverse view; note that th2[2] is the dicalycal theca in *Pseudisograptus* (adapted from Maletz & Mitchell, 1996, and Maletz & Zhang, 2003).

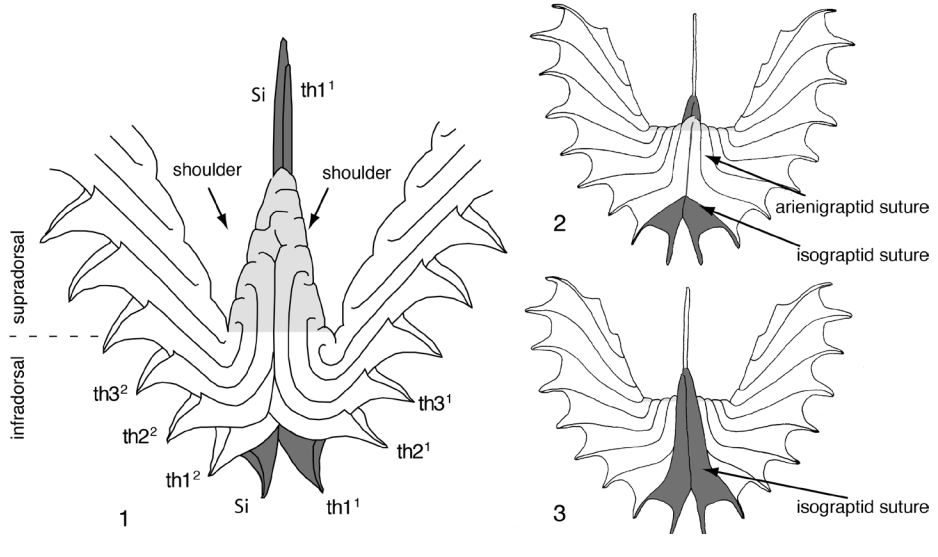


FIG. 207. The arienigraptid manubrium. *1, Pseudisograptus manubriatus* subsp., showing large manubrium with sloping manubrium shoulders, thecal notation, and division of supradorsal and infradorsal; *2–3, Arienigraptus zhejiangensis* YU & FANG, 1981a; *2,* reverse view, small manubrium wedge and nearly horizonal manubrium shoulders, arienigraptid suture between th1[2] and th2[1], isograptid suture visible below; *3,* obverse view, showing isograptid suture; manubrium wedge or supradorsal part of manubrium (*light gray*); first thecal pair (*dark gray*); *Si*, sicula (new).

The thecal length determines the growth patterns and development of the manubrium. The thecae are parallel sided in taxa with a large manubrium (Fig. 208.1) but widen more quickly in taxa with a reduced manubrium (Fig. 208.5–208.6). The arienigraptid proximal structure consists of parallel-downward and distally outward-growing proximal thecae, the manubrium wedge (Fig. 202.3, Fig. 207.1). This is a complex and difficult-to-decipher construction of unknown use in all arienigraptids.

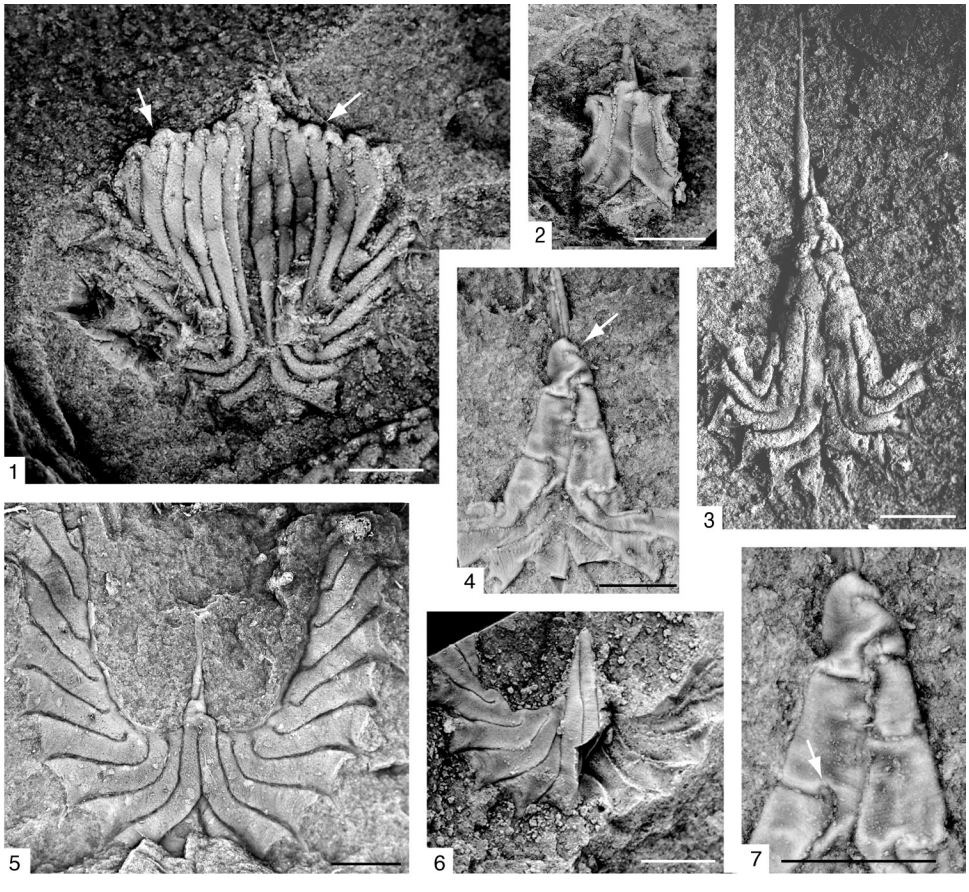


Fig. 208. Examples of manubrium construction. *1, Arienigraptus* sp., LO 12244, Krapperup drill core, Scania, Sweden, specimen with low supradorsal part and long infradorsal part of manubrium, showing prothecal folds (*arrows*); *2, A. zhejiangensis* Yu & Fang 1981a, PMU 29983, juvenile, Krapperup drill core at 59.30–59.35 m; *3, Pseudisograptus manubriatus* ssp., PMU 28978, latex cast; *4, 7, Pseudisograptus* sp., PMU 29984, coated, Krapperup drill core at 60.67–60.68 m, showing left-handed origin of th1^2 (*arrow* in *4*) and construction of manubrium with intrathecal folds (*arrow* in *7*); *5, A. zhejiangensis* Yu & Fang, 1981a, PMU 29985, coated, Lovisefred drill core, Scania, Sweden, 472.58–472.59 m; *6, Arienigraptus* sp. with strongly reduced manubrium, PMU 29986, coated, Krapperup drill core at 58.75–58.77 m; all specimens in reverse view, except (*6*), which shows the obverse view; scale bars, 1 mm (new).

The massive structure of the manubrium is a completely new development in a few derived taxa of the isograptids. In some taxa, this structure is modified by a complex of overlapping distal thecae (Fig. 207.1, Fig. 208.3). All thecal origins are dorsal and are characterized by the development of intrathecal folds in most arienigraptids (Fig. 208.4, Fig. 208.7). Other taxa clearly develop prothecal folds at the origins of the thecae (Fig. 208.1). The connection between these two types of thecal modification is unclear.

The shape of the manubrium is quite variable (Fig. 208). In *Pseudisograptus,* the manubrium form a massive triangular feature around the sicula positioned above the base of the stipes (Fig. 202.3, Fig. 208.3). The manubrium has long, sloping shoulders with variable inclination. In Darriwilian species of *Arienigraptus,* the manubrium shoulders are typically horizontal (or nearly horizontal) and the downward growth of the initial thecae is reduced (Fig. 208.1, Fig. 206).

As the stratigraphically oldest arienigraptid species, *Arienigraptus hastatus* Harris, 1933

already has a conspicuous and highly complex manubrium; however, the exact evolutionary origin of the structure is unknown. Cooper and Ni (1986) first described the construction of the manubrium from three-dimensionally preserved material of a number of *Pseudisograptus manubriatus* specimens.

Subfamily ISOGRAPTINAE Harris, 1933

[Harris, 1933, p. 85]

Two-stiped, reclined to scandent or proximally scandent, dipleural Glossograptina with isograptid symmetry; sicula conical, commonly elongated, widening gradually toward the aperture, with small prosicula; origin of th1[1] in lower part of prosicula; proximal development type isograptid, dextral; thecae simple, widening tubes, typically with distinct rutellum. *Middle Ordovician* (*Dapingian, Isograptus lunatus* Biozone–*Darriwilian, Nicholsonograptus fasciculatus* Biozone): worldwide.

Isograptus Moberg, 1892a, p. 345 [**Didymograptus gibberulus* Nicholson 1875, p. 271; M]. Reclined, two-stiped isograptids; thecae simple with rutellate apertures, shorter and wider in earlier species, with thecal length increasing in later species; proximal development type isograptid, dextral, with low prosicular origin of th1[1], rarely sinistral. *Middle Ordovician* (*lower Dapingian, Isograptus lunatus* Biozone–*Darriwilian, Levisograptus austrodentatus* Biozone): worldwide.——Fig. 209,*1a*. **I. gibberulus* (Nicholson), lectotype, SM A17779, Randal Craig, Skiddaw, Cumbria (English Lake District), UK, scale bar, 1 mm (Rushton, 2000c, Atlas, Folio 1.34).——Fig. 209,*1b*. *I. spjeldnaesi* Maletz, 2011a, holotype, T878-1, left-handed specimen, scale bar, 1 mm (Maletz, 2011a, fig. 6A).——Fig. 209,*1c*. *I. mobergi* Maletz, 2011a, holotype, SGU 5249, scale bar, 1 mm (Maletz, 2011a, fig. 6).

Cardiograptus Harris & Keble in Harris, 1916, p. 66 [**C. morsus;* M] [=*Paracardiograptus* Mu & Lee, 1958, p. 399 (type, *P. hsui,* OD), syn. by Maletz & Mitchell, 1996, p. 650]. Scandent, biserial isograptids with increasing thecal length distally; thecae simple with distinct rutella; proximal development derived-isograptid type, dextral, with origin of th1[1] low in the prosicula. *Middle Ordovician* (*upper Dapingian, Cardiograptus morsus* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, USA, Canada, Argentina——Fig. 210,*2a*. **C. morsus,* NMV P32148, Chinaman's Creek, Yapeenian 2, Victoria, Australia, scale bar, *5* mm (new).——Fig. 210,*2b*. *C. amplus* Hsü, 1947, NIGP 136152, SEM photograph, reverse view, scale bar, 1 mm (Fortey, Zhang, & Mellish, 2005, fig. 10A).——Fig. 210,*2c–d*. *C. hsui* (Mu & Lee), Ningkuo Shale, Western Chekiang, China; *2c,* holotype, NIGP 9733, proximal end in reverse view; *2d,* paratype, NIGP 9734, proximal end in obverse view; scale bars, 1 mm (Mu & Lee, 1958, pl. 1,*14*).

Oncograptus T. S. Hall, 1914, p. 109 [**O. upsilon;* M] [=*Otricograptus* Percival, Quinn, & Glen, 2011, fig. 4; *nomen nullum;* misspelling]. Initially scandent, biserial isograptid; two distally diverging stipes with increasing thecal length and overlap; thecae simple tubes with distinct rutella; proximal development of derived-isograptid type, dextral, with origin of th1[1] low in prosicula. *Middle Ordovician* (*upper Dapingian, Oncograptus* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, USA, Canada, Argentina, Ireland.——Fig. 210,*1*. **O. upsilon,* holotype, NMV P31177, Victoria, Australia, scale bar 5 mm (new).

Parisograptus Chen & Zhang, 1996, p. 86 [**Isograptus curvithecatus* Hsü, 1959b, p. 168; OD; =*Isograptus forcipiformis* Ruedemann, 1904, p. 699, syn. by Maletz & Zhang, 2003, p. 301]. Reclined, two-stiped isograptids; crowded and dorsally stacked origins of early thecae with upward and downward early growth on reverse side; colony initially biserial, dipleural; proximal development type isograptid, dextral, with origin of th1[1] in lower part of prosicula; thecae of uniform length and overlapping, with rutella elongated proximally and rutella of sicula and th1[1] united in some species; fusellum attenuated in most species. *Middle Ordovician* (*Dapingian, Isograptus maximus* [=*Arienigraptus hastatus*] Biozone)–*Darriwilian, Nicholsonograptus fasciculatus* Biozone): Australia, New Zealand, China, UK, Sweden, Norway, USA, Canada, Argentina.——Fig. 209,*2a*. **P. curvithecatus* (Hsü), holotype, scale bar, 1 mm (Hsü, 1959b, fig. 2).——Fig. 209,*2b*. *P. forcipiformis* (Ruedemann, 1904), lectotype, NYSM 5881, Ash Hill Quarry, Mount Merino, Hudson, New York, USA, scale bar, 1 mm (new).——Fig. 209,*2c*. *P. caduceus* (Salter in Bigsbyi, 1853), NIGP 12523, reverse view, scale bar, 1 mm (Maletz & Zhang, 2003, fig. 1A).

Procardiograptus Xiao, Xia, & Wang, 1985, p. 435 [**Cardiograptus* (*Procardiograptus*) *uniformis;* OD]. Scandent, biserial isograptid with conspicuous, heart-shaped axial cavity in proximal portion; stipes with increasing thecal length and overlap; thecae simple tubes with distinct rutella; proximal development derived-isograptid type, dextral, with origin of th1[1] low in the prosicula. *Middle Ordovician* (*upper Dapingian, Oncograptus magnus* Biozone–*Cardiograptus amplus* Biozone): China.——Fig. 209,*3a–b*. **P. uniformis; 3a*, NIGP 124849, Hengtang, Zhejiang Province, China; *3b*, NIGP 124851 Chenjiawu, Zhejiang Province, China; scale bars, 1 mm (adapted from Chen, Zhang, & Mitchell, 1995, fig. 26B,D, respectively).

Proncograptus Xiao, Xia, & Wang, 1985, p. 434 [**Oncograptus* (*Proncograptus*) *forcatus;* OD].

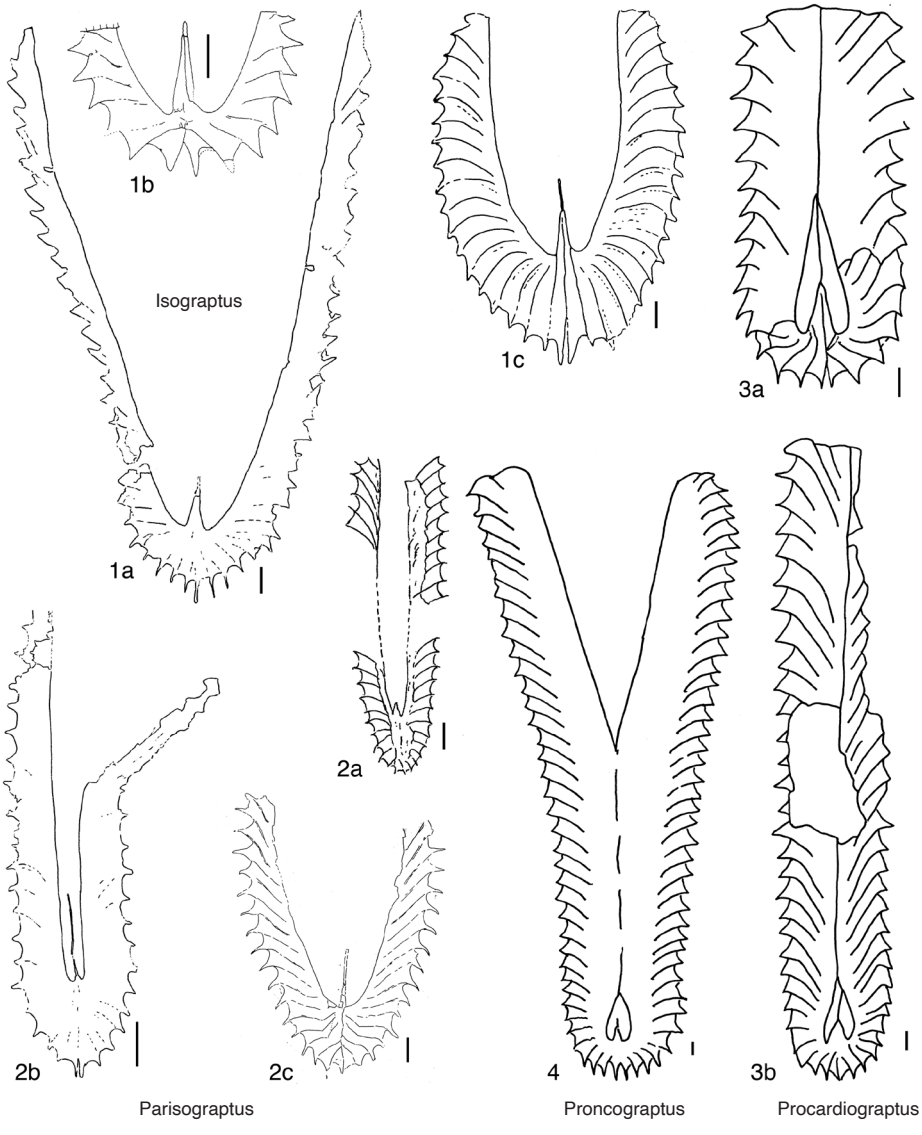


FIG. 209. Isograptidae (Isograptinae) (p. 316–317).

Initially scandent, biserial isograptid with conspicuous, heart-shaped axial cavity in the proximal portion; two diverging stipes with distally increasing thecal length; thecae simple tubes with distinct rutella; proximal development of derived-isograptid type, dextral with origin of th1[1] low in the prosicula. *Middle Ordovician* (*upper Dapingian*, *Oncograptus magnus* Biozone): China.——FIG. 209,*4*. *P. robustus* (XIAO, XIA, & WANG, 1985), holotype, Jiangxi Province, scale bar, 1 mm (adapted from Xiao, Xia, & Wang, 1985, fig. 3).

Subfamily ARIENIGRAPTINAE Yu & Fang, 1981

[Arienigraptinae YU & FANG, 1981a, p. 29] [=Pseudisograptinae COOPER & NI, 1986, p. 323]

Two-stiped, reclined glossograptids with isograptid or maeandrograptid symmetry, manubrium invariably present; sicula conical, elongated, largely parallel sided, with short or elongated, conical prosicula;

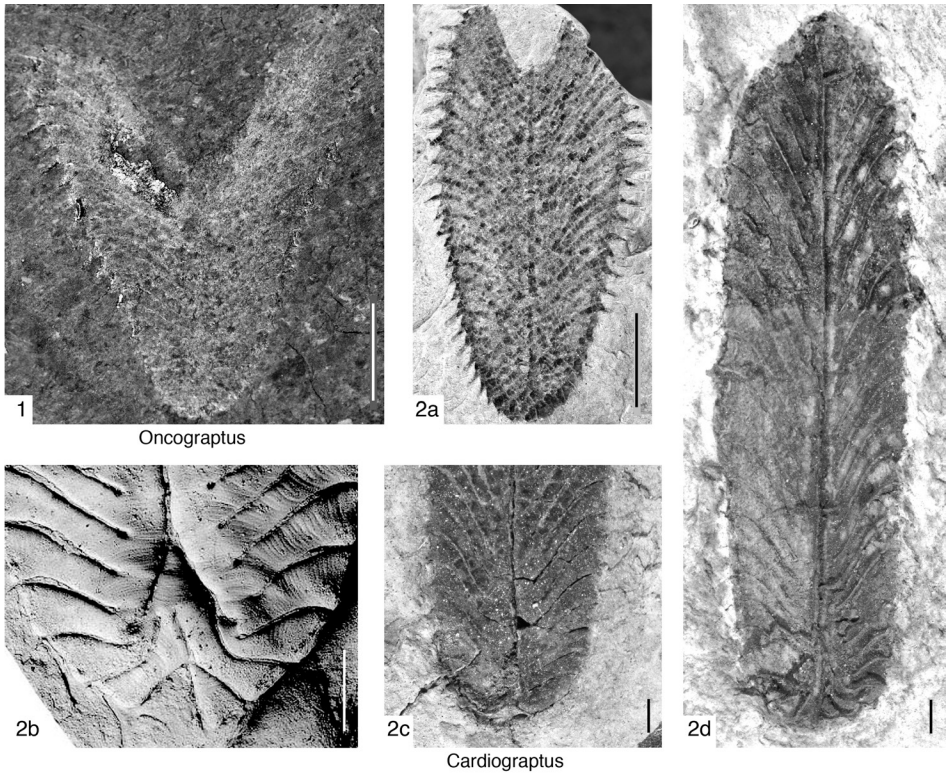


FIG. 210. Isograptidae (Isograptinae) (p. 316).

origin of th1[1] in lower part of prosicula; proximal development isograptid type, dextral; origin of th1[2] right- or left-handed or with delayed dicalycal theca; thecae simple, ranging from parallel sided to slightly widening tubes, commonly with distinct rutella, but some lacking lateral apertural elaborations or with low lateral lappets. *Middle Ordovician* (*Dapingian, Isograptus maximus* [=*Arienigraptus hastatus*] Biozone–*Darriwilian, Levisograptus dentatus* Biozone): worldwide.

YU and FANG (1981a, fig. 2) referred the Arienigraptinae to the family Kalpinograptidae based on their interpretation that *Kalpinograptus* derived from *Pseudisograptus*. The genus *Kalpinograptus* can be referred to the Glossograptidae based on the development of its sicula and the proximal end construction with a monopleural development (FINNEY, 1978). The development is very different from the proximal development of the manubriate *Arienigraptus*.

COOPER and NI (1986) erected the subfamily Pseudisograptinae, in which they also included the closely related biserial, dipleural genera *Exigraptus* and *Apiograptus*. Following MALETZ (2014b), the latter are interpreted in this revision as the earliest Axonophora, based on the presence of a biserial, dipleural colony retaining the manubrium, and, thus, are separated from the Arienigraptinae.

The subfamily Arienigraptinae, including *Arienigraptus* and *Pseudisograptus,* can be defined as the paraphyletic partial clade, based on a reclined, two-stiped isograptid with the presence of a manubrium as the defining synapomorphy (MALETZ & MITCHELL, 1996). It excludes the biserial, dipleural Axonophora. The synapomorphies of the Arienigraptinae include 1) a manubrium with the arienigraptid suture between

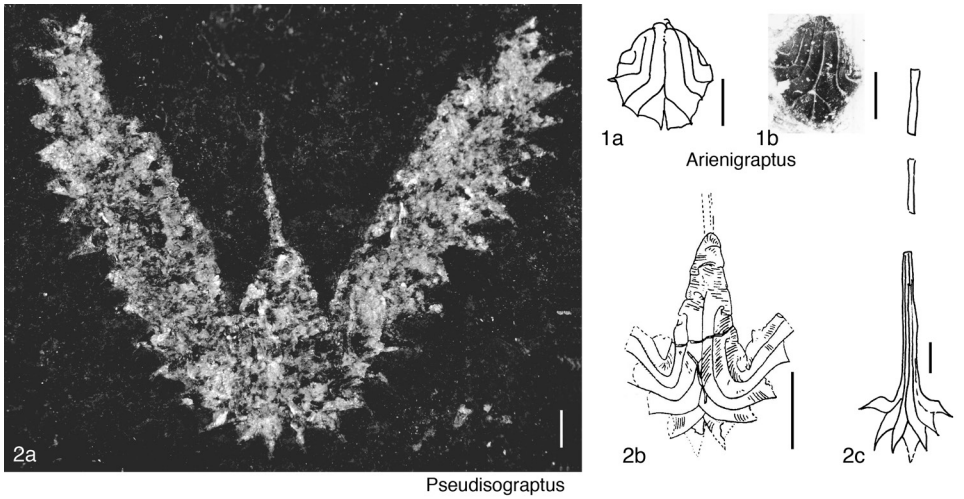


FIG. 211. Isograptidae (Arienigraptinae) (p. 319).

th1[2] and th2[1] on the reverse side (Fig. 207.2); 2) an elongated, slender thecae; and 3) a simple, distal thecal apertures lacking the extended rutella of most Isograptidae. The proximal development type is isograptid, dextral with a low prosicular origin of th1[1]. The derived genus *Pseudisograptus* bears thecae of the advanced manubriate type (Fig. 204.3), typically with slight lateral lappets (Fig. 204.4) and a delayed dicalycal theca at th2[1] or a later one. It also shows a left-handed origin of th1[2] (Fig. 206), a character that MITCHELL (1987, p. 355) considered a synapomorphy of the Diplograptina, even though it was present already in the isograptid genus *Pseudisograptus*.

Arienigraptus YU & FANG, 1981a, p. 29 [**A. jiangxiensis;* OD]. Two-stiped, reclined manubriate isograptids with simple arienigraptid proximal structure and isograptid symmetry; th1[2] and th2[1] cover sicula and th1[1] in reverse view, showing arienigraptid suture; proximal development type isograptid, dextral; manubrium wedge of highly variable dimensions; th1[2] with right-handed origin; thecae simple to advanced manubriate; stipes typically poorly developed. *Middle Ordovician* (*Dapingian, Isograptus maximus* [=*Arienigraptus hastatus*] Biozone–*Darriwilian, Holmograptus lentus* Biozone): Australia, New Zealand, China, UK, Sweden, Norway, USA, Canada, Russia, Argentina, Peru.——FIG. 211,*1a–b*. **A. jiangxiensis; 1a*, drawing of holotype, NIGP 50011 (adapted from Ni, Xiao, & Chen, 1991, fig. 4g); *1b*, photograph of holotype (new; provided by Ni Yunan, 1994). Scale bars, 1 mm.

Pseudisograptus BEAVIS, 1972, p. 202 [**Didymograptus caduceus* var. *manubriatus* T. S HALL, 1914, p. 108; OD] [=*Xiushuigraptus* YU & FANG in YANG & others, 1983, p. 406 (type, *X. songxiensis;* M), syn. by MALETZ & MITCHELL, 1996, p. 653]. Two-stiped, reclined, manubriate isograptids with complex arienigraptid proximal structure and isograptid to maeandrograptid symmetry; arienigraptid suture between th1[2] and th2[1] usually covered by overlap of later thecae; manubrium wedge of highly variable dimensions; proximal development type isograptid, dextral, with delayed dicalycal theca; sicula strongly elongated; th1[2] with left-handed origin; thecae of advanced manubriate style; stipes sometimes poorly developed; intrathecal folds present. *Middle Ordovician* (*upper Dapingian, Oncograptus upsilon* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, Russia, UK, Norway, Sweden, USA, Canada, Argentina.——FIG. 211,*2a*. **P. manubriatus manubriatus* (T. S. HALL), holotype, NMV P31176 scale bar, 1 mm (VandenBerg & Maletz, 2016, fig. 1A).——FIG. 211,*2b*. *P. manubriatus janus* COOPER & NI, 1986, reverse view, scale bar, 1 mm (Cooper & Ni, 1986, fig. 17B).——FIG. 211,*2c*. *P. songxiensis* (YU & FANG), holotype NIGP 50021, scale bar, 1 mm (adapted from Yang & others, 1983, fig. 1).

Family GLOSSOGRAPTIDAE Lapworth, 1873

[Glossograptidae LAPWORTH, 1873b, table 1, facing p. 555] [=Corynoideae RUEDEMANN, 1908, p. 233; Cryptograptidae HADDING, 1915b, p. 332; Corynoididae BULMAN, 1945, p. 22, *nom. correct. pro* Corynograptidae HOPKINSON & LAPWORTH, 1875, p. 633; =Kalpinograptidae JIAO, 1977, p. 289]

Two-stiped, scandent graptoloids with isograptid symmetry and monopleural development based on dextral torsion of the stipes around sicula; proximal development type isograptid, dextral; prosicular and occasional

metasicular origin of th1[1]; sicula tubular, widening toward the aperture, with small prosicula; thecae simple, widening tubes with distinct rutella; lateral apertural thecal spines common; lacinia in a few taxa, attached to the lateral apertural spines; attenuation of fusellum and reduction of number of thecae in colony common. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Katian, Dicellograptus complexus* Biozone): worldwide.

The family Glossograptidae is the monophyletic clade based on the scandent, monopleural colony shape as defining synapomorphy (Maletz & Mitchell, 1996). It includes a small group of biserial, monopleural taxa with a simple isograptid proximal development that is covered by the later growth of the colony. Thus, in this group, proximal development and thecal growth patterns are hard to verify and have long been a matter of debate (Bulman, 1945; Strachan, 1985; Maletz & Mitchell, 1996). Some of the younger members (e.g., *Corynoides, Corynites*) are included herein, even though their colony development is so reduced that they lack important characteristics for an analysis. Maletz, Carlucci, and Mitchell (2009, p. 14) defined the taxon as "the common ancestor of *Glossograptus acanthus* Elles & Wood, 1908 and the first species to have a monopleural arrangement of the stipes."

MORPHOLOGY

In well-preserved specimens, Glossograptidae can be distinguished from other biserial taxa by the presence of pronounced ventral rutella and the characteristic paired proximal spines. For most members, details of the early development of tubaria are unknown because they were enclosed by the two scandent stipes.

The proximal development in all Glossograptidae appears to be of the isograptid, dextral type, with th1[2] as the dicalycal theca. The proximal development type of the Glossograptidae is known from a number of flattened juveniles and is difficult to interpret, with some details remaining conjectural (Finney, 1978; Maletz & Mitchell, 1996). Relief specimens and isolated juveniles of *Glossograptus* show the sicula and th1[1] as a symmetrical pair (Ni & Cooper, 1994, fig. 1–2; Maletz & Mitchell, 1996). The origin of th1[1] is variably placed in the prosicula (*Paraglossograptus*, *Corynoides*, *Corynites*) or in the metasicula (*Cryptograptus*). The high prosicular origin of th1[1] in *Paraglossograptus* is unusual because it occurs in the lower part of the prosicula in most dichograptids and in the ancestral Isograptidae. A higher prosicular origin of th1[1] is also present in members of the Anisograptidae (Hutt, 1974a).

In *Paraglossograptus*, th1[1] grew downward from a point high on the prosicula along the ventral side of the sicula before it gave rise to a dextral development of th1[2] (Fig. 212.3). The sicula and th1[1] formed a symmetrical pair, surrounded by dextral coiling of the two scandent stipes. The initial thecae formed a considerable glossograptid bulge through the curved overlap of these elongated proximal thecae before shorter, distal thecae grew immediately upward from their beginning (Ni & Cooper, 1994; Maletz & Mitchell, 1996). The proximal development of *Cryptograptus* is more difficult to understand, but it appears to follow a similar path. The origin of th1[1] is in the metasicula, and th1[2] initially grew upward, forming a large loop, and then across the sicula and downward. As with the other genera, the sicula and th1[1] formed a symmetrical pair, but the glossograptid bulge was not developed, because the proximal thecae were short and thecal overlap was low (Fig. 213).

The thecal growth that produced the biserial, monopleural colony shape of the Glossograptidae was initiated by the dextral torsion of the two stipes around the sicula (Fig. 214), as was demonstrated in the partial monopleural development of *Bergstroemograptus crawfordi* (Fig. 214.2–214.3). Whittington and Rickards (1969) described chemically isolated material of *B. crawfordi* under the name *Skiagraptus* sp., but Keller (1956, pl. 1, *4–5*) identified the

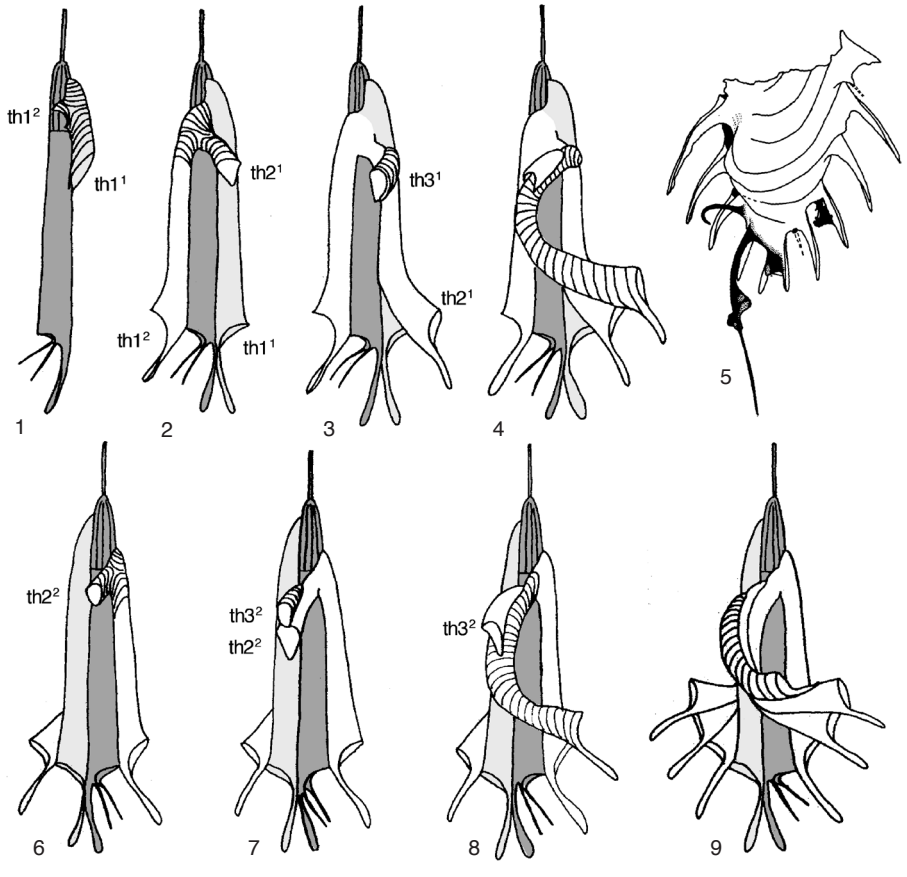


FIG. 212. Early ontogeny of *Paraglossograptus*. *1–4,* reverse view; *6–9,* obverse view; *8–9,* showing development of glossograptid bulge (adapted from Maletz & Mitchell, 1996, fig. 4); *5, P. holmi* (BULMAN, 1931), isolated specimen, western Newfoundland, showing glossograptid bulge (adapted from WHITTINGTON & RICKARDS, 1969, fig. 2C).

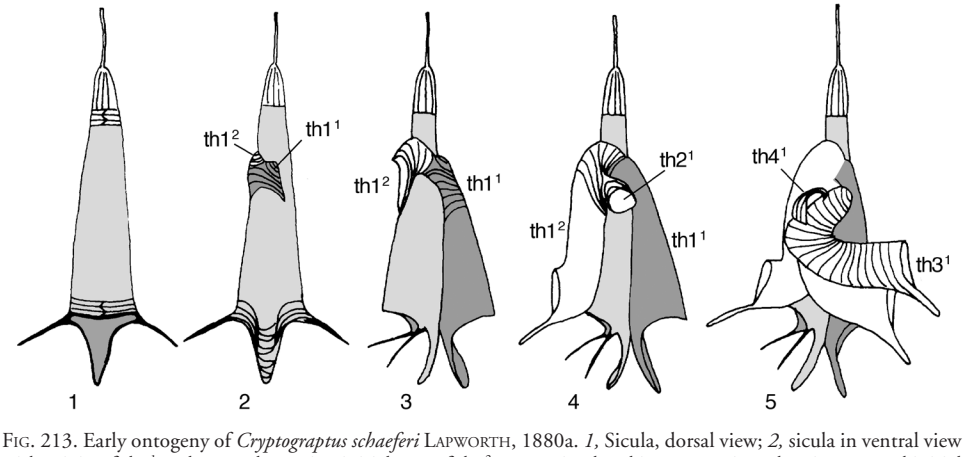


FIG. 213. Early ontogeny of *Cryptograptus schaeferi* LAPWORTH, 1880a. *1,* Sicula, dorsal view; *2,* sicula in ventral view with origin of th1[1] and upward-growing initial part of th1[2]; *3,* proximal end in reverse view, showing upward initial growth from th1[1] and arch of th1[2]; *4,* proximal end in reverse view, showing initial growth of th2[1]; *5,* proximal end with fully developed th3[1] and origin of th4[1]; *light gray,* metasicula, *dark gray,* th1[1]; reconstructions based on flattened, chemically isolated specimens from western Newfoundland (adapted from Maletz & Mitchell, 1996, fig. 4).

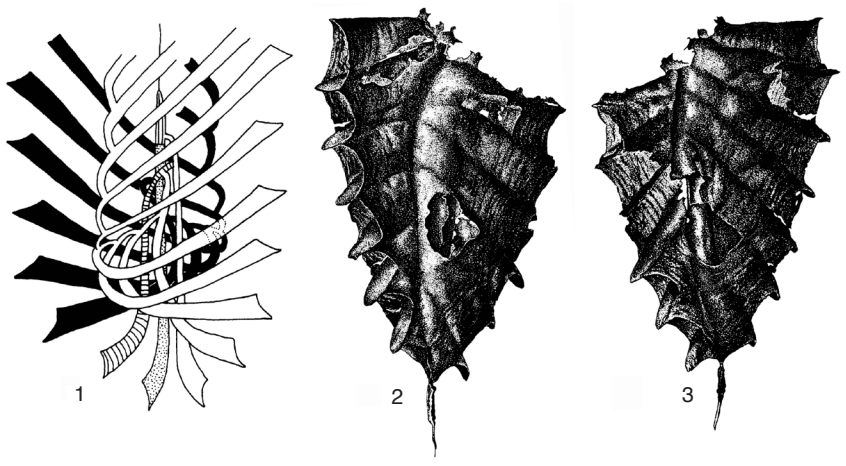


FIG. 214. Monopleural development of the Glossograptidae. *1,* Thecal diagram of *Glossograptus* sp. (adapted from MALETZ & MITCHELL, 1996, fig. 1); *2–3, Bergstroemograptus crawfordi* (HARRIS, 1926), isolated specimen in obverse and reverse views showing the dextral (clockwise) torsion of the stipes (Whittington & Rickards, 1969, fig. 9: illustrated as *Skiagraptus* sp.).

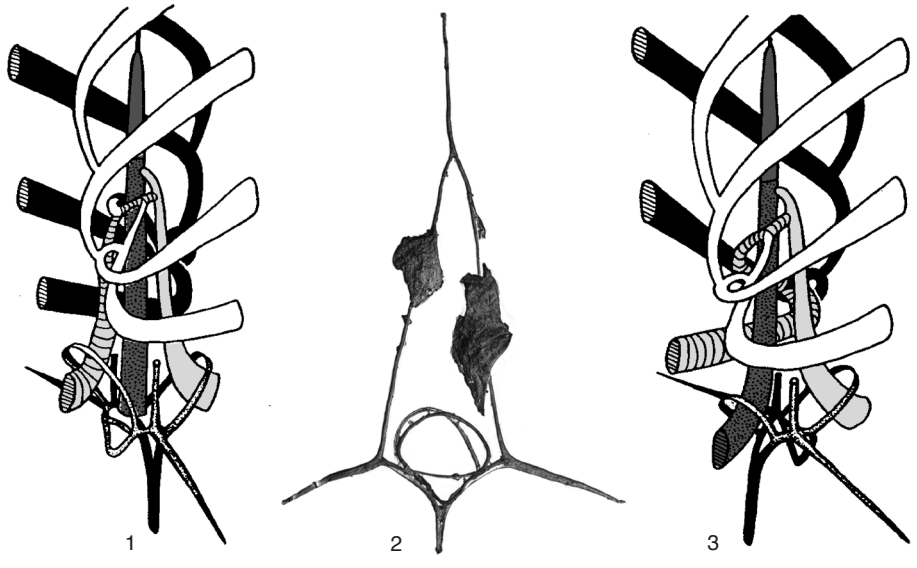


FIG. 215. *Cryptograptus* proximal development. *1,* Interpretation of STRACHAN (1985); *2, Cryptograptus* sp., (new; photo by Denis Bates); *3,* interpretation of MALETZ & MITCHELL (1996); *dark gray,* sicula; *light gray,* th1[1]; *light gray with stripes,* th1[2] (*1, 3,* adapted from Maletz & Mitchell, 1996, fig. 7).

species as *Phyllograptus anna* HALL, 1865. In completely monopleural colonies of the genus *Glossograptus* (Fig. 214.1), the sicula is fully enveloped by the two stipes, with only the aperture visible, and the colonies look identical in obverse and reverse views.

The proximal development of the genus *Cryptograptus*, as mentioned earlier, has been difficult to interpret (Fig. 215). In derived taxa of the genus, the fusellum of the initial thecae, including the sicula, is reduced and preserved as a framework of

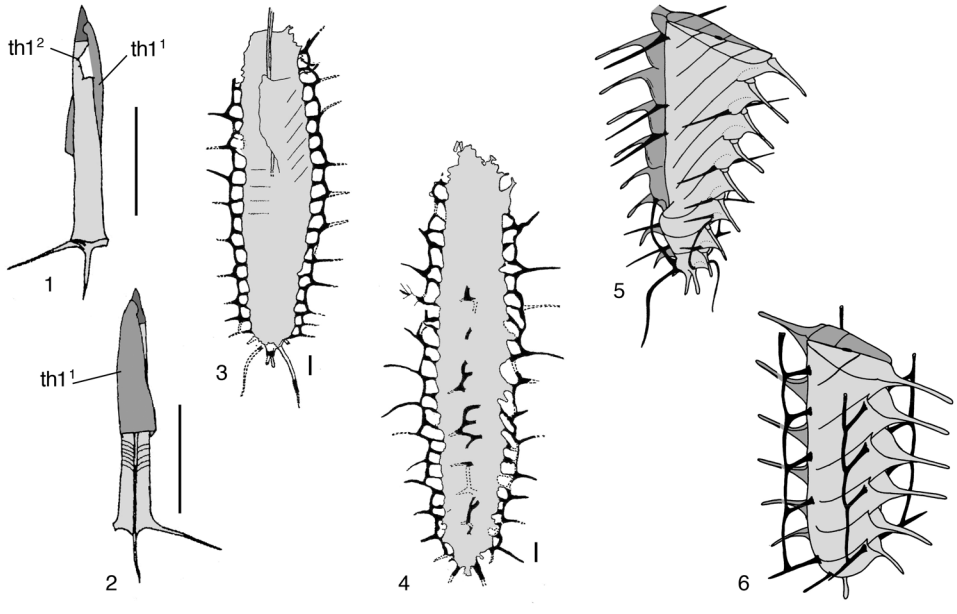


FIG. 216. Thecal spines and lacinia. *1–2, Glossograptus ciliatus* EMMONS, 1855, OSU 33142, sicula with lateral apertural spines, pointed rutellum and early growth of th1[1] and th1[2] (adapted from Finney, 1978, fig. 3); *3, Paraglossograptus tentaculatus* (HALL, 1865), GSC 950b, syntype showing lacinia development and connection to lateral apertural thecal spines (Rickards, 1972, fig. 1a); *4, Paraglossograptus tentaculatus* (HALL, 1865), NMVP 14406, holotype of *Lasiograptus etheridgei* HARRIS, 1924, showing lacinia (Rickards, 1972, fig. 1b); *5, Paraglossograptus holmi* (BULMAN, 1931), reconstruction showing position of lateral apertural spines and prominent glossograptid bulge (adapted from Whittington & Rickards, 1969, fig. 6a); *6, Paraglossograptus proteus* (HARRIS & THOMAS, 1935), reconstruction showing lacinia, lateral apertural spines on sicula and th1[1] not shown (adapted from Whittington & Rickards, 1969, fig. 6b). Scales bars, 1 mm in *1–4*.

lists only (Fig. 215.2). Different interpretations have been proposed to understand the construction. BULMAN (1945) and STRACHAN (1985) preferred the presence of a centrally positioned sicula (Fig. 215.1) as an explanation. However, MALETZ and MITCHELL (1996) suggested isograptid symmetry of the proximal end with the sicula and th1[1] as a symmetrical pair (Fig. 215.3), based on isolated specimens of *C. schaeferi* from the Table Head Group of western Newfoundland. These specimens clearly demonstrate the isograptid symmetry of the sicula and th1[1] (MALETZ & MITCHELL, 1996, fig. 5), thus strengthening the case for its descent from an isograptid ancestor.

The Glossograptidae are characterized by paired lateral apertural spines on the sicula and typically also on later thecae. They may not be present on each thecal pair, but they are regularly distributed and form the basis for the four ladderlike strings of mesh (the lacinia) in the genus *Paraglossograptus* (Fig. 216.6). The development of the lacinia is variable, and the spines usually protrude from the meshwork (Fig. 216.3–216.4).

A reduction in the colony size occurred in a number of taxa of the Glossograptidae. In early taxa, mature colonies reached considerable size; stipe length could be several centimeters in the isograptids and more than 3 cm in *Glossograptus* and *Cryptograptus*. However, a decrease in colony size was already apparent in the genera *Nanograptus* and *Sinoretiograptus*, with *Nanograptus* having colonies only 3–4 mm long, comprising only about five or six thecae. The diminution in these taxa is not associated with other changes in the colony development; it appears that their growth was suddenly arrested.

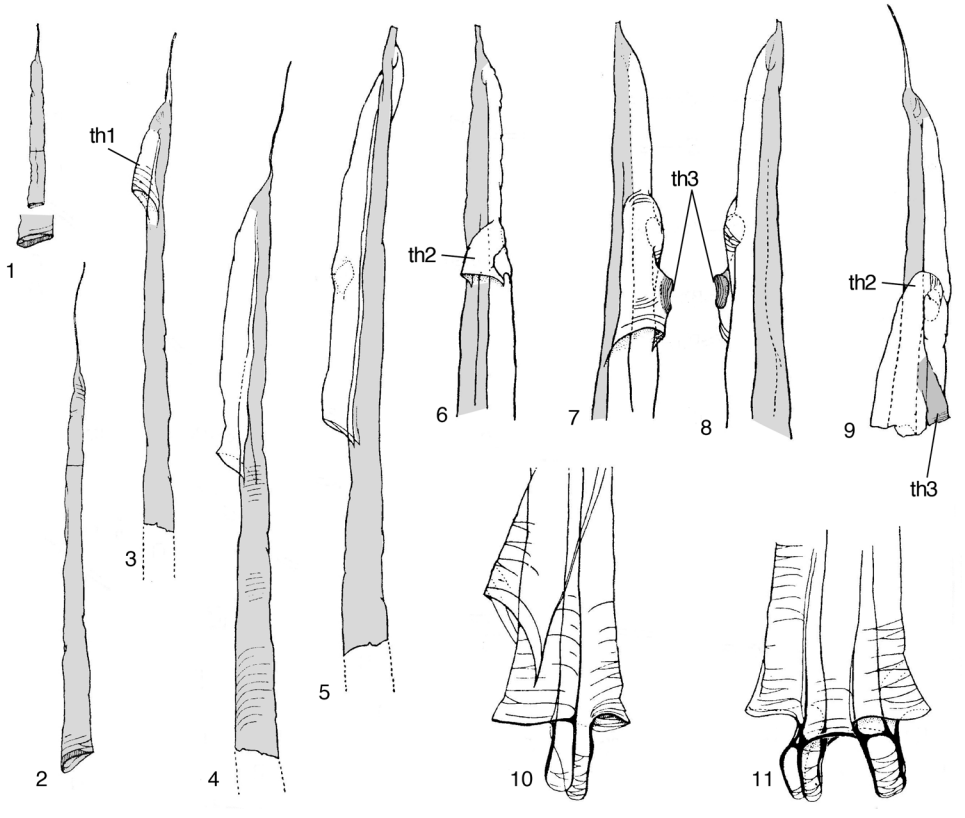


FIG. 217. Ontogeny of the genus *Corynoides*. *1–2,* Sicula development, showing length of prosicula; *3–5,* initial growth of th1; *6–9,* growth of th2; *10–11,* apertures of sicula, th1, and th2 (Bulman, 1947, fig. 39–40).

An even more drastic diminution is apparent in the colonies of *Corynoides* and *Corynites*, which have tiny tubaria consisting of only two or three thecae. However, the most important character that distinguishes these taxa from other Glossograptidae is the extreme elongation and attenuation of the thecae, with lengths up to 12 mm but widths generally not exceeding 0.2 mm. The most distal theca, usually th2[1], is reduced to a small appendage that bends away from the colony in *Corynoides* and is coiled in *Corynites*. BULMAN (1955, p. 81; 1970, p. 119) included these genera in a separate family, the Corynoididae, which he later placed in the Didymograptina (BULMAN 1970). FINNEY (1978) suggested that the Corynoididae be included as a separate family in the Glossograptina. MALETZ and MITCHELL (1996) advocated the inclusion of *Corynoides* and *Corynites* in the Glossograptidae, instead of the Corynoididae.

BULMAN (1945, 1947) was first to describe isolated specimens of *Corynoides* from the Caradoc of Laggan Burn, Scotland (Fig. 217); these possess an elongated, slender prosicula and a long metasicula with a high prosicular origin of the first theca (th1[1]), suggesting a relationship with *Glossograptus*. Another typical glossograptid character in *Corynoides* is the development of the lamelliform rutellum, identified as a lamelliform virgella by BULMAN (1945, 1947).

EVOLUTION

A detailed cladistic analysis of the Glossograptidae has not been attempted, and the classification herein is based on data provided by MALETZ and MITCHELL (1996) and MALETZ, CARLUCCI, and MITCHELL

(2009). The simple thecae and isograptid symmetry of the Glossograptidae indicates a close relationship to the Isograptidae (FINNEY, 1978; MALETZ & MITCHELL, 1996), as does the proximal development.

The earliest Glossograptidae, from the basal Darriwilian, already possessed the biserial, monopleural colony development, and transitional taxa have not been recognized in older strata. The genus *Bergstroemograptus*, shown at the base of the clade by MALETZ and MITCHELL (1996) and MALETZ, CARLUCCI, and MITCHELL (2009), possesses the partial monopleural development of a glossograptid, but the taxon is unlikely to represent the base of the clade, given that it is only known from the middle Darriwilian. Nevertheless, *Bergstroemograptus* can be taken as a guide to understanding the early evolution of the clade. The genus *Cryptograptus,* with its metasicular origin of th1[1], separated at an early stage in the evolution of the group, but the remaining taxa maintained a prosicular origin of th1[1].

As discussed earlier, *Corynoides* and *Corynites* have extremely reduced colonies and are difficult to relate to other taxa, as many indicative characters may be missing. However, the prosicular origin of th1[1] indicates a relationship with *Glossograptus* or *Kalpinograptus*. This relationship is also supported by the elongation of the sicula, which is present, for example, in *Kalpinograptus spiroptenus* JIAO, 1977. These genera might be related to the Dichograptina, but this seems unlikely, given the long gap between the extinction of the Dichograptina and the appearance of *Corynoides* and *Corynites*.

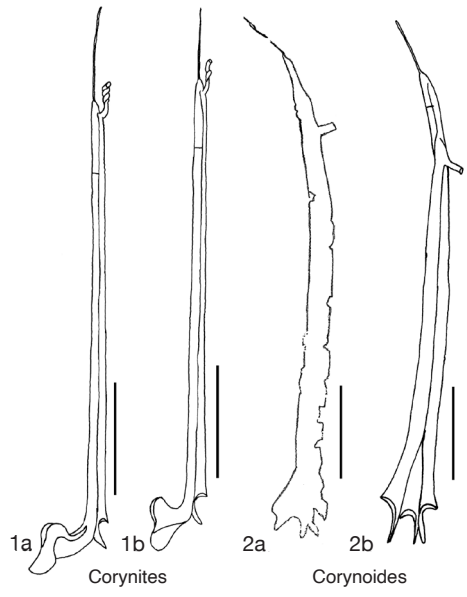


FIG. 218. Glossograptidae (p. 325–326).

Glossograptus EMMONS, 1855, p. 108, *nom. correct.* HALL, 1865, p. 59, original spelling as *Glossograpsus* changed in ICZN Opinion 650, 1963 [**G. ciliatus;* SD LAPWORTH, 1873b, table opposite p. 555] [=*Lonchograptus* TULLBERG, 1880a, p. 313 (type, *L. ovatus,* M), syn. herein]. Monopleural, scandent glossograptid formed through dextral torsion of stipes around sicula, typically with considerable glossograptid bulge; paired lateral apertural spines on sicula and variably developed on later thecae; thecal rutella extended and commonly modified; origin of th1[1] through resorption foramen in middle to lower part of prosicula; proximal development type isograptid, dextral. [The genus *Lonchograptus* TULLBERG, 1880a, from the *Didymograptus geminus* (=*Pterograptus elegans*) Biozone of southern Sweden (EKSTRÖM, 1937), is regarded as a synonym of *Glossograptus;* however, the type is extremely poorly preserved and lacks features to differentiate it from *Glossograptus*.] *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone): worldwide.——FIG. 220,*2a*. **G. ciliatus,* NYSM 7202, Normanskill Shale, Glenmont, New York, scale bar, 5 mm (Ruedemann, 1908, pl. 27,*1*).——FIG. 220,*2b*. *G. acanthus* ELLES & WOOD, 1908, NIGP 116481, specimen showing glossograptid bulge, Chenjiawu, Jiangxi, China, scale bar, 1 mm (Ni & Cooper, 1994, fig. 1).——FIG. 220,*2c*. *G. ovatus* (TULLBERG, 1880a), holotype, LO 408T, scale bar, 1 mm (Tullberg, 1880a, pl. 11,*1*).

Bergstroemograptus FINNEY & CHEN, 1984, p. 1198 [**Cardiograptus crawfordi* HARRIS, 1926, p. 57; OD]. Leaf-shaped, dipleural glossograptid with initial monopleural development covering sicula completely on both sides; rutella of sicula and th1[1] united; distal thecae distinctly widening, short. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone–*Nicholsonograptus fasciculatus* Biozone): Australia, China, UK, Sweden, USA, Canada, Russia, Argentina.——FIG. 219,*2a–b*. **B. crawfordi* (HARRIS), paratypes; *2a*, NMV P13360; *2b*, NMV P13359; scale bars, 1 mm (Finney & Chen, 1984, fig. 3C–D).

Corynites KOZŁOWSKI, 1956b, p. 260 [**C. wyszogradensis;* OD]. Strongly reduced colony consisting of elongated sicula with single adnate theca and vestigial, coiled second theca; sicular aperture with elaborate apertural flanges; origin of th1[1] in upper

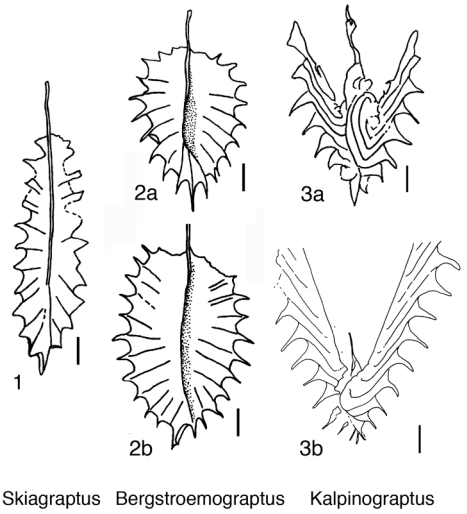


FIG. 219. Glossograptidae (p. 325–328).

part of prosicula. *Upper Ordovician* (?*Sandbian*): Poland, Germany (glacial erratic boulder).——FIG. 218,*1a*. **C. wyszogradensis,* reconstruction of holotype, scale bar, 1 mm (Kozłowski, 1956b, fig. 1).——FIG. 218,*1b*. *C. divnoviensis,* reconstruction of holotype, scale bar, 1 mm (Kozłowski, 1953, fig. 1).

Corynoides NICHOLSON, 1867a, p. 108 [**C. calicularis;* M] [=*Corynograptus* NICHOLSON in HOPKINSON & LAPWORTH, 1875, p. 633]. Strongly reduced colony consisting of elongated sicula and two adnate thecae with extended rutella; a fourth vestigial theca may be present; origin of th1[1] in the upper part of prosicula. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Diplacanthograptus spiniferus* Biozone): worldwide.——FIG. 218,*2a–b*. **C. calicularis; 2a,* BMHM Q62, lectotype (Zalasiewicz, 2000a, Atlas, Folio 1.14); *2b,* reconstruction; scale bars, 1 mm (new).

Cryptograptus LAPWORTH, 1880a, p. 174 [**Diplograpsus tricornis* CARRUTHERS, 1858, p. 468; OD] [=*Tonograptus* WILLIAMS, 1992, p. 1727, pl. 3 (type, *T. subulatus,* OD), syn. by MALETZ & MITCHELL, 1996, p. 653]. Monopleural, scandent glossograptid formed through dextral torsion of stipes around sicula; paired lateral apertural spines restricted to sicula; origin of th1[1] through resorption foramen in metasicula; th1[2] initially growing upward and across reverse side of sicula; proximal development type isograptid, dextral; sicula and early thecae reduced to several bars and lists in biostratigraphically younger species. *Middle Ordovician* (*lower Darriwilian, Undulograptus austrodentatus* Biozone)–*Upper Ordovician* (*Katian, Dicranograptus kirki* Biozone): worldwide.——FIG. 220,*1a*. **C. tricornis* (CARRUTHERS), lectotype, NHMUK Q1299, Hartfell Spa, Hartfell Shales, Scotland, scale bar, 5 mm (Elles & Wood, 1908, pl. 32, fig. 12A).——FIG. 220,*1b*. *C. insectiformis* RUEDEMANN, 1908, juvenile, MCZ 106835, showing reduction of fusellum, Viola Springs Limestone, Arbuckle Mountains, Oklahoma, USA, scale bar, 1 mm (Maletz & Mitchell, 1996, fig. 6.5).——FIG. 220,*1c*. *C. schaeferi* LAPWORTH, 1880a, GSC 87720, nematularium, holotype of *T. subulatus* WILLIAMS, 1992, western Newfoundland, Canada, scale bar, 1 mm (new).

Kalpinograptus JIAO, 1977, p. 290 [**K. spiroptenus;* OD] [=*Apoglossograptus* FINNEY, 1978, p. 489, *nom. nud.*]. Initially monopleural glossograptid formed through dextral torsion of stipes around sicula; two distally diverging stipes; glossograptid bulge conspicuous; origin of th1[1] through resorption foramen in initial part of prosicula; proximal development type isograptid, dextral. *Middle Ordovician* (*upper Darriwilian, Nicholsonograptus fasciculatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Australia, China, Sweden, Norway, Canada, USA, Argentina, Peru.——FIG. 219,*3a*. **K. spiroptenus,* syntype, scale bar, 1 mm (adapted from Jiao, 1977, fig. 4–5).——FIG. 219,*3b*. *Kalpinograptus* sp., GSC 113324, Table Head Group, western Newfoundland, Canada, scale bar, 1 mm (Maletz & Mitchell, 1996, fig. 2,*1*).

Nanograptus HADDING, 1915b, p. 328 [**N. lapworthi;* SD BULMAN, 1929, p. 179] [=*Rogercooperia* SHERWIN & RICKARDS, 2000, p. 162 (type, *Petalograptus? phylloides* ELLES & WOOD, 1908, p. 284, OD), syn. herein]. Glossograptid with rounded, finite colony consisting of ~8–10 thecae; sicula with metasicular origin of first theca; glossograptid bulge reduced and restricted to two thecal pairs; slender lateral apertural spines on sicula. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Australia (New South Wales), Sweden, Scotland.——FIG. 221,*1a–b*. **N. lapworthi; 1a*, lectotype (selected herein), LO 2746t (new); *1b*, paratype, LO 2743t (on slab), previously unfigured specimen showing long, dorsally projecting sicula, origin of th1[1] not visible; scale bars, 1 mm (new).——FIG. 221,*1c–d*. *N. phylloides* (ELLES & WOOD); *1c*, paratype, flattened juvenile (new); *1d*, lectotype (selected by SHERWIN & RICKARDS, 2000, p. 162), GSE 5495, flattened specimen; scale bars, 1 mm (new).

Paraglossograptus MU in MU & others, 1962, p. 97 [**P. typicalis;* OD]. Monopleural, scandent glossograptid with conspicuous development of simple lacinia with ladderlike structure; lacinia only present in the proximal part in certain species. [GANIS (2005, p. 803) discussed the availability of the genus name *Paraglossograptus* that appeared first in Hsü, 1959b]. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone–*Pterograptus elegans* Biozone): Australia, New Zealand, China, Norway, USA, Canada, Argentina.——FIG. 220,*3a*. **P. typicalis*, holotype, NIGP 10635, scale bar, 5 mm (Mu & Lee, 1960, fig. 127).——FIG. 220,*3b*. *P. tentaculatus* (HALL, 1865), GSC 138686, isolated, flattened specimen, Cow Head Group, western

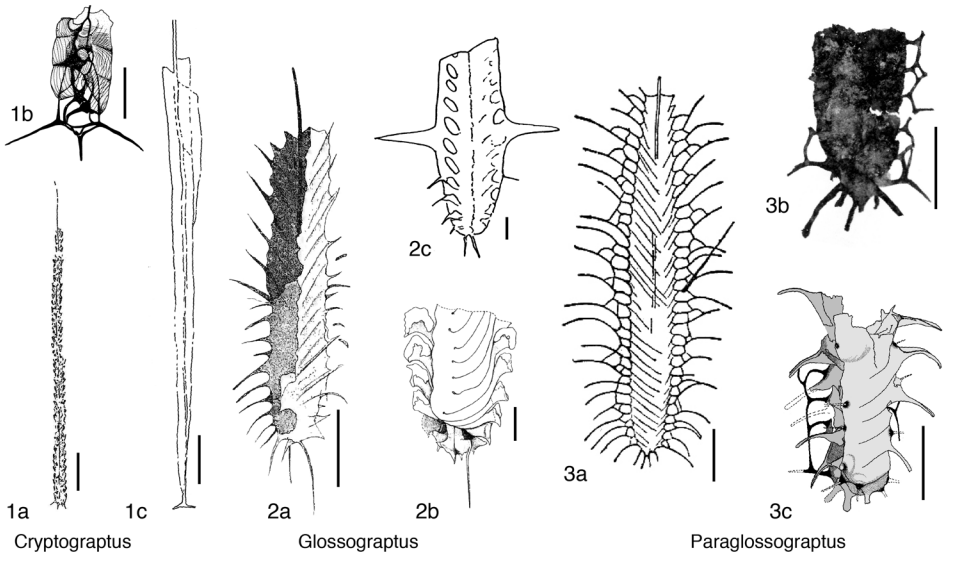


FIG. 220. Glossograptidae (p. 325–328).

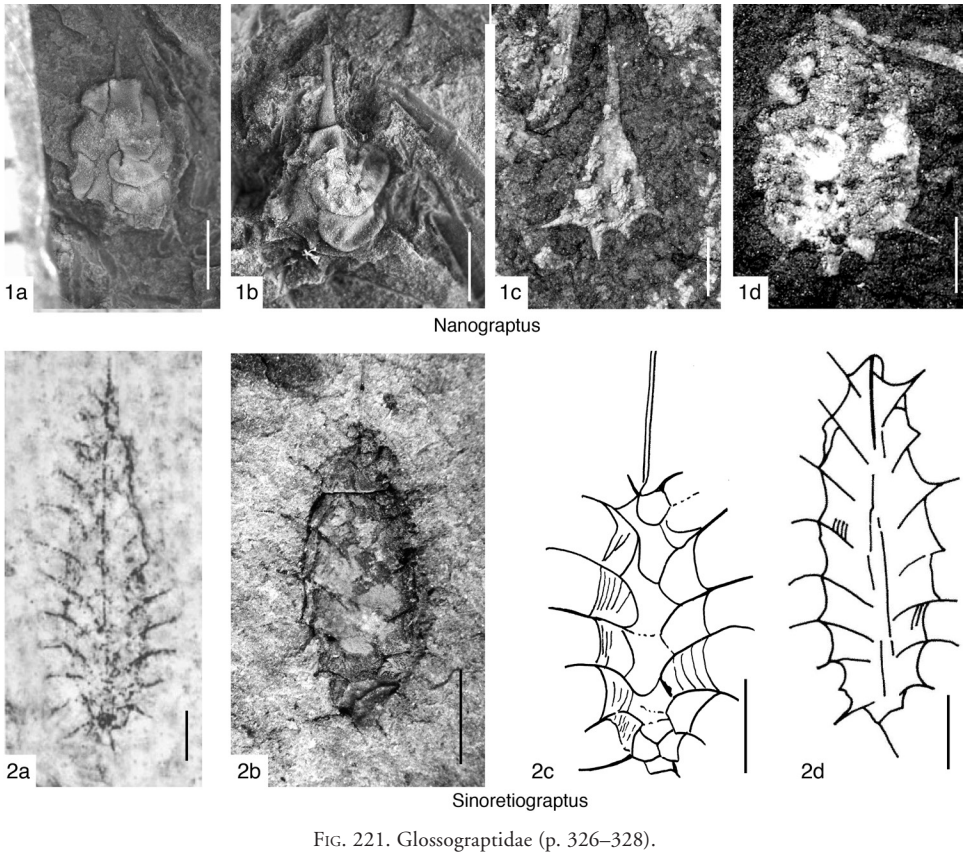


FIG. 221. Glossograptidae (p. 326–328).

Newfoundland, Canada, scale bar, 1 mm (new).——Fig. 220,*3c*. *P. proteus* (Harris & Thomas, 1935), GSC 23949, Daniels Harbour, western Newfoundland, Canada, scale bar, 1 mm (adapted from Whittington & Rickards, 1969, fig. 7).

Sinoretiograptus Mu & others, 1974, p. 164 [**S. mirabilis;* OD; =*Rogercooperia paucispinosus* Sherwin & Rickards, 2000, p. 163, herein]. Glossograptid with slender, elongated, probably finite colony consisting of ~8–10 thecal pairs; sicula with metasicular origin of first theca; glossograptid bulge reduced and restricted to two thecal pairs; slender spine-like rutella on all thecae; development unknown. *Upper Ordovician* (*Katian, Dicellograptus complexus* [=?*Dicellograptus ornatus*] Biozone): China, Australia.——Fig. 221,*2a–d. *S. mirabilis; 2a,* NMV P63643, Warbisco Shale, eastern Victoria, Australia (VandenBerg, 2003, fig. 2a); *2b–c,* holotype, NIGP 21406, late Katian, Wufeng Shale, Wangjiawan, Yichang, South China (new; drawing by Charles Mitchell); *2d,* AMF 103320, Keenan's Bridge, New South Wales, Australia (Sherwin & Rickards, 2000, fig. 2a). All scale bars, 1 mm.

Skiagraptus Harris, 1933, p. 108 [**Diplograptus gnomonicus* Harris & Keble in Harris, 1916, p. 66; OD]. Small, slender, scandent, dipleural(?) glossograptid with rutella of sicula and th1[1] united; thecae short; fusellum attenuated. *Middle Ordovician* (*upper Dapingian, Oncograptus upsilon* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): New Zealand, Australia, China, Norway, USA, Canada, Argentina.——Fig. 219,*1. *S. gnomonicus* (Harris & Keble), NMV P73118, scale bar, 1 mm (Finney & Chen, 1984, fig. 3A).

SUBORDER AXONOPHORA

Jörg Maletz

Suborder AXONOPHORA Frech, 1897

[Axonophora Frech, 1897, p. 607] [=Virgellina Fortey & Cooper, 1986, p. 639, *partim* (see Maletz, 2010a, p. 416); =suborder Diplograptacea Lapworth in Mitchell, 1987, p. 367; =order Diplograptoidea in Mitchell & others, 2007, p. 332]

Graptoloids with nema as leading rod followed by or engulfed in growth of thecal rows; colonies either biserial, dipleural, or uniserial; proximal development complex, with pro- or metasicular origin of th1[1], dicalycal theca delayed from position at th1[2] or lacking altogether; characteristic cross bars connect interthecal septa to nema in many taxa and form ring with aboral lists at base of interthecal septa. *Middle Ordovician* (*Dapingian, Oncograptus upsilon* Biozone)–*Lower Devonian* (*Pragian, Uncinatograptus yukonensis* Biozone): worldwide.

Frech (1897) introduced the name Axonophora for uniserial and biserial graptolites with a nema leading the growth of the stipe. The term has been accepted by some scientists, especially in Russian and Chinese literature (e.g., Obut, 1964; Mu, 1974), but it fell into disuse in western taxonomy (Bulman 1955, 1970; Rigby, 1986) and was only reintroduced by Maletz, Carlucci, and Mitchell (2009). Frech (1897) largely misinterpreted the colony development, following Ruedemann's (1895) reconstructions of synrhabdosomes. However, Frech recognized the central position of the nema in the growth of the graptolite colony. In discussing the early evolution of the axonophorans, Fortey, Zhang, and Mellish (2005, p. 1255) preferred the name Virgellina for this clade. Mitchell and others (2007) called the same clade Diplograptoidea. Maletz, Carlucci, and Mitchell (2009, fig. 6) separated the early biserials of the *Levisograptus austrodentatus* (Harris & Keble, 1932) group (see Maletz, 2011c) as stem axonophorans and even included the Arienigraptidae *sensu* Maletz and Mitchell (1996) in their Pan-Axonophora. This definition separates the *Levisograptus austrodentatus* group—which, in the past, has generally been accepted as the earliest biserials or axonophorans—from the remaining axonophorans.

The concept used herein (Fig. 222) identifies all biserial, dipleural graptolites as axonophorans. The defining synapomorphy of the Axonophora, then, is the biserial, dipleural colony construction engulfing a central nema between the dorsal sides of the two stipes. The Axonophora comprise all biserial, dipleural taxa derived from the two-stiped genus *Pseudisograptus* and the derived uniserial Monograptidae. The stem group is formed by *Apiograptus* and *Levisograptus,* bearing a pattern U astogeny. However, a trichotomy within the Diplograptina indicates remaining problems with this interpretation (see Mitchell & others, 2007). Based on a number of tubarium features, Maletz (2011d, fig. 3) preferred the origin of the Climacograptidae from a neograptine ancestor close to *Undulograptus,* thus, independent from the genus *Archiclimacograptus* and the Diplograptina. As a solution has not been proposed, the Climacograptidae are here retained in the Diplograptina. Further research is necessary to document the precise relationships of the three clades.

MORPHOLOGY

In the Axonophora, the nema gained a new importance and was used as the rod along which the stipes grew, while in non-axonophoran graptoloids the stipes did not need a leading rod and the nema was free and commonly relatively short and inconspicuous (Fig. 223.1). A long nema engulfed between the two laterally connected stipes is visible in biserial, monopleural Glossograptidae specimens (Maletz & Zhang,

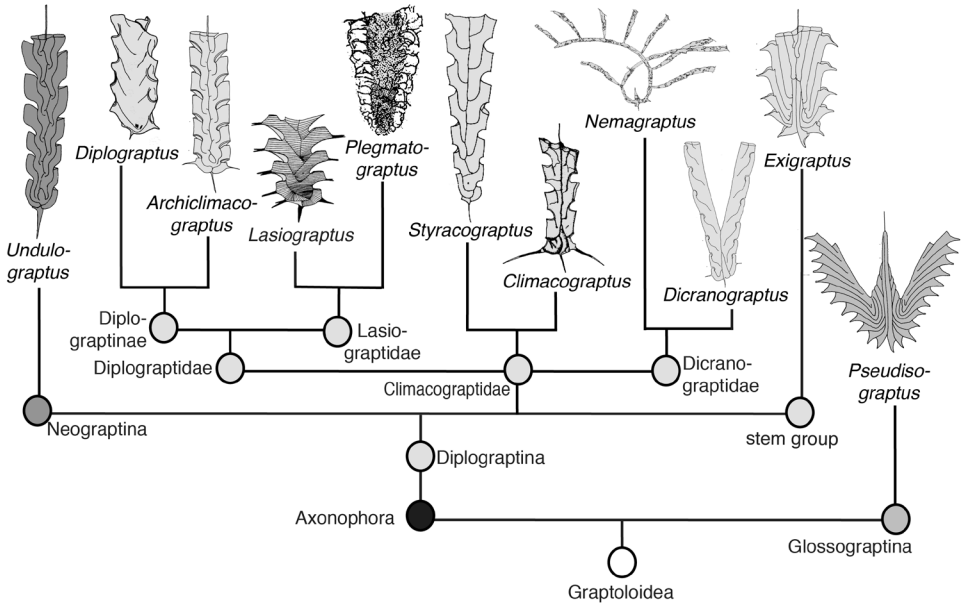


FIG. 222. Diagram of the Axonophora, showing the unresolved trichotomy within the Diplograptina leading to the Diplograptidae, Climacograptidae, and Dicranograptidae. Specimens not to scale (new).

2016). Early Axonophora were invariably biserial, dipleural (Fig. 223.2) but the biserial tubarium shape was lost in the Silurian monograptids (Fig. 223.3). In specimens of both groups, the nema extends distally beyond the thecate part of the tubarium.

The prosicula with the typical spiral line and the metasicula formed from fuselli is recognizable in the Axonophora. KRAFT (1926) differentiated the nema prosiculae (cauda) from the conus in *Rectograptus gracilis* (ROEMER, 1861) and in an indeterminate monograptid, ?*Heisograptus micropoma* (JAEKEL, 1889). He stated that the cauda is very short in monograptids but does not differ otherwise from the development in *Rectograptus*. The cauda has not been differentiated in later descriptions of isolated materials of axonophorans. Information on the number and development of the longitudinal rods on the prosicula is not available for most axonophoran taxa. The prosicula appears to be reduced in some climacograptids, where it is preserved in the form of a single rod or two rods united distally to form a normal nema (MITCHELL, 1987).

The nema was secreted in fusellar increments as a spine from the cauda of the prosicula (BATES, 1987a). The differentiation of the nema and virgula (RICKARDS, 1996) cannot be upheld, and the virgula in older literature should be regarded as identical to the nema. Nematularia are common in the Axonophora and may have various shapes (MÜLLER & SCHAUER, 1969; MÜLLER, 1975). Few nematularia are known from chemically isolated material of the Diplograptina, and many details of their development and use are still uncertain. They may have formed as two- and three-vaned structures (Fig. 223.5–223.6), as is seen in a number of examples (e.g., BULMAN, 1947; URBANEK, KOREN', & MIERZEJEWSKI, 1982; MITCHELL & CARLE, 1986). MALETZ and others (2011) illustrated the heart-shaped nematularium of *Archiclimacograptus decoratus* (HARRIS & THOMAS, 1935) from western Newfoundland produced from fusellar or microfusellar material. In the Lasiograptidae, paired lateral spines or scopulae with variably formed vanes with fusellar construction are present in a number of species (Fig. 223.4), but are

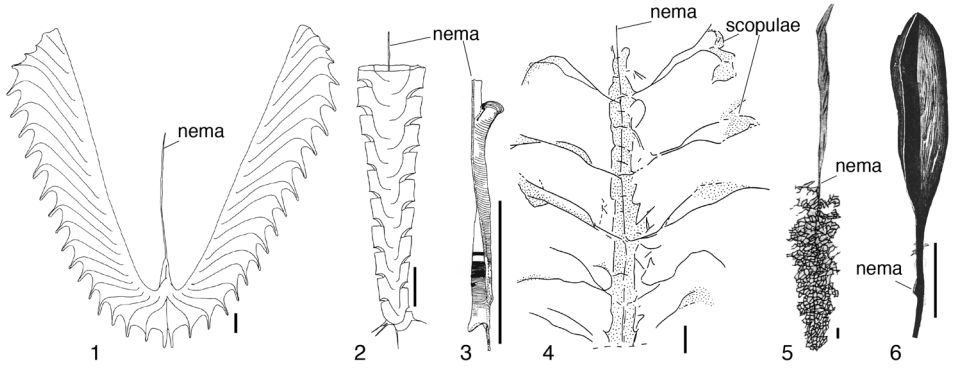


FIG. 223. Nema and nematularium development in the Graptolithina. *1, Isograptus divergens* HARRIS, 1933, completely free nema between two reclined stipes (new); *2, Amplexograptus praetypicalis* RIVA, 1987, nema incorporated in colony, visible at distal end (new); *3, Lobograptus imitator* URBANEK, 1966, nema visible on dorsal side of stipe (Urbanek, 1966, pl. 28D); *4, Neurograptus fibratus* (LAPWORTH, 1876a), NIGP 127015, part of colony showing paired scopulae, Kalpin, China (Chen & others, 2000, fig. 6); *5, Phormograptus laqueus* (ROSS & BERRY, 1963), holotype showing long nematularium (Ruedemann, 1934, pl. 15,*10*); *6, Pseudoclimacograptus scharenbergi* (LAPWORTH, 1876a), three-vaned nematularium (Bulman, 1947, pl. 9). Scale bars, 1 mm.

best known in chemically isolated material of *Orthoretiolites hami* (BATES & KIRK, 1991).

The origin of the ventral virgella of the Axonophora from a rutellum can be documented in all steps leading to the final apertural virgellar spine (MALETZ, 2010a; MALETZ, LENZ, & BATES, 2016). It occurred in the glossograptid *Isograptus* MOBERG, 1892a, in which the rutellum is often considerably extended, leading to the lamelliform rutellum of *Arienigraptus* and the Glossograptidae. A lanceolate virgella has been recognized in chemically isolated material of the genus *Levisograptus* (Fig. 224.1–224.4). The genus *Apiograptus* may still have possessed a lamelliform rutellum, but isolated material is not available.

PROXIMAL DEVELOPMENT

The proximal development and structure is quite complex in axonophorans and becomes successively simpler. Quite a number of proximal development types have been described for biserial graptolites, based on the origins and growth directions of proximal thecae (MITCHELL 1987, 1990; MELCHIN & MITCHELL, 1991; MELCHIN, 1998; MELCHIN & others, 2011). The development of relief specimens of the oldest axonophorans (*Apiograptus*, *Levisograptus*) can easily be related to the manubriate isograptids, because the remains of the manubrium are still present, even though often considerably reduced in size (Fig. 225.1). Relief specimens of *Apiograptus* have a low prosicular origin of th1[1] (ZHANG, 1993; MITCHELL & MALETZ, 1995, fig. 3N) as a symplesiomorphic character and not the typical metasicular origin of th1[1] of derived axonophorans. The manubrium is reduced but retains the initial parallel-sided downward growth of the proximal thecae (Fig. 225.2). The proximal development is comparable to the pattern U astogeny in all other features. The manubrium is lost in the genus *Levisograptus,* and the last remains of the manubrium exist only as an exposed patch of thecal origins on the reverse side of the colony (Fig. 225.3–225.4). The dicalycal theca appears to be th2[2], but apart from a few relief specimens, isolated juveniles are not available to confirm this construction. The delayed dicalycal theca th2[2] is also present in the genus *Pseudisograptus* (see COOPER & NI, 1986). *Levisograptus primus* (LEGG, 1976) and *Levisograptus austrodentatus* bear a pattern U astogeny, the most complex type described from axonophorans (MITCHELL, 1990).

Initially, the two stipes of the axonophorans were folded over the apex of the sicula

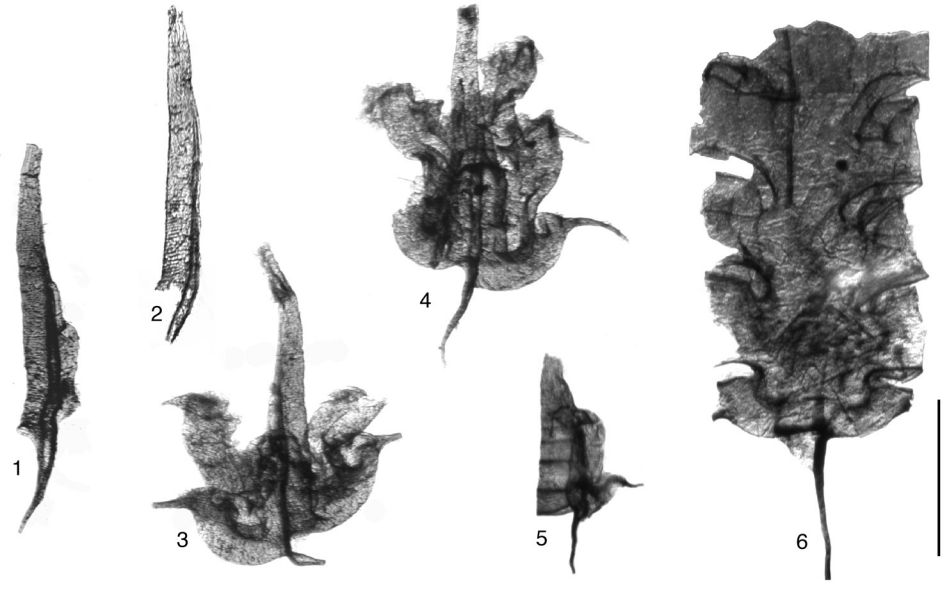


FIG. 224. The virgellar spine development in early Axonophora, infrared photos. *1–4, Levisograptus sinicus* (MU & LEE, 1958), Cow Head Group, western Newfoundland; *1,* GSC 133381, nearly complete sicula with lanceolate virgella and part of first theca; *2,* GSC 133380, juvenile sicula with tip of lanceolate virgella broken, showing thickened rims; *3,* GSC 133386, small specimen with five thecae and strongly bent lanceolate virgella; *4,* GSC 133378, specimen with three thecal pairs, some parts broken (*1–4,* Maletz, 2010a, fig. 5,*b,a,g,h,* respectively); *5–6, Archiclimacograptus* MITCHELL, 1987, West Bay Centre Quarry, western Newfoundland; *5,* GSC 140112, juvenile, showing virgellar spine and dark banding on sicula (new); *6,* GSC 140113 (new). All specimens are flattened, chemically isolated from shales. Scale bar, 1 mm for all specimens.

and grew parallel to each other, forming the median septum with the nema integrated in the layer. The precise construction of the median septum is far from being understood, and the reconstruction of BULMAN (1970, fig. 46), as well as the interpretation of GOLDMAN and others (2011) in climacograptids, suggest a single layered construction. The median septum varies considerably in shape due to the thecal style of the colony. Due to the presence of intrathecal folding (MALETZ, LENZ, & BATES, 2016), the median septum may be undulating or even zigzag shaped (Fig. 226.2).

Intrathecal folds are common in earlier axonophorans but easily overlooked because the short bars connected to the median septum are only recognizable in well-preserved relief material (Fig. 226.1). The intrathecal folds represent a temporary stop and change in growth direction at the base of the metathecae and the introduction of the median septum. A short lateral bar is commonly visible, around which the interthecal septum bends. The position of this part of the cross bar is clearly marked in *Urbanekograptus retioloides* (URBANEK, 1959, pl. 2) to be above the origin of the prothecae and can be recognized as the cross bars connected to the median septum in taxa with intrathecal folding (Fig. 226.3). The ventral parts of these cross bars (Fig. 226.2) anchor the nema and stabilize the median septum. The robust strengthening cross bars connect the nema with the lateral walls in many taxa and are connected to the thickened bases of the interthecal septae, the aboral lists (Fig. 226.2). BULMAN (1932a) illustrated the thickened cross bars from chemically isolated material in *Archiclimacograptus* (?) *skagensis* (JAANUSSON & SKOGLUND, 1963) and *Haddingograptus eurystoma* (JAANUSSON, 1960) (Fig. 226.4–226.5), showing that they are part of the median septum construction.

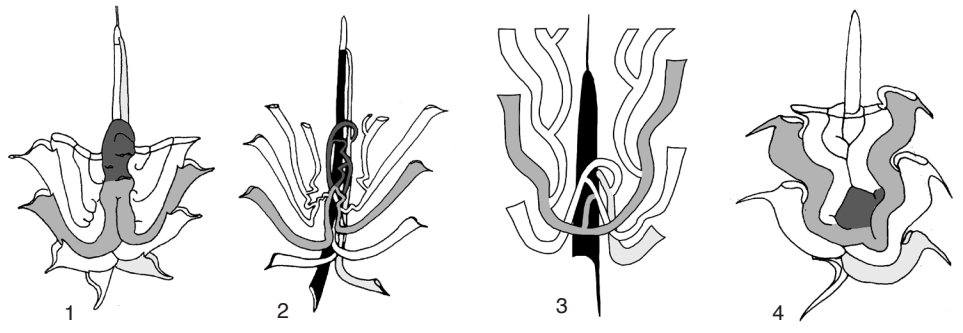


FIG. 225. Proximal development, pattern U astogeny. *1, Apiograptus uniformis* (MU in MU & others, 1979), reverse view, reconstruction (new drawing, adapted from Mitchell & Maletz, 1995, fig. 3N); *2,* pattern U astogeny of *Apiograptus* COOPER & MCLAURIN, 1974 with conspicuous downward growth of proximal thecae (manubrium in *light and dark gray*) and prosicular origin of th1[1] (new); *3,* pattern U astogeny (adapted from Mitchell, 1990, fig. 11,*1C*); *4, Levisograptus sinicus* (MU & LEE, 1958), reverse view showing remains of manubrium, reconstruction (new).

In derived axonophorans, a median septum may be absent, and the thecae grow alternately to form a unistipular, biserial colony (MELCHIN, NACZK-CAMERON, & KOREN', 2003). These either have an unconnected nema freely wandering through the colony, or the nema is attached to the center of the interthecal septae through a short central bar. BULMAN (1932c) described the development of the unistipular colony of *Geniculograptus typicalis* (HALL, 1865) in some detail and illustrated the connection of the interthecal septae to the nema (Fig. 226.6–226.7). The aboral list is modified into a V-shaped form with the tip connected to the nema. The median septum may also be delayed and not present in the proximal end in many diplograptines (i.e., *Amplexograptus*, *Hustedograptus, Orthograptus;* see MITCHELL, 1987).

THECAL STYLES

In the literature, the thecal shapes of biserial axonophorans are frequently described by referring to typical genera. The terminology ranges from dichograptid, glyptograptid, and orthograptid to climacograptid and lasiograptid thecal styles (BULMAN, 1970, fig. 41–42). These styles are not used herein; it is preferred to describe the thecal features independent of any named genera, following MALETZ, BATES, and others (2014). Thus, the thecal descriptions are based on constructional features, the shape, presence/absence or style of the geniculum, genicular additions and also of apertural modifications. The profile of the ventral thecal wall may be straight or nearly so (Fig. 227.1) or may have a geniculum that is rounded (Fig. 227.2) or angular (Fig. 227.3–227.4). The position of the geniculum may vary considerably and can be close to the underlying thecal aperture or close to the overlying aperture. In cases in which the geniculum is close to the thecal aperture above, the term pseudogeniculum has been used (see MITCHELL, MALETZ, & GOLDMAN, 2009).

Thecal apertures can be quite variably adorned with lappets, spines, or other features. These can be restricted to the sides of the thecal apertures or to the ventral apertural margins. In the Peiragraptinae, for example, lateral apertural lobes or lappets can be modified into horns (Fig. 227.1) and eventually into paired apertual spines, as in the *Orthograptus quadrimucronatus* (HALL, 1865) group (GOLDMAN, 1995). Geniculate thecae often bear conspicuous flanges or collars (Fig. 227.4a), sometimes completely surrounding the thecal aperture. A ventral notch (Fig. 227.4b) in the aperture is commonly formed, supporting the paired lateral lobes of many species. In addition, a genicular notch (Fig. 227.3b) may also be present. Thecal apertures may be

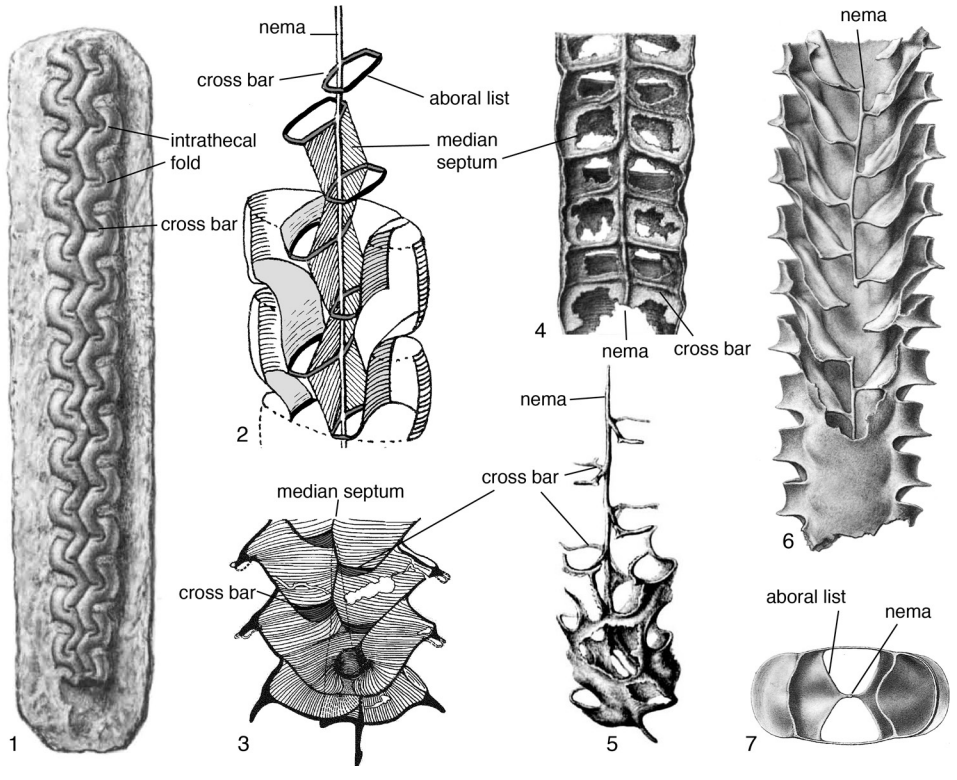


Fig. 226. Median septum development. *1,* Climacograptid indet., relief specimen showing zigzag median septum and intrathecal folding (Bulman, 1932a, pl. 3,*34*); *2,* part of colony showing integration of median septum, nema, crossbars, and aboral list (adapted from Bulman, 1970, fig. 46); *3, Urbanekograptus retioloides* (Wiman, 1895), reconstruction showing the cross bars and intrathecal folding, prothecal parts of third and fourth thecal pair in *gray,* note change of growth direction at this point (Urbanek, 1959, pl. 5A); *4–5, Haddingograptus oliveri* (Bouček, 1973); *4,* fragment showing cross bars from inside, fusellum of median septum largely preserved (Bulman, 1932a, pl. 1); *5,* proximal end in lateral view, showing connecting bars in distal part of colony where fusellum is missing (Bulman, 1932a, pl. 2); *6–7, Geniculograptus typicalis* (Hall, 1865), unistipular colony; 6, distal colony fragment with partially preserved nema and V-shaped attachment to base of interthecal septa; *7,* cross section of a colony showing connection of interthecal septa to nema in center (*6–7,* adapted from Bulman, 1932b, pl. 4,5).

introverted, horizontal, or everted, but these features are often modified by preservational aspects or the development of lateral lobes and horns (Fig. 227.1) and, thus, may be unreliable. All these thecal features can be modified independently and do not provide a useful guide for taxonomy.

Infraorder DIPLOGRAPTINA Lapworth, 1880

[*nom. correct.* Obut, 1957, p. 17, *ex* Diplograpta Lapworth, 1880f, p. 191, *non* order Diplograptoidea in Mitchell & others 2007; *non* superfamily Diplograptoidea, Štorch & others 2011, fig. 6] [=Diplograptina, Jaanusson, 1960, p. 321, *partim,* excl. Monograptidae]

Biserial axonophorans with pattern U astogeny or derived one, excluding taxa of the Neograptina; early taxa with manubrium and prosicular origin of th1[1], but metasicular origin of th1[1] in derived taxa; proximal end wide and rounded to highly asymmetrical, generally provided with virgellar spine and additional apertural spines, at least on first thecal pair; tubarium may be secondarily multiramous to single stiped; fusellum attenuated in some taxa, in which also reticulum and sometimes a lacinia develop (Lasiograptidae); thecae geniculate or non-geniculate with intrathecal folds and

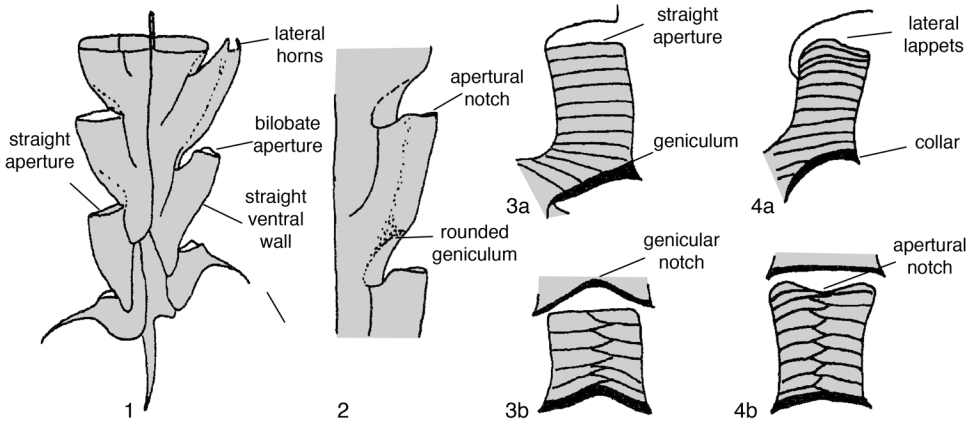


FIG. 227. The thecal morphology in biserial axonophorans (adapted from Maletz, 1997a, fig. 7).

complete median septum in earlier taxa; interthecal septa long and undulating in early taxa, becoming successively shorter in later ones; characteristic cross bars connect interthecal septa to nema in many taxa and form ring with aboral lists at base of interthecal septa. *Middle Ordovician* (*Dapingian, Exigraptus clavus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

MALETZ, CARLUCCI, and MITCHELL (2009) and ŠTORCH and others (2011) differentiated two major clades in the Axonophora, which ŠTORCH and others (2011, p. 368) identified as the Diplograptina and the Neograptina and recognized the earliest taxon of the Neograptina as *Undulograptus formosus* (MU & LEE, 1958), a typical axonophoran with a pattern C astogeny (see MITCHELL & others, 2007, fig. 1), most probably derived from a diplograptine ancestor. Whereas MITCHELL and others (2007) and MALETZ, CARLUCCI, and MITCHELL (2009) suggested separating a paraphyletic stem group to define the Diplograptina and Neograptina as two monophyletic taxa, it is preferred herein to include their stem group in the Diplograptina, generating a paraphyletic taxon from which the Neograptina originated.

The concept used here for the Diplograptina is nearly identical to the order Diplograptoidea of MITCHELL and others (2007, fig. 1A), but includes the genus *Apiograptus* COOPER & MCLAURIN, 1974 and thus follows the opinion of HARRIS and THOMAS (1935, p. 303) who identified *Apiograptus crudus* (HARRIS & THOMAS, 1935) as the earliest biserial graptolite and suggested a relationship to the genus *Isograptus* MOBERG, 1892a. ŠTORCH and others (2011) included the superfamilies Dicranograptoidea, Diplograptoidea, and Climacograptoidea in the Diplograptina, interpreted here as family level taxa (Fig. 222). The detailed relationships of the Diplograptina and Neograptina are still uncertain, because the early evolution of the axonophorans is poorly known (MALETZ, 2011c).

STEM GROUP DIPLOGRAPTINA

The early axonophorans having the remains of the pseudisograptid manubrium are herein referred to an unnamed stem group taxon. This stem group is characterized by a pattern U astogeny, lost in the Diplograptidae, in which early taxa have a pattern C astogeny. A pattern A to pattern C astogeny occurs in the basal members of the Neograptina. The genus *Apiograptus* retains a prosicular origin of th1[1], a remnant of the origin through a pseudisograptid ancestor, lost in *Levisograptus*.

Apiograptus COOPER & MCLAURIN, 1974, p. 80 [*(?) *Glossograptus crudus* HARRIS & THOMAS, 1935, p. 303; OD] [=*Exigraptus* MU in MU & others, 1979, p. 128 (type, *E. clavus,* OD), syn. by NI &

Xiao, 1994, p. 15]. Diplograptina with strongly developed manubrium and pattern U astogeny; proximal end rounded, with maeandrograptid to isograptid symmetry; thecae elongated, tube-like, with widening apertures, long rutella, and sometimes with low lateral apertural lappets; sicula probably with lamelliform rutellum and low prosicular origin of th1[1]; proximal development of pattern U astogeny. *Middle Ordovician* (*upper Dapingian*, *Cardiograptus morsus* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, Sweden.——Fig. 229,*1a–c*. **A. crudus* (Harris & Thomas)*; 1a,* lectotype, NMV P31960 (new; provided by A. H. M. VandenBerg); *1b,* topotype, NMV P27485, Chinaman's Creek, Muckleford, Victoria, Australia (Cooper & McLaurin, 1974, fig. 2h); *1c,* topotype, NMV P30515, juvenile showing large manubrium (new). Scale bars, 1 mm.

Levisograptus Maletz, 2011c, p. 856 [**Fucoides dentatus* Brongniart, 1828, p. 70; OD]. Diplograptina with pattern U astogeny; tubarium parallel sided to distally widening; proximal end broad, fairly symmetrical; manubrium structure reduced, lacking downward growth of thecae or manubrium lacking altogether; thecae long and doubly sigmoidal in shape; supragenicular thecal walls vertical to outwardly inclined; apertural spines at least on first thecal pair, rarely on distal thecae; thecae bear rounded or flowing geniculum and incipient to well-developed lateral apertural lappets. *Middle Ordovician* (*upper Dapingian, Exigraptus clavus* Biozone–*Darriwilian, Holmograptus lentus* Biozone): worldwide.——Fig. 229,*4a–c*. **L. dentatus; 4a,* neotype (selected by Bulman, 1963b, p. 672), GSC 943, distal end omitted; *4b,* GSC 134280, associated with neotype; *4c,* GSC 134266, reverse view in low relief; Lévis, Québec, Canada (Maletz, 2011c, fig. 3A–B, 5G, respectively). Scale bars, 1 mm.——Fig. 229,*4d. L. austrodentatus* (Harris & Keble, 1932), GSC 102618, Begins Hill, Lévis, Québec, obverse view, scale bar, 1 mm (Maletz, 1997b, fig. 7C).

Family DIPLOGRAPTIDAE Lapworth, 1873

[Diplograptidae Lapworth, 1873b, table 1 facing p. 555; =superfamily Diplograptoidea Lapworth in Štorch & others, 2011]

Diplograptina with pattern C astogeny or derived one, excluding derived Lasiograptidae; proximal end without manubrium; metasicular origin of th1[1]; proximal end wide and rounded to highly asymmetrical, generally provided with virgellar spine and additional apertural spines on at least first thecal pair; thecae variable, typically with complex apertural or genicular additions; long, double sigmoid thecae with intrathecal folds and complete median septum in earlier taxa; tubarium with attenuated fusellum in some taxa. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

The Diplograptidae is a paraphyletic family from which the Lasiograptidae originated (Fig. 222). The precise origin and differentiation of the Climacograptidae (see discussion in Maletz, 2011d) and the Dicranograptidae (see Maletz, 1998b) remains unclear. In their cladistic interpretation, Mitchell and others (2007) placed them at the base of an unresolved trichotomy within the Diplograptina.

The concept of the family Diplograptidae has changed considerably during the time of its use. Lapworth (1873b) introduced the taxon for all biserial, dipleural graptolites, but stated that this arrangement was provisional and essentially artificial. As used by Mitchell and others (2007), it includes most of the Orthograptidae of Mitchell (1987), except for the Lasiograptinae, now recognized as the family Lasiograptidae (Mitchell & others, 2007). Even though a number of taxa are well known from isolated material, many questions still remain open on the internal structure of the tubarium in members of the clade.

Mitchell, Maletz, and Goldman (2009) revised the genus *Diplograptus* (the name giver of the Diplograptidae) and considered it as nesting among the main plexus of the Orthograptidae of Mitchell (1987), a clade of biserials with a pattern G or a derived astogeny and possessing paired antivirgellar spines. As the authors stated, except for the proximal end pattern, the genus might better fit with the archiclimacograptids. Štorch and others (2011) defined their superfamily Diplograptoidea as the clade including a stem lineage with the genera *Eoglyptograptus* and *Pseudamplexograptus* and the two families Diplograptidae and Lasiograptidae.

Subfamily DIPLOGRAPTINAE Lapworth, 1873

[Diplograptinae Lapworth, 1873b, table 1 facing p. 555, *ex* Diplograptidae Lapworth, 1873b]

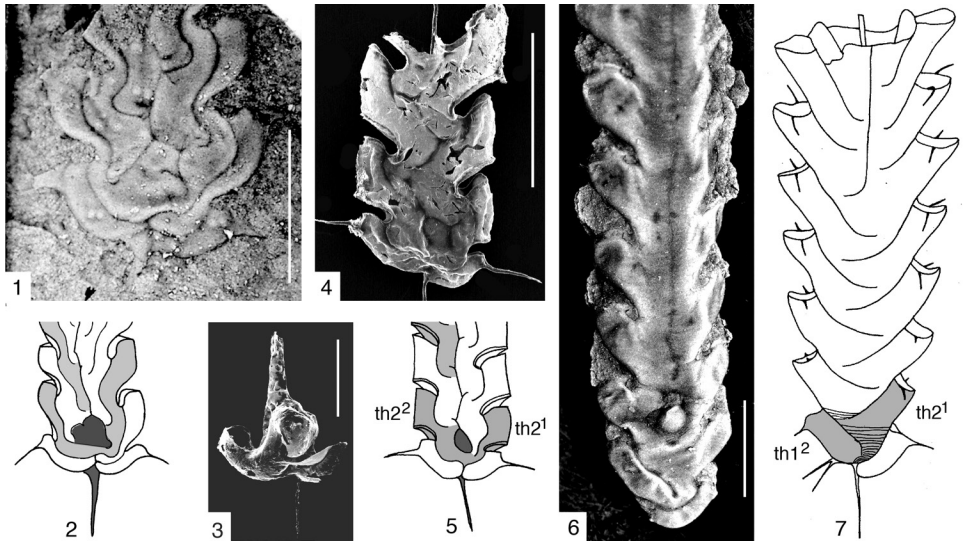


Fig. 228. Proximal development in the Diplograptina. *1, Levisograptus sinicus* (Mu & Lee, 1958), PMU 31733, pattern U astogeny, latex cast, coated, Fågelsång-3 drill core at 56.28–56.30 m, Scania, Sweden (Maletz & Ahlberg, 2018, fig. 6G); *2, Levisograptus austrodentatus* (Harris & Keble, 1932), reverse view, pattern U astogeny, reconstruction (new); *3–5, Archiclimacograptus decoratus* (Harris & Thomas, 1935); *3,* GSC 139286a, reverse view, showing upward-growing flange, Daniels Harbour, Table Head Group, western Newfoundland (new); *4,* GSC 139286b, small specimen in reverse view, Daniels Harbour, western Newfoundland (new); *5,* reconstruction of pattern C astogeny (new); *6, Diplograptus pristis* (Hisinger, 1837), LO 2354t, reverse view (new); *7, Orthograptus quadrimucronatus* (Hall, 1865), reverse view, reconstruction, showing pattern G astogeny (based on Maletz, 2011b, fig. 2B). Scale bar 0.5 in 3, all other scale bars, 1 mm.

Biserial diplograptids with pattern C or derived astogeny, excluding taxa of the Lasiograptidae; proximal end with metasicular origin of th1[1]; proximal end square to highly asymmetrical, generally provided with virgellar spine and additional apertural spines on first thecal pair; thecae variable, commonly with complex apertural or genicular additions; intrathecal folds and complete median septum in earlier taxa. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

The early evolution of the Diplograptinae is unclear because detailed information on the proximal development and thecal construction of most basal axonophorans—and thus, the connection to the stem group taxa—is not available. The proximal development of the Diplograptinae varies considerably. Whereas taxa of the stem group had a pattern U astogeny (Fig. 228.1–228.2), early Diplograptinae possessed a pattern C astogeny (Fig. 228.3–228.5), and younger taxa may have had a derived pattern G astogeny (Fig. 228.6–228.7). Species with pattern C or derived astogeny usually had an upward-growing flange (Fig. 228.3) uniting with the downward-growing initial part of th2[1], forming the paired openings for the growth of th2[1] and th2[2] (Fig. 228.5). In derived taxa, th1[2] and th2[1] may have formed a conspicuous arch in the pattern G astogeny (Fig. 228.7). The evolutionary origin of the upward-growing flange is uncertain as it has not been detected in any species with a pattern U astogeny and appears to be lacking in species with the derived pattern B astogeny (see Mitchell, 1987).

Diplograptus M'Coy, 1850, p. 270, *nom. correct.* Hall, 1865, p. 109, original spelling as *Diplograpsis* changed in ICZN Opinion 650, 1963] [**Prionotus pristis* Hisinger, 1837, p. 114; SD Gurley, 1896, p. 78]. Diplograptines with bluntly rounded

proximal end; th1[1] and th1[2] with subapertural or apertural spines; tubarium with or without median septum and alternating thecal origin; thecal gradient with proximally geniculate to distally straight, outward-inclined ventral sides and everted thecal apertures; proximal development probably of pattern G astogeny. *Upper Ordovician* (*upper Katian, Pleurograptus linearis* Biozone–*Hirnantian, Normalograptus extraordinarius* Biozone): China, Europe, UK, Estonia, Sweden, Canada, USA, Russia (Siberia).——Fig. 229,*9a–c*. **D. pristis* (Hisinger); *9a*, holotype, NRM-PZ Cn 59728, Draggabro, Dalarna, Sweden (new; drawing by John F. Riva); *9b,* GIT 708-1, infrared photo, obverse view, showing sicular length; *9c*, GIT 708-1, reverse view, Paasvere drill core, Estonia (*b–c,* Mitchell, Maletz, & Goldman, 2009, fig. 1E–2E). Scale bars, 1 mm.

Archiclimacograptus Mitchell, 1987, p. 387; *ex* subgenus *Pseudoclimacograptus* (*Archiclimacograptus*) Mitchell, 1987, p. 387, Maletz, 1997a, p. 52 [**Pseudoclimacograptus angulatus sebyensis* Jaanusson, 1960, p. 330; OD]. Diplograptines with a pattern C astogeny; square proximal end with apertural to subapertural spines on first thecal pair, an arch connecting th1[2] and th2[1], and early origin of th3[1] on reverse side; exposed part of the crossing canal of th1[2] small; dicalycal theca is th2[1] or later one; thecae with distinct geniculae, variably developed lateral apertural lappets and variably long thecal overlap; intrathecal septa originate from median septum, indicating intrathecal folds; gradual shape change common in development of geniculae, lateral apertural lappets, and shape and length of septa along tubarium. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone)–*Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone): worldwide.——Fig. 229,*8a–b*. **A. sebyensis* (Jaanusson); *8a,* obverse view, reconstruction of holotype (Jaanusson, 1960, fig. 7D); *8b,* PMO 138.785, proximal end in reverse view (Maletz, 2011d, fig. 2). Scale bars, 1 mm.

Mesograptus Elles & Wood, 1907, p. 258 [**Graptolithus foliaceus* Murchison, 1839, p. 694; OD (type based on distal fragment), =*Diplograptus* (*Mesograptus*) *multidens* Elles & Wood, 1907, p. 261, Hughes, 1989, p. 54]. Diplograptines with robust, parallel-sided to distally distinctly widening tubarium; thecae geniculate throughout or geniculum lost distally; thecal excavations deep and semicircular to somewhat restricted; apertures horizontal to everted; supragenicular wall short and commonly of similar height to that of thecal excavations; proximal development and median septum unknown, but possibly pattern C astogeny; first thecal pair with subapertural to median spines. *Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone): UK, Sweden, China, Russia. [The distribution of the genus may indicate a high latitude faunal element.]——Fig. 229,*7a–b*. **M. foliaceus* (Murchison); *7a,* NHMUK PM 1288, proximal part of lectotype of *Diplograptus* (*Mesograptus*) *multidens* Elles & Wood; *7b*, second specimen on NHMUK PM 1288, obverse view; scale bars, 1 mm (new; drawings by John F. Riva).

Oepikograptus Obut & Sennikov, 1984b, p. 110 [**Diplograptus bekkeri* Öpik, 1927, p. 28; OD] [=*Fenhsiangograptus* Hong, 1957, p. 495 (type, *F. fenhsianensis,* OD), syn. herein]. Diplograptines with distinctly biform thecae; proximal thecae spined, distal ones geniculate; median septum complete without indications of intrathecal folds; proximal end of pattern G astogeny, with apertural spines on variable number of proximal thecal pairs; thecal apertures provided with lateral lappets; sicula extensively exposed on the obverse side of the tubarium. *Middle Ordovician* (*Darriwilian, Jiangxigraptus vagus* Biozone or *Sandbian, Nemagraptus gracilis* Biozone): China, Estonia, Latvia, Spain, Sweden, Syria. [The distribution of the genus may indicate a high latitude faunal element.]——Fig. 229,*5a*. **O. bekkeri* (Öpik), holotype, TUG 1087-8, Kohtla, Estonia, scale bar, 1 mm (new; provided by Ursula Toom).——Fig. 229,*5b. O. fenshiangensis* (Hong, 1957), holotype, scale bar, 1 mm (Hong, 1957, pl. 5,*7*).

Prorectograptus Li, 1994, p. 66 [**Cryptograptus uniformis* Chen in Mu & others, 1979, p. 132; M]. Diplograptines with square proximal end and parallel-sided colony; thecae with straight, everted ventral thecal sides and everted apertural margins, possessing strong rutella or apertural spines; proximal development unknown. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone): China.——Fig. 229,*3*. **P. uniformis* (Chen in Mu & others), lectotype (selected herein), NIGP 32333, scale bar, 1 mm (new).

Pseudamplexograptus Mitchell, 1987, p. 389 [**Lomatoceras distichum* Eichwald, 1840, p. 101; OD (lectotype illustrated by Jaanusson, 1960, pl. 5,*5*)]. Diplograptines with broad and nearly parallel-sided tubarium; thecae geniculate throughout or geniculum lost distally; thecal excavations deep and semicircular to somewhat restricted; apertures horizontal to introverted; supragenicular wall short and commonly of similar height to that of thecal excavations; pattern C astogeny with early origin of th3[1]; dicalycal theca th2[1] with complete median septum and intrathecal folding; first thecal pair with apertural or subapertural spines. [Taxon may be synonymous to *Mesograptus.*] *Middle Ordovician* (*upper Darriwilian, Pseudamplexograptus distichus* Biozone): UK, Estonia, Latvia, Sweden, Norway, China, Russia. [The distribution of the genus may indicate a high latitude faunal element].——Fig. 229,*6a–c*. **P. distichus* (Eichwald) isolated specimens, Öland, Sweden; *6a*, NRM-PZ Cn 2355; *6b–c*, NRM-PZ 111 (Holm collection), juvenile in reverse (*b*) and obverse (*c*) views, showing pattern C astogeny (Bulman, 1932a, pl. 4,*19–20,* pl. 5,*1*, respectively). Scale bars, 1 mm.

Urbanekograptus Mitchell, 1987, p. 389 [**Climacograptus retioloides* Wiman, 1895, p. 276;

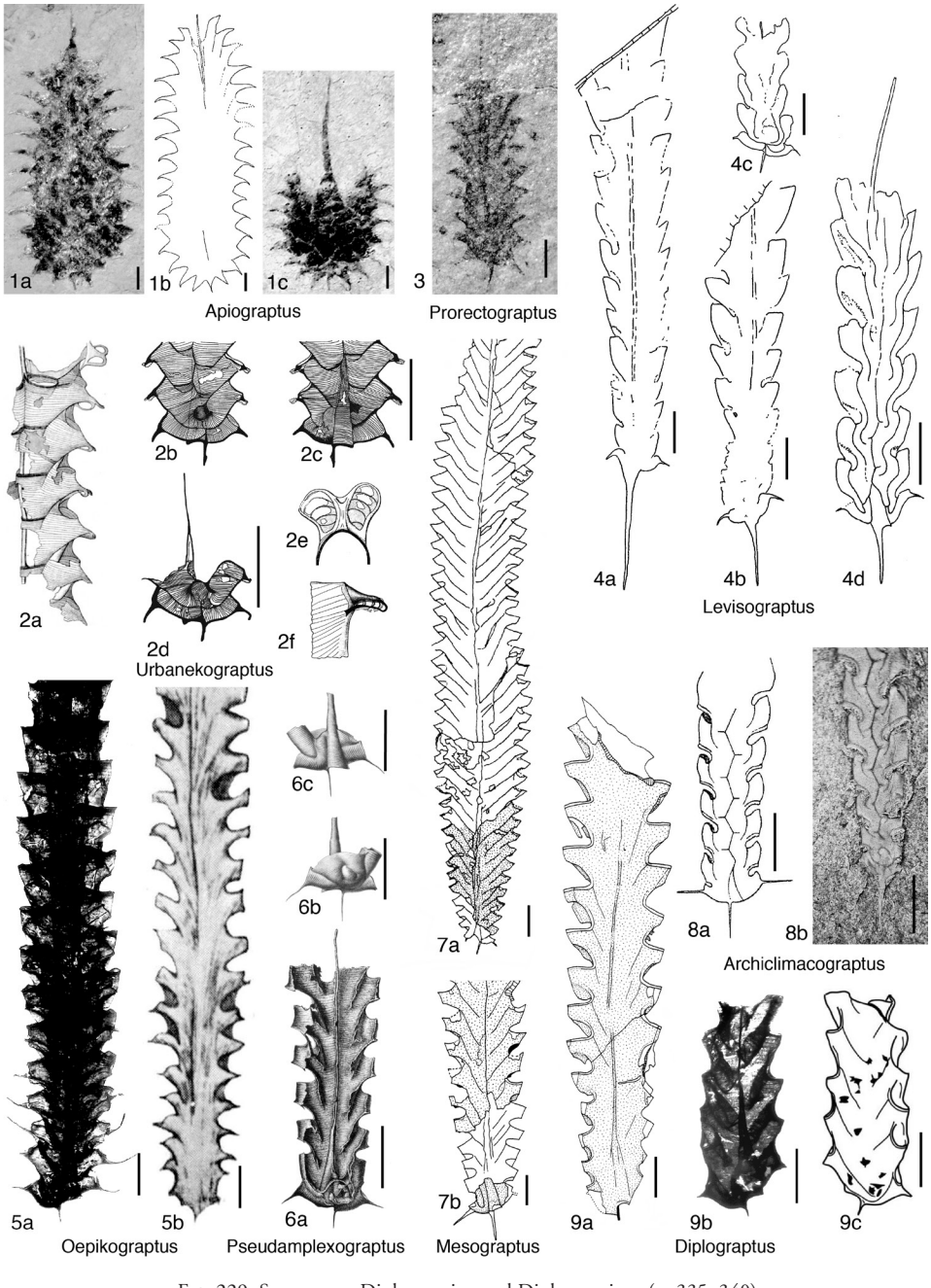


FIG. 229. Stem group Diplograptina and Diplograptinae (p. 335–340).

OD]. Diplograptines with nearly symmetrical, square proximal end and pattern C astogeny with th2[2] as the dicalycal theca; aperturtal spines on first thecal pair; later thecae with prominent paired subapertural lobes; intrathecal folds present; median septum undulating. *Middle Ordovician* (*upper Darriwilian, Dicellograptus vagus* Biozone) or *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Poland, Sweden (glacial boulders).——FIG. 229,*2a–f.* **U. retioloides* (WIMAN) *2a,* holotype,

fragment, Grisslehamn, Wäddö, northeast of Stockholm, Sweden, glacial boulder (Wiman, 1895, pl. 9,*4*); *2b–c,* proximal end in reverse (*b*) and obverse (*c*) views, glacial boulder 0.31, Poznan Czerwonak, Poland; *2d,* juvenile with complete sicula, proximal development in reverse view; *2e–f,* detail of apertural lobes from the side (*f*) and above (*e*) (*2b–2f,* Urbanek, 1959, from text-pl. 4, 5, and 7, respectively). Scale bars, 1 mm.

Subfamily PEIRAGRAPTINAE Jaanusson, 1960

[Peiragraptinae Jaanusson, 1960, p. 322] [=Orthograptinae Mitchell, 1987, p. 380] [=Eoglyptograptinae Mitchell, 1987, p. 396; revised from misspelling as Eoglyptograptidae subfamily *nov.*]

Septate to aseptate diplograptids with straight median septum; onset of median septum often considerably delayed; interthecal septae in aseptate taxa attached to nema by central bar, but contact may be lost in younger taxa, in which nema is free; proximal development of pattern A astogeny or derived one (patterns B, G, F, K); often strongly asymmetrical proximal end with sicula extensively exposed on obverse side in younger taxa; sicula bearing paired antivirgellar spines in younger taxa; thecae variable, with straight to strongly geniculate ventral wall; apertures frequently with paired processes, lobes, horns, or spines; genicular modifications common; fusellum reduced in some taxa. *Middle Ordovician* (*Darriwilian,* ?*Holmograptus lentus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

Jaanusson (1960) based his subfamily Peiragraptinae on the genus *Peiragraptus,* which is now regarded as an abnormal taxon or population of distally uniserial axonophorans of general diplograptid relationships. Mitchell (1987) emended the subfamily and referred a number of additional genera to the subfamily, based on the strongly geniculate thecae and the derived proximal development with a pattern G astogeny. Mitchell (1987) separated the genera *Orthograptus* and *Hustedograptus* in the subfamily Orthograptinae. Mitchell and others (2007) and Štorch and others (2011) eliminated the subfamilies Orthograptinae and Peiragraptinae and referred all genera to the Diplograptidae instead. Maletz (2014b) differentiated the Diplograptinae and the Orthograptinae in the family Diplograptidae.

Early peiragraptines bear a pattern A astogeny (Fig. 230.1a–c), but during the evolution of the group, patterns G and K became the standard, and the dicalycal theca was delayed or even eliminated in species without a median septum. Another important change occurred in the development and shape of th1[1]. A typical U-shaped th1[1] with a space between the downward- and upward-growing parts of the theca was present in species with a pattern G astogeny on the obverse side of the colony (Fig. 230.2a–c). This gap was filled by the initial part of th2[1]. In pattern K astogeny species (Fig. 230.4a–c), th1[1] filled this gap by reversing its growth direction, growing vertically upward. Pattern F astogeny species tightened the loop so that the dorsal part of the th1[1] aperture became attached to the ventral side of the sicula (Fig. 230.3a–c). In flattened material, these proximal development patterns may be impossible to tell apart.

Peiragraptus Strachan, 1954, p. 509 [**P. fallax;* OD]. Peiragraptines with square proximal end; subsequently slightly curved uniserial tubarium based on stipe 1; prominent antivirgellar spines and subapertural spine on th1[1] but not on th1[2]; thecae with outward-inclined ventral thecal walls, rounded geniculum and everted apertures possessing paired apertural horns; proximal development comparable to pattern G astogeny. *Upper Ordovician* (*Katian*): Canada (Anticosti Island, boulder).——Fig. 232,*4a–c.* **P. fallax,* Observation Cliff, Anticosti Island, probably from Vaureal Formation, Canada; *4a,* holotype, BU 682, reverse view; *4b,* paratype, BU 679, juvenile, obverse view; *4c,* paratype, BU 680, juvenile, reverse view; scale bars, 1 mm (*a–c,* Strachan, 1954, fig. 2).

Amplexograptus Elles & Wood, 1907, p. 267 [**Diplograptus perexcavatus* Lapworth, 1876a, pl. 2,*38;* OD]. Peiragraptines with square proximal end, prominent antivirgellar spines and subapertural spine on th1[1], but not on th1[2]; thecae geniculate, often with short, outward-inclined supragenicular walls; median septum delayed or lacking; pattern G astogeny; thecal apertures horizontal, with lateral apertural lappets. *Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone–*Katian, Diplacanthograptus caudatus* Biozone): worldwide.—— Fig. 231,*1a–b.* **A. perexcavatus* (Lapworth); *1a,* neotype, BU 1297a; *1b*, BU 1297b, proximal end of unfigured specimen from neotype slab; scale bars, 1 mm (new; drawings by John F. Riva).——

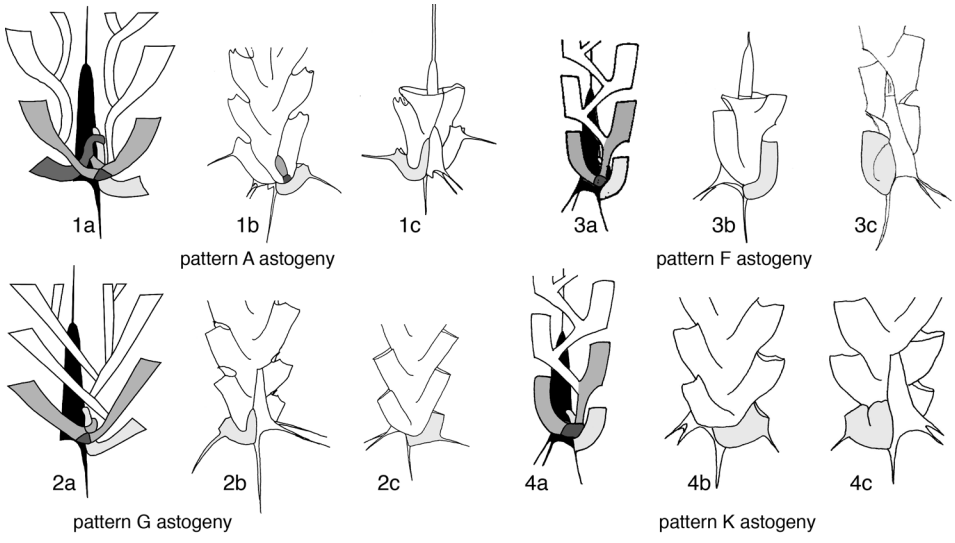


FIG. 230. Proximal development in the Peiragraptinae. *1,* pattern A astogeny (*a*), *Hustedograptus uplandicus* (WIMAN, 1895) in reverse (*b*) and obverse (*c*) views, showing exposed patch of crossing canal of th1[2], note the paired antivirgellar spines; *2,* pattern G astogeny (*a*), *Rectograptus* (PŘIBYL, 1949) in reverse (*b*) and obverse (*c*) views; *3,* pattern F astogeny (*a*), *Geniculograptus pygmaeus* (RUEDEMANN, 1925c) in reverse (*b*) and obverse (*c*) views; *4,* pattern K astogeny (*a*), *Anticostia hudsoni* (JACKSON, 1971) in reverse (*b*) and obverse (*c*) views. All specimen illustrations are reconstructions, not to scale. Proximal details shaded for easier access (new).

FIG. 231,*1c. A. leptotheca* BULMAN, 1946, BU 1299, holotype of *A. fallax* BULMAN, 1962; scale bar, 1 mm (new; drawing by John F. Riva).——FIG. 231,*1d. A. maxwelli* DECKER, 1935b, MCZ 115921, isolated specimen, note distal origin of median septum, Bromide Formation, Oklahoma, USA, scale bar, 1 mm (Goldman, Campbell, & Rahl, 2002, fig. 2,*11*).

Anticostia STEWART & MITCHELL, 1997, p. 219 [**A. macgregorae;* OD]. Peiragraptines with rounded, asymmetrical proximal end, distally widening tubarium, prominent antivirgellar spines and subapertural spine on th1[1] but not on th1[2]; thecae with straight, outward-inclined ventral wall to strongly geniculate with vertical supragenicular wall; median septum lacking; proximal development of pattern K astogeny; thecal apertures horizontal to introverted, often with lateral lappets. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.——FIG. 231,*2a–b. *A. macgregorae;* holotype, GSC 115740, reverse (*a*) and obverse (*b*) views, Vaureal Formation, Anticosti Island, Quebec, Canada, scale bar, 1 mm (Stewart & Mitchell, 1997, fig. 5a–b).

Arnheimograptus MITCHELL, 1987, p. 382 [**Glyptograptus lorrainensis anacanthus* MITCHELL & BERGSTRÖM, 1977, p. 262; OD]. Peiragraptines with rounded, asymmetrical proximal end, parallel-sided to distally widening aseptate tubarium; prominent antivirgellar spines, but lacking apertural spines on first thecal pair; thecae with straight outward-inclined to strongly geniculate ventral wall with vertical supragenicular walls; proximal development of pattern F astogeny; thecal apertures horizontal to introverted. *Upper Ordovician* (*Katian, Paraorthograptus manitoulinensis* Biozone [=*Pleurograptus linearis* Biozone, see GOLDMAN, BERGSTRÖM & MITCHELL,1995]): USA. [The distribution of the genus indicates a low latitude endemic faunal element.]——FIG. 231,*5a–c. *A. anacanthus* (MITCHELL & BERGSTRÖM) Cincinnati region, Ohio, USA; *5a,* OSU 31663, holotype (Mitchell & Bergström, 1977, fig. 4); *5b,* SMF 75832, broken proximal end in reverse view; *5c,* SMF 75833, obverse view (new). Scale bars, 1 mm.

Eoglyptograptus MITCHELL, 1987, p. 396 [**Fucoides dentatus* BRONGNIART, 1828, *sensu* BULMAN, 1963b (=*E. gerhardi* MALETZ, 2011c, p. 859); OD]. Robust peiragraptines with distinctly asymmetrical proximal end and distally widening colony; apart from a typically elongated virgella, proximal end bears single apertural spine on th1[1]; proximal development of pattern B astogeny; thecae with rounded to angular geniculum and outward-inclined apertures, commonly with slight lateral lobes, median septum straight to undulating; interthecal septae short, no intrathecal folds. *Middle Ordovician, Darriwilian* (*Holmograptus lentus* Biozone–*Jiangxigraptus vagus* Biozone): China, UK, Norway, Sweden.——FIG. 231,*4a–b. *E. gerhardi* (MALETZ), NRM-PZ Cn 1280, holotype, Öland, Sweden, scale bars, 1 mm (Bulman, 1936a, pl. 3,*1–2*).

Geniculograptus MITCHELL, 1987, p. 381 [**Climacograptus typicalis* HALL, 1865, p. 57; OD] [=*Uticagraptus* RIVA, 1987, p. 932, obj.]. Peiragraptines with

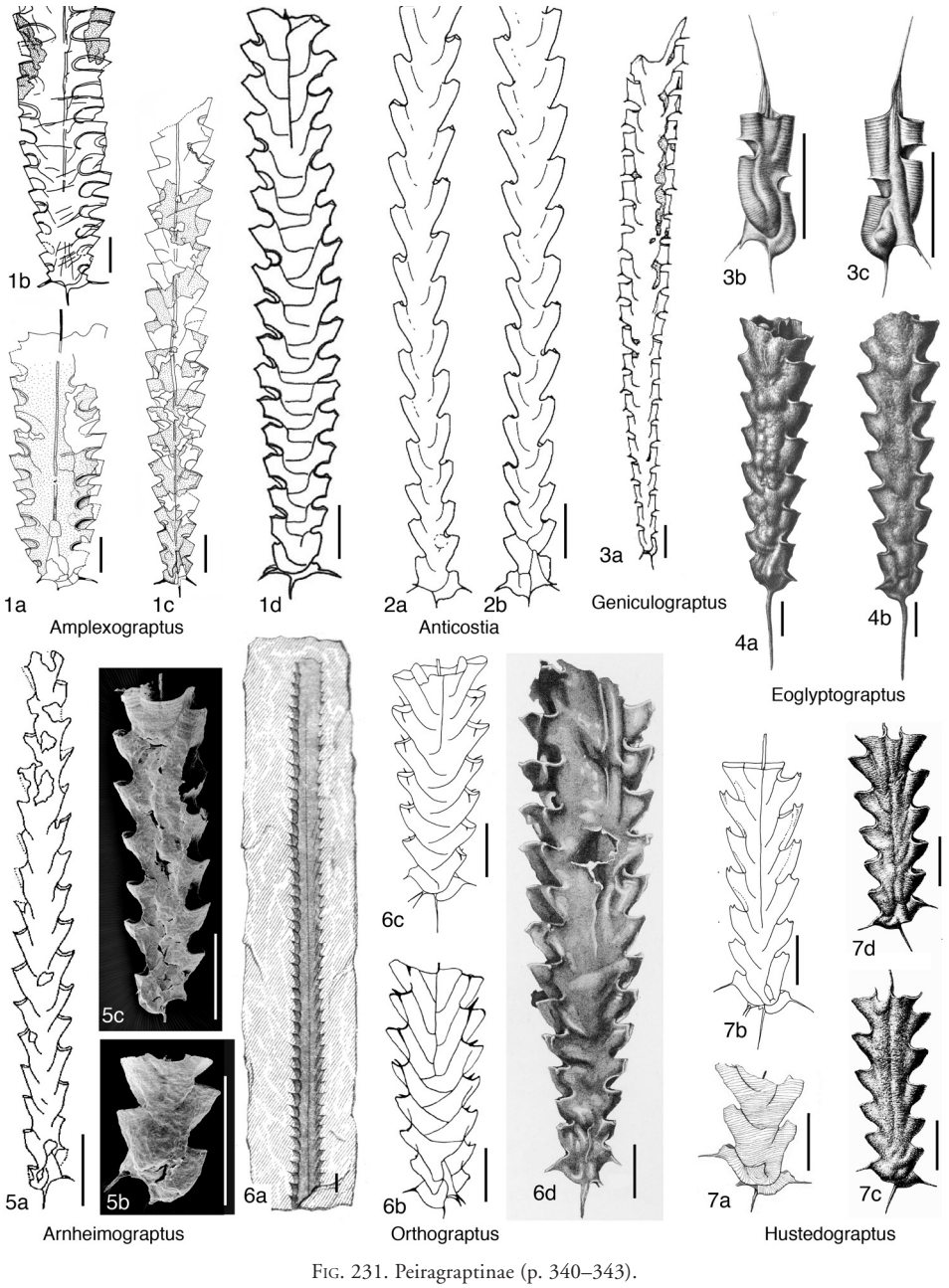


FIG. 231. Peiragraptinae (p. 340–343).

aseptate, gradually widening to nearly parallel-sided tubarium and narrow, pointed proximal end, bearing the virgella and two antivirgellar spines; geniculate thecae with slightly outwardly inclined supragenicular walls, bearing a variably prominent genicular flange; proximal development of pattern F astogeny; thecae with straight aperture, generally with low lateral apertural lobes. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone–*Climacograptus tubuliferus* Biozone): USA (Eastern), Canada (Eastern).——FIG. 231,*3a–c*. **G. typicalis* (HALL); *3a,* lectotype, AMNH 39957, Eden Shale, Cincinnati, Ohio, scale bar, 1 mm (Riva, 1987, fig. 7b); *3b–c,* reverse (*b*) and obverse (*c*) views of chemically isolated specimen, Cincinnati, Ohio, USA, scale bars, 1 mm (Bulman, 1932c, pl. 2,*22a–b*).

Hustedograptus Mitchell, 1987, p. 380 [**Diplograptus uplandicus* Wiman, 1895, p. 274; OD). Slender to robust peiragraptines with square, symmetrical to strongly asymmetrical proximal end, bearing apertural spines on sicula and first thecal pair; paired antivirgellar spines in stratigraphically younger species; median septum straight, commonly delayed; thecae regularly with rounded geniculum, distally with straight ventral wall; apertures simple or with paired lateral lappets; proximal development of pattern A astogeny. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——Fig. 231,*7a–b*. **H. uplandicus* (Wiman); *7a,* holotype, reverse view (Wiman, 1895, pl. 9,*1*); *7b,* reconstruction in reverse view based on isolated material in Mitchell collection, Buffalo, New York, USA (new); scale bars, 1 mm.——Fig. 231,*7c–d. H. bulmani* Mitchell, Brussa, & Maletz, 2008, holotype, NRM-PZ Cn 59946, reverse (*c*) and obverse (*d*) views, scale bars, 1 mm (Bulman, 1936a, pl. 3,*10–11*).

Orthograptus Lapworth, 1873b, table 1, opposite p. 555, *ex* subgenus *Diplograptus* (*Orthograptus*) Lapworth, 1873b, table 1, opposite p. 555 [**Graptolithus quadrimucronatus* Hall 1865, p. 144; OD]. Peiragraptines with proximally rounded to strongly asymmetrical tubarium and apertural spines on the first thecal pair; median septum delayed; proximal development of pattern G astogeny; thecae with straight to slightly sigmoidal ventral walls; thecal apertures generally bearing paired spines or horns, rarely unadorned; fusellum may be attenuated. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Pleurograptus linearis* Biozone): worldwide.——Fig. 231,*6a–c*. **O. quadrimucronatus* (Hall); *6a,* syntype, GSC 1898a, Lake St. John, Quebec, Canada (Hall, 1865, pl. 13,*1*); *6b–c,* MCZ 9472/5, isolated specimen in reverse (*c*) and obverse (*b*) views showing delay of median septum (adapted from Mitchell, 1987, fig. 9G–H). Scale bars, 1 mm.——Fig. 231,*6d. O. apiculatus* (Elles & Wood, 1907), Laggan Burn, Scotland, scale bar, 1 mm (Bulman, 1946, pl. 6,*2*).

Paraorthograptus Mu & others, 1974, p. 160 [**P. typicus;* OD; =*Climacograptus innotatus* var. *pacificus* Ruedemann, 1947, p. 429, see Williams, 1982a, p. 41] [=*Pacificograptus* Koren', 1979, p. 70, obj.]. Peiragraptines with square proximal end, prominent antivirgellar spines and subapertural spine on th1[1], but not on th1[2]; thecae geniculate, with outward-inclined supragenicular walls; median septum lacking; proximal development of pattern G astogeny; thecal apertures horizontal or outward inclined with or without apertural cusps; geniculum adorned with paired spines, lobes, or collar. *Upper Ordovician* (*Katian, Paraorthograptus pacificus* Biozone–*Hirnantian, Normalograptus persculptus* Biozone): Australia, China, UK, Czech Republic, Canada, USA.——Fig. 232,*1a–c*. **P. typicus; 1a*, counterpart of holotype, NIGP 21418a, associated with specimen of *Appendispinograptus supernus* (Elles & Wood, 1906) (Riva, 1988, fig. 5a); *1b,* holotype of *P. pacificus* (Ruedemann), USNM 102838, Phi Kappa Formation, Idaho, USA (Riva, 1974c, fig. 2f); *1c,* GSC 104924, infrared photo, Cape Phillips Formation, Cornwallis Island, Arctic Canada (Melchin & Anderson, 1998, fig. 1,*1*). Scale bars, 1 mm.——Fig. 232,*1d. P. manitoulinensis* (Caley, 1936), GSC 56900, reverse view, Manitoulin Island, Ontario, Canada, scale bar, 1 mm (Riva, 1988, fig. 5i).

Pararetiograptus Mu in Mu & others, 1974, p. 163 [**P. sinensis;* OD] [=*Orthoretiograptus* Mu in Wang & others, 1977, p. 345 (type *O. denticulatus,* OD), syn. by Štorch & others, 2011, p. 342; =*Pseudoreteograptus* Mu in Mu & others, 1993, p. 231 (type, *P. nanus,* OD), syn. by Štorch & others, 2011, p. 343]. Peiragraptines with square proximal end, prominent antivirgellar spines and subapertural spine on th1[1], but not on th1[2]; fusellum attenuated and may be lacking distally, where represented by thickened lists; thecae with outward-inclined ventral walls; incipient geniculum only in proximal thecae; lateral apertural lappets on proximal thecae; median septum lacking; proximal development possibly of pattern K astogeny (Štorch & others, 2011, p. 341); thecal apertures horizontal. [Genus name was misspelled as *Parareteograptus* in Mu, 1974, p. 233 and Štorch & others, 2011, p. 341.] *Upper Ordovician, Katian* (*Dicellograptus ornatus* Biozone–*Paraorthograptus pacificus* Biozone): China, USA).——Fig. 232,*3a–b*. **P. sinensis;* 3a, NIGP 83257, Wufeng Shale, China; *3b,* USNM 542746, long specimen, Nevada, USA (Štorch & others, 2011, fig. 18b and 14s, respectively). Scale bars, 1 mm.——Fig. 232,*3c–d. P. denticulatus* (Mu in Wang & others, 1977); *3c*, NIGP 57854, holotype; *3d,* NIGP 57807; scale bars, 1 mm (Mu & others, 1993, fig. 39a–b).——Fig. 232,*3e. P. nanus* (Mu in Mu & others, 1993), NIGP 57734, paratype, scale bar, 1 mm (Mu in Mu & others, 1993, fig. 38).

Rectograptus Přibyl, 1949, p. 25 [**Diplograptus pristis* var. *truncatus* Lapworth, 1877, p. 133; OD]. Peiragraptines with square proximal end, distally widening or largely parallel-sided tubarium, prominent antivirgellar spines and subapertural spine on th1[1] but not on th1[2]; thecae with or without geniculum on proximal thecae or straight, outward-inclined ventral thecal walls and straight, everted apertures; sometimes with low lateral lappets on thecal apertures that may be lost distally; median septum lacking; proximal development of pattern G astogeny. *Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone–*Hirnantian, Paraorthograptus pacificus* Biozone): worldwide.——Fig. 232,*2a*. **R. truncatus* (Lapworth) holotype (Lapworth, 1877, pl. 6,*17a* [specimen not identified, see Strachan, 1997, p. 72]).——Fig. 232,*2b–d. R. gracilis* (Roemer, 1861); *2b*, neotype, GPIT 1056/3, infrared photo, scale bar, 1 mm (Eisenack 1959, fig. 1); *2c–d*, NRM-PZ Cn 654, 885, isolated specimens, glacial boulder, Sweden, scale bars, 1 mm (Bulman, 1932a, pl. 7,*11* and 7,*10,* respectively).

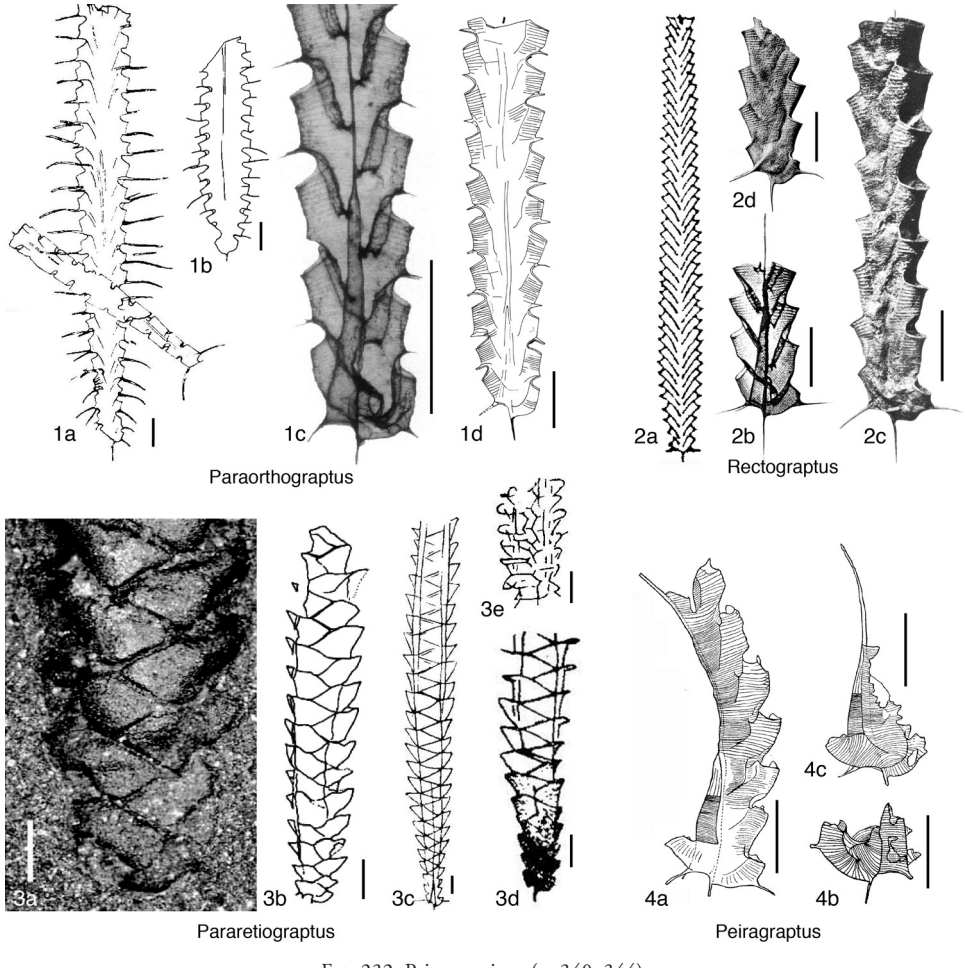


FIG. 232. Peiragraptinae (p. 340–344).

Family LASIOGRAPTIDAE Lapworth, 1879

[Lasiograptidae LAPWORTH, 1879c, p. 454] [=Hallograptidae MU, 1950b, p. 182; =Archiretiolitinae BULMAN, 1955, p. 88]

Biserial axonophorans with proximal development of pattern A astogeny or derived one (pattern L of MITCHELL and others, 2007); median septum complete to variable to lacking; thecal fusellum attenuated to absent; thecae with prominent lists (clathrium) and commonly bearing lacinia derived from genicular and lateral nemal spines or scopulae; thecae geniculate to highly stylized; polygonal reticulum may be present. *Upper Ordovician* (*Sandbian,* ?*Nemagraptus gracilis* Biozone–*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

MITCHELL, (1987, p. 382) defined the Lasiograptidae at the subfamily level and emended the diagnosis of LAPWORTH (1879c). MITCHELL and others (2007) and ŠTORCH and others (2011, p. 346) discussed the Lasiograptidae, based on a cladistic analysis. The taxon incorporates the genera previously included in the Archiretiolitinae as possible relatives of the Silurian Retiolitidae (see BULMAN, 1955).

BATES (1990) indicated that *Orthoretiolites*, *Phormograptus,* and *Pipiograptus* may not be closely related due to differences in their colony construction. Along with differently shaped thecae, *Orthoretiolites* has the nema embedded into the obverse side of the tubarium and lacks a lacinia. BATES and KIRK (1986) suggested that *Pipiograptus* may have

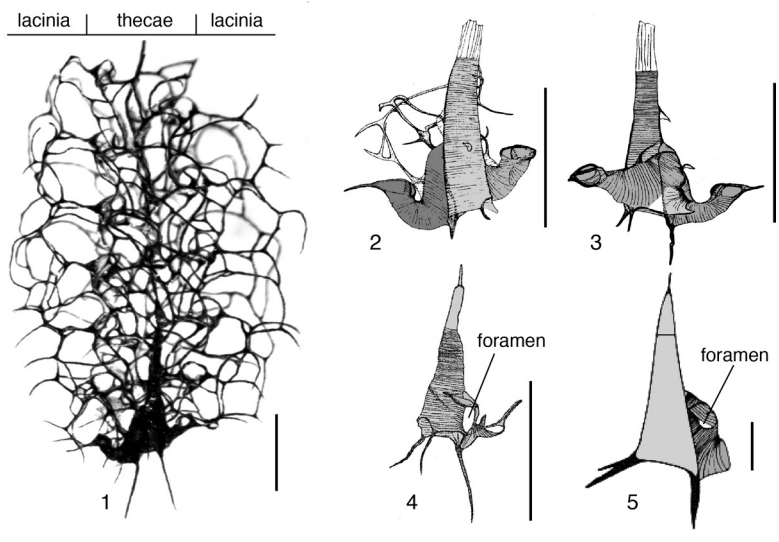


FIG. 233. Tubarium development in Lasiograptidae. *1–3,* Fusellum reduction and lacinia in *Pipiograptus hesperus* WHITTINGTON, 1955; *1,* photo of larger specimen, vaguely showing the thecal outline remains of the fusellum (Maletz, 2017a, fig. 11,8J); *2–3,* isolated paratype specimens showing part of proximal development, specimens from Viola Limestone, Oklahoma, USA (Whittington, 1955, fig. 12–13); *4*, *Orthoretiolites hami* WHITTINGTON, 1954, showing foramen for th1^2 (Whittington, 1954, fig. 5); *5*, *Lasiograptus harknessi* (NICHOLSON, 1867b), juvenile, showing foramen for th1^2 (Rickards & Bulman, 1965, fig. 3B). Scale bars, 0.5 mm.

been derived from a form such as *Dicaulograptus hystrix* (BULMAN, 1932a) based on the thecal construction, whereas MITCHELL (1988) discussed the constructional details in *Brevigraptus* and *Dicaulograptus* as indicating convergent evolution.

The proximal development is unknown in most Lasiograptidae due to the reduction of the fusellum. MITCHELL and others (2007) noted a pattern L astogeny in the Lasiograptidae, but this pattern has never been described. The proximal development in *Orthoretiolites*, *Brevigraptus,* and *Pipiograptus* is characterized by the lack of a reverse wall of th1^1 separating the foramen for th1^2 from the sicula (Fig. 233.3), thus differing from the development in taxa with a pattern G or pattern L astogeny (Fig. 233.5) (MITCHELL, 1987).

FUSELLUM REDUCTION

In many graptolites that are not phylogenetically closely related, the fusellum is reduced independently and is seldom preservable in fossils, e.g., in the Silurian Retiolitidae (LENZ & others, 2018), in the Abrograptidae (MALETZ, ZHANG, & VANDENBERG, 2018), or in some Glossograptina (see *Cryptograptus* in MALETZ & ZHANG, 2016). A reduction of the fusellum is also visible, for example, in some climacograptids (MITCHELL, 1987) in the lack of a preservable prosicula in a number of genera (e.g., *Diplacanthograptus* MITCHELL, 1987).

A reduction of the thickness of the thecal walls is common in members of the Lasiograptidae (Fig. 233.1) but should not be confused with the presence of the lacinia, a secondary development formed from branching lists outside the original tubarium construction (BATES & KIRK, 1991). In the early lasiograptids (e.g., *Hallograptus*, *Lasiograptus*), the fusellum is attenuated but is preservable in the fossil record, and it is possible to easily recognize the proximal development and thecal style. Other taxa show an extreme reduction of the fusellum, with the thecae visible only as an outline of thecal lists (clathrium), associated in some with the development of a variably formed reticulum. This development should not be confused with the lacinia developed from thecal spines and surrounding at least

parts of the colonies. In *Pipiograptus* (Fig. 233.1–233.3), the sicula and the first thecal pair preserve the fusellum, but the later thecae do not. A further reduction leads to the complete loss of preservable fusellum of the colonies; and as a result, the proximal development is not easy to discern. Only the sicula is completely preserved in all taxa of the clade.

THE LACINIA

The lacinia is a development of a meshwork of lists outside the fusellar walls of the tubarium. The presence of a lacinia (Fig. 233.1) is well known from chemically isolated material of a number of lasiograptids (e.g., WHITTINGTON, 1955; MITCHELL & others, 2007), but the details of the construction of the lacinia are unknown. BATES and KIRK (1991) demonstrated the development of the lacinia surrounding the colonies on all sides in the genera *Pipiograptus* and *Phormograptus*. The lacinia is attached to the tubarium by lateral apertural spines and spines originating from the sides of the colonies, often termed scopulae. There appears to be no membrane associated with the lacinia in the manner of the ancora sleeve of the retiolitids (LENZ & others, 2018), and the rods of the lacinia have circular cross sections (BATES, 1987a; BATES & KIRK, 1987). Most lacinate taxa are known only from flattened shale specimens, which makes the interpretation of the construction difficult and unreliable, leaving details of their evolutionary relationships unexplained.

Lasiograptus LAPWORTH, 1873b, p. 559 [**L. costatus;* OD] [=*Thysanograptus* ELLES & WOOD, 1908, p. 325 (type, *Diplograptus harknessi* NICHOLSON, 1867b, p. 262), syn. by BULMAN, 1970, p. 126]. Lasiograptids with proximally widening, distally parallel-sided tubarium and rounded proximal end; median septum complete; proximal development of pattern G astogeny; thecae showing inwardly inclined supragenicular wall and single or paired genicular or mesial spines; clathria weakly developed in some taxa; possibly paired septal processes or scopulae visible in scalariform view in some taxa. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Katian, Climacograptus bicornis* Biozone): worldwide(?).——FIG. 234,*3a. *L. costatus*, BU 1341, lectotype, Dob's Linn, Scotland (adapted from Hughes, 2000, Atlas, Folio 1.35).——FIG. 234,*3b–c. L. harknessi; 3b,* isolated specimen, reverse view, Laggan Burn, Ayrshire, UK (Bulman, 1947, pl. 8,*11*); *3c,* reconstruction in reverse view (Rickards & Bulman, 1965, fig. 3). Scale bars, 1 mm.

Archiretiolites EISENACK, 1935, p. 74 [**A. regimontanus;* M]. Lasiograptids with highly asymmetrical proximal end; proximal end astogeny unknown; sicula with single antivirgellar spine; tubarium reduced to clathrial lists and coarse reticulum with the sicula and the initial part of th1[1] preserved as complete fusellum; presence of lacinia uncertain; central virgella attached to clathrial thecal lists. *Upper Ordovician* (*Sandbian, ?Nemagraptus gracilis* Biozone): Estonia, Germany, Sweden (glacial boulder).——FIG. 234,*1a–d. *A. regimontanus; 1a–c,* holotype, proximal end in reverse (*a*) and obverse (*b*) views, complete specimen in obverse view (*c*); *1d,* juvenile, showing development of thecal lists in th1[1]; scale bars, 1 mm (Eisenack, 1935, pl. 6).

Brevigraptus MITCHELL, 1988, p. 450 [**B. quadrithecatus;* OD). Small lasiograptids with finite growth, bearing maximum of five to six thecae; fusellum attenuated and clathria well developed; sicula with single antivirgellar spine; proximal development probably of pattern G astogeny; thecae with birds-head construction of the apertures, bearing branched subapertural or mesial spines; lateral spines present on reverse and obverse side of tubarium; lacinia lacking. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone): USA.——FIG. 234,*7a–c. *B. quadrithecatus; 7a–b,* holotype, MCZ 9437, in obverse (*a*) and reverse (*b*) views; *7c,* MCZ 9438, reverse view; Carter County, Oklahoma, USA; scale bars, 1 mm (adapted from Mitchell, 1988, fig. 5,*11–13*).

Hallograptus LAPWORTH, 1876a, p. 7 [**Diplograptus bimucronatus* NICHOLSON, 1869, p. 236]. Lasiograptids with proximally widening, distally parallel-sided tubarium and square proximal end; proximal development possibly of pattern A astogeny; thecae with short, inwardly inclined supragenicular walls and single or paired genicular spines; clathria weakly developed; paired septal processes or scopulae visible in scalariform view. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide(?).——FIG. 234,*2a. *H. bimucronatus* (NICHOLSON) Glenkiln Shale, Scotland, scale bar, 1 mm (Bulman, 1970, fig.93,*2a*).——FIG. 234,*2b–d. H. mucronatus* (HALL, 1847); *2b*, Glenkiln Shale, Scotland (Bulman, 1970, fig. 93,*2b*); *2c–d,* isolated specimens in reverse view, showing possible pattern A astogeny, Dalby Limestone, Skövde, Västergötland, Sweden, scale bars, 1 mm (new; drawings by C. E. Mitchell).

Neurograptus ELLES & WOOD, 1908, p. 320, =*Neurograptus* LAPWORTH in HOPKINSON & LAPWORTH, 1875, p. 641, *nom. nud.* [**Retiolites fibratus* LAPWORTH, 1876a, fig. 62]. Lasiograptids

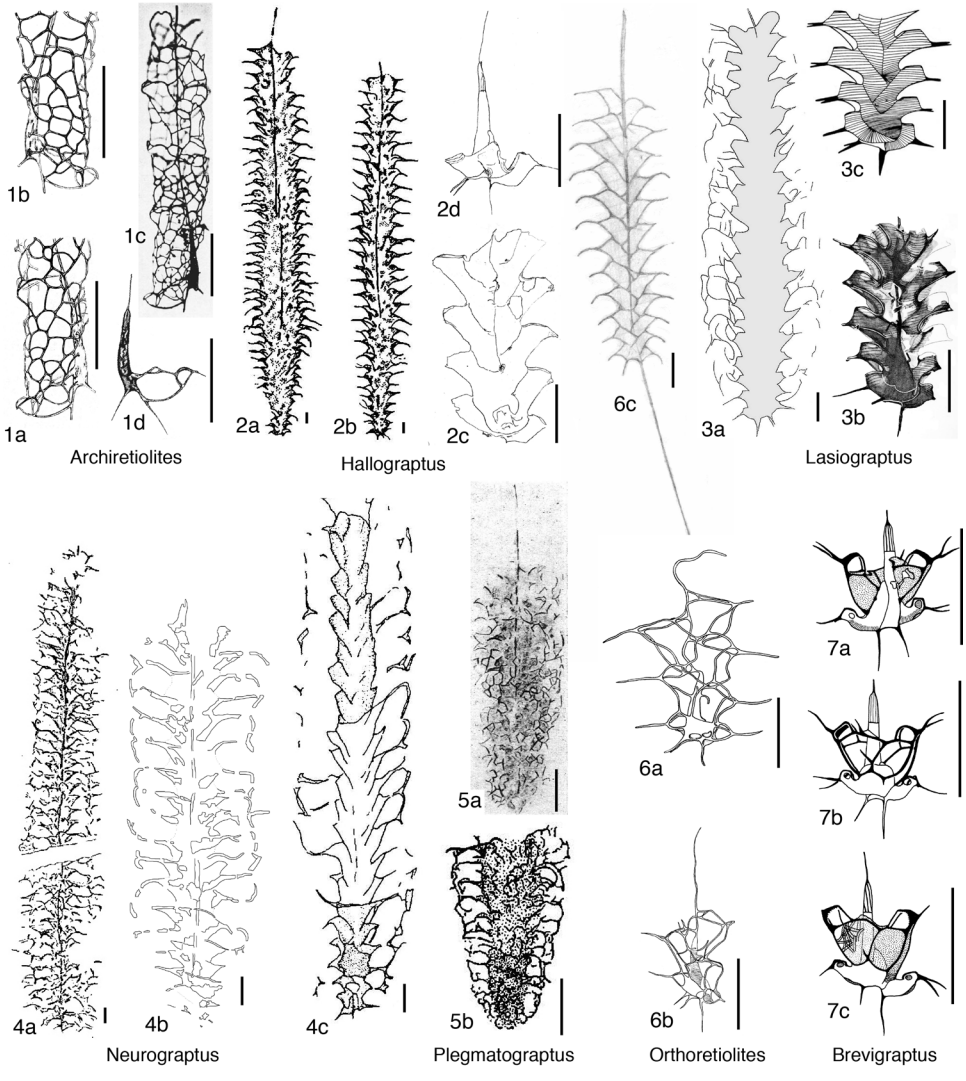


FIG. 234. Lasiograptidae (p. 346–349).

with proximally widening, distally parallel-sided tubarium and square proximal end; proximal development probably of pattern G astogeny; thecae with single or paired apertural spines as the base of a simple lacinia development on the ventral tubarium sides; septal processes or scopulae visible in scalariform view. [BULMAN (1929, p. 179) selected *Lasiograptus margaritatus* LAPWORTH, 1876a (pl. 2,*60*) as genolectotype of *Neurograptus* in consent with G. ELLES. The species may be a synonym of *N. fibratus* (VANDENBERG & COOPER, 1992, p. 82).] *Upper Ordovician* (*Katian, Dicranograptus clingani* Biozone): Australia, China, UK, Norway, Canada, USA.——FIG. 234,*4a–c*. **N. margaritatus* (LAPWORTH); *4a,* BU 1351, holotype of *Retiolites fibratus* LAPWORTH, 1876a (Elles & Wood, 1908, pl. 34,*5a*); *4b,* lectotype, BU 1353a, Dob's Linn, Scotland (Wilkinson, 2018a); *4c,* PMO 108.905, obverse view, Oslo Region, Norway (Williams & Bruton, 1983, fig. 24c). Scale bars, 1 mm.

Nymphograptus ELLES & WOOD, 1908, p. 320, *ex* subgenus *Lasiograptus* (*Nymphograptus*) ELLES & WOOD, 1908, p. 320 [**L.* (*N.*) *velatus;* OD] [=*Yangzigraptus* MU in YANG & others, 1983, p. 492 (type, *Y. yangziensis,* OD), syn. herein]. Lasiograptids with strongly developed lacinia on reverse and obverse sides formed from septal bars (scopulae) extending far outward and upward from

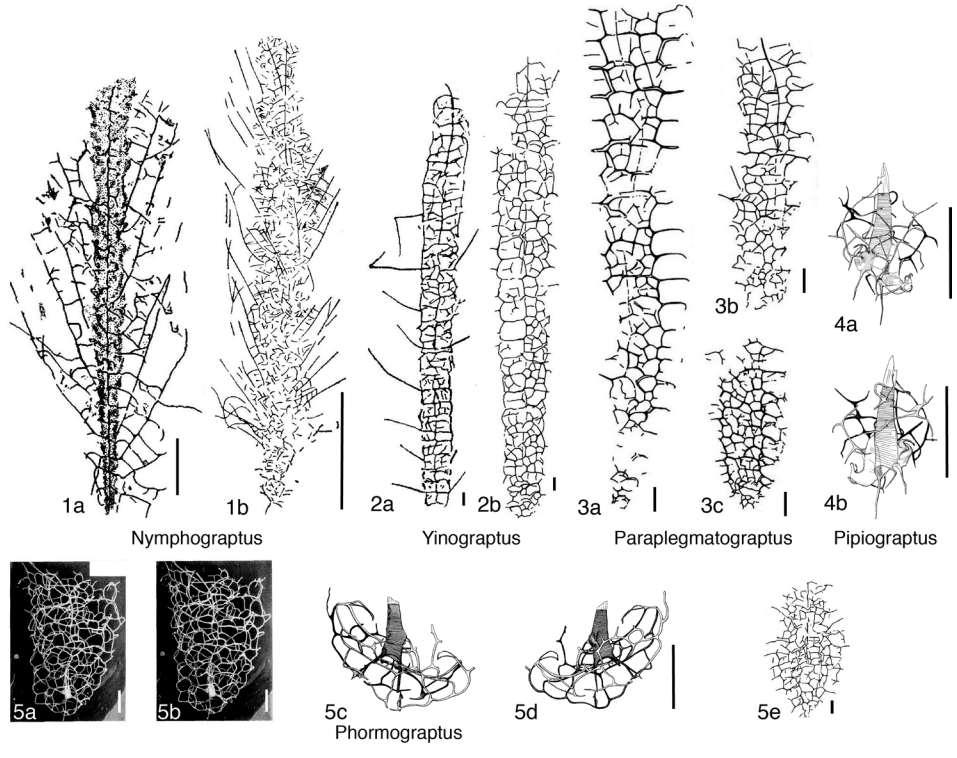


FIG. 235. Lasiograptidae (p. 348–349).

thecate part of the tubarium; fusellum strongly attenuated; thecal style and proximal development unknown. *Upper Ordovician* (*Katian, Dicellograptus anceps* Biozone): Kazakhstan, China, UK.——FIG. 235,*1a. *N. velatus* (ELLES & WOOD), BGS GSE 10856, lectotype (selected by KOREN', TZAI, & MIKHAILOVA, 1980, p. 164), Ettrickbridge End, Scotland, UK, scale bar, 10 mm (Bulman, 1970, fig. 93,*4*).——FIG. 235,*1b. N. yangziensis* (MU & others, 1993), holotype, NIGP 57843, scale bar, 10 mm (Mu & others, 1993, fig. 59).

Orthoretiolites WHITTINGTON, 1954, p. 613 [**O. hami;* OD]. Lasiograptids with strongly reduced fusellum and thickened clathrial lists outlining colony; nema embedded into obverse wall of colony; proximal development unknown; thecal apertures simple, outward inclined with centrally positioned single apertural spine which may be branched distally; paired nemal spines or scopulae present at regular distances along nema. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone): Australia, Canada, USA.——FIG. 234,*6a–b*. **O. hami,* Oklahoma, USA; *6a,* holotype, MCZ 511; *6b,* paratype, MCZ 512h; scale bars, 1 mm (Whittington, 1954, fig. 4,*12*).——FIG. 234,*6c*. *Orthoretiolites* sp., GSC 141089a, flattened specimen with long virgella, Bald Mountain core, Quebec, Canada, scale bar, 1 mm (new, original drawing by John F. Riva).

Paraplegmatograptus MU & LIN, 1984, p. 66 [*non Paraplegmatograptus* MU, 1963b, p. 365, *nom. nud.*, ŠTORCH & others, 2011, p. 348] [**P. uniformis* MU in WANG, 1978, p. 210; OD]. Lasiograptids with obverse and reverse walls reduced to irregular clathrium consisting of lateral lists, indistinct dorsal lists, and well-defined reticulum; prominent lacinia that surrounds sicular aperture and is confined to apertural margins of colony; nema possibly unconnected. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Hirnantian, Metabolograptus extraordinarius* Biozone): China, USA.——FIG. 235,*3a–c*. **P. uniformis*, Vinini Formation, Nevada, USA. *3a,* USNM 542769, long fragment in lateral view; *3b,* USNM 542705, proximal end; *3c,* USNM 542766; scale bars, 1 mm (Štorch & others, 2011, fig. 16,*a,c,q,* respectively).

Phormograptus WHITTINGTON, 1955, p. 846 [**P. sooneri;* OD] [=*Arachniograptus* ROSS & BERRY, 1963, p. 159 (type, *A. laqueus,* M), syn. by ŠTORCH & others, 2011, p. 348]. Lasiograptids with thecal framework consisting of lightly thickened dorsal lists, apertural lists, and aboral lists; dorsal lists linked to nema by scopular spines; ventral lists absent; lacinia encloses entire tubarium forming complex, and usually dense, three-dimensional mesh along obverse and reverse side of colony and with regular apertural openings along pleural

margin of colony; proximal development unknown as only sicula is fully sclerotized. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone–*Metabolograptus persculptus* Biozone): China, Czech Republic, USA.——Fig. 235,*5a–d*. **P. sooneri; 5a–b,* stereopair of small specimen (Bates & Kirk, 1987, fig. 4a); *5c–d,* holotype in reverse (*c*) and obverse (*d*) views, Oklahoma, USA (Whittington, 1955, fig. 17–18). Scale bars, 1 mm.——Fig. 235,*5e. P. connectus* (Mu in Wang & others, 1977), USNM 542742, small specimen showing colony shape, Vinini Formation, Nevada, USA, scale bar, 1 mm (Štorch & others, 2011, fig. 16b).

Pipiograptus Whittington, 1955, p. 839 [**P. hesperus;* OD]. Lasiograptids with sicula, much of th1[1] and th 1[2] and initial part of th2[1] sclerotized; later thecae coarsely reticulate, clathrium not clearly differentiated from extensive development of lacinia; thecal characters imperfectly known, but th2[1] with initial downward direction of growth; proximal development type probably of pattern G astogeny. *Upper Ordovician, Katian* (*Diplacanthograptus caudatus* Biozone): USA.——Fig.235,*4a–b*. **P. hesperus,* holotype, MCZ 521, in reverse (*a*) and obverse (*b*) views, Oklahoma, USA, scale bars, 1 mm (Whittington, 1955, fig. 12–13).

Plegmatograptus Elles & Wood, 1908, p. 340, *ex* subgenus *Retiolites* (*Plegmatograptus*) Elles & Wood, 1908, p. 340 [**Retiolites* (*Plegmatograptus*) *nebula* Elles & Wood, 1908, p. 337, 340; OD]. Lasiograptids with reticulum and well-developed lacinia; fusellum strongly attenuated or lacking; details of development unknown. *Upper Ordovician* (*Katian, Dicranograptus clingani* Biozone–*Pleurograptus linearis* Biozone): Australia, China, UK, USA.——Fig. 234,*5a–b*. **P. nebula; 5a,* lectotype (selected by Williams, 1982b, p. 253), BGS GSE 5615, Hartfell Shale, Scotland, UK (Elles & Wood, 1908, fig. 222b); *5b,* BGS GSE 5539, Hartfell Shale, Scotland (Bulman, 1970, fig. 95,*4*). Scale bars, 1 mm.

Yinograptus Mu in Mu & Chen, 1962b, p. 112 [**Gothograptus*? *disjunctus* Yin & Mu, 1945, p. 216; OD] [=?*Sunigraptus* Mu in Mu & others, 1993, p. 247 (type, *S. regularis,* OD), syn. herein; based on poor, indeterminable fragments]. Lasiograptids with obverse and reverse walls reduced to regular clathrium consisting of lateral lists and dorsal lists; sparse planar reticulum linked to nema by prominent spines or scopulae; scopulae project outward from lateral walls at regular intervals, generally at every fourth thecal pair; somewhat delicate lacinia surrounds the sicular region and is confined to apertural margins of colony more distally; proximal development unknown. *Upper Ordovician* (*upper Katian, Dicellograptus ornatus* Biozone–*Paraorthograptus pacificus* Biozone): China; USA.——Fig. 235,*2a–b*. **Y. disjunctus; 2a,* holotype, NIGP 57816, apertural view showing scopular spines (Mu & others, 1993, fig. 53a); *2b,* USNM 542767, lateral view, Roberts Mountains, Nevada, USA (Štorch & others, 2011, fig. 16o). Scale bars, 1 mm.

Family CLIMACOGRAPTIDAE Frech, 1897

[Climacograptidae Frech, 1897, p 607, *nom. transl. ex.* Familie Climacograptidi Frech, 1897, p. 607] [=superfamily Climacograptoidea Frech *sensu* Štorch & others, 2011, p. 353; =Pseudoclimacograptidae Mitchell, 1987 (in press version), Fortey & Cooper, 1986, p. 652, *nom. nud.*]

Biserial, dipleural axonophorans; metasicular origin of th1[1]; proximal end square to highly asymmetrical, generally provided with virgellar spine as only proximal end spine, but secondarily developed thecal spines on first thecal pair or only on th1[1] may be present; proximal development type of pattern C astogeny or progressively more derived pattern; tubarium commonly twisted longitudinally; thecae with distinct geniculum; intrathecal folds externally expressed through crossbars and with strongly zigzag-shaped median septum in early taxa; straight median septum and straight, short thecae with crossbars in derived taxa; median septum may be delayed or lacking altogether; parasiculae and parathecae common. *Middle Ordovician* (*lower Darriwilian, Levisograptus dentatus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

The family Climacograptidae originally included the genus *Climacograptus,* the Dicranograptidae, and Glossograptidae. It also included the monograptid genus *Monoclimacis* and was based entirely on the climacograptid (geniculate) thecal outline (see Frech, 1897). Bulman (1955, 1970) included the genus *Climacograptus* in the Diplograptidae, whereas Štorch and others (2011), in their latest revision, referred the climacograptids to the superfamily Climacograptoidea.

A recent cladistic analysis of the Climacograptidae does not exist. The analysis of Cone (2004) was discussed in Štorch and others (2011) but has never been published. The family Climacograptidae (Fig. 236) includes a well-defined group of derived Darriwilian to Hirnantian (Upper Ordovician) taxa united by a number of synapomorphies, but the early members are less easily defined and analyzed. Mitchell and others

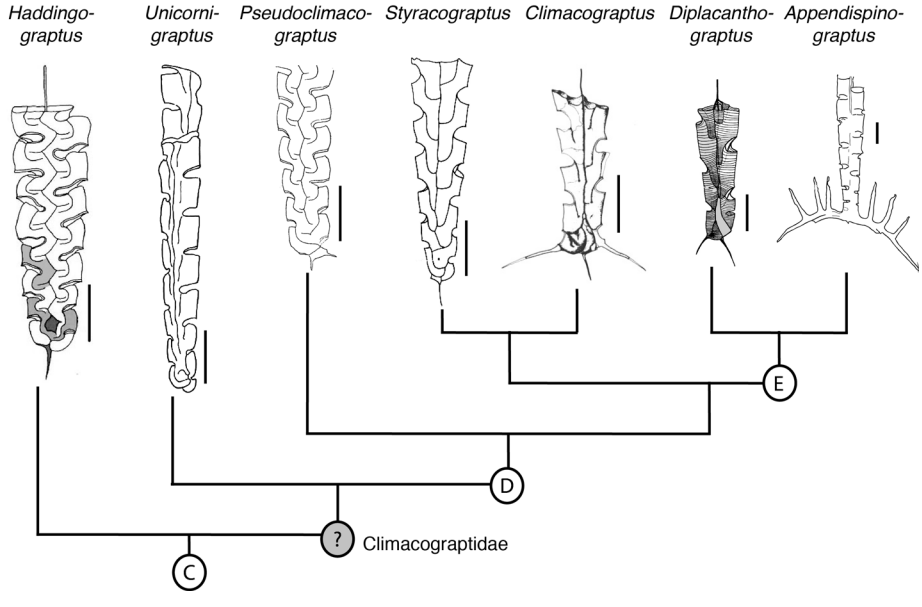


FIG. 236. Interpretation of the evolutionary relationships of the Climacograptidae, showing presence of the proximal development patterns C–E, scale bars, 1 mm (new; based on data from CONE, 2004; MITCHELL & others, 2007; MALETZ, 2011b).

(2007) performed a cladistic analysis of the Axonophora but did not publish any data supporting the analysis and did not provide a definition of the family Climacograptidae. ŠTORCH and others (2011, fig. 6) modified the cladistic tree of MITCHELL and others (2007) to define the Neograptina but also did not include data to support the diagram. Thus, the basis for the differentiation of the Diplograptina and Neograptina is unclear, as is the inclusion of early taxa referred to the Neograptina by ŠTORCH and others (2011) and the position of the Climacograptidae.

ŠTORCH and others (2011, fig. 6) discussed *Undulograptus formosus* (MU & LEE, 1958) as the earliest member of the Neograptina and, thus, of the Normalograptidae; whereas MALETZ (2011d, fig. 3) and MALETZ (2014b) regarded the genera *Undulograptus, Oelandograptus,* and *Proclimacograptus* as early member of the Climacograptidae. MALETZ (2011d) suggested a derivation of *Pseudoclimacograptus* and its descendants from an ancestor such as *Haddingograptus* (Fig. 236). Instead of an inclusion with the Diplograptina, the Climacograptidae then may alternatively be referred to the Neograptina. In this interpretation, the mesial to subapertural spines on the derived Climacograptidae would have originated secondarily from a spineless ancestor.

CHEN and GOLDMAN (in CHEN & others, 2016) referred the genus *Unicornigraptus* with its pattern C astogeny to the Climacograptidae. The species of this genus has a virgellar spine and a spine on th1[1] but not on th1[2] and represent the earliest climacograptids. Their development resembles the development in *Pseudoclimacograptus scharenbergi* (LAPWORTH, 1876a), with its pattern D astogeny, but still bears an exposed patch of the crossing canal of th1[2], indicating a typical pattern C astogeny (Fig. 236).

MORPHOLOGY

Sicular Development

The sicula of the Climacograptidae is short (less than 1.5 mm long) and widens rapidly in all members of the clade from which the sicula is known in isolated speci-

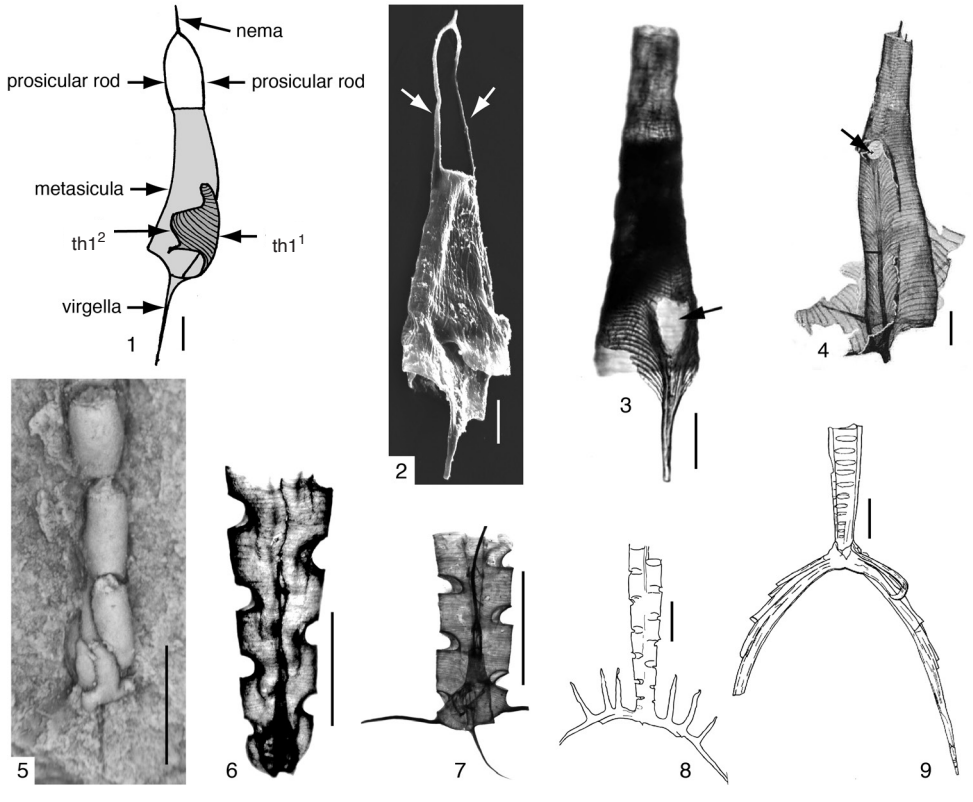


FIG. 237. The sicula and proximal development in the Climacograptidae. *1, Diplacanthograptus spiniferus* (RUEDEMANN, 1912), sicula showing curvature and initial parts of th1[1] and th 1[2] (Mitchell, 1987, fig. 7E); *2, Diplacanthograptus spiniferus*, SMF 75834, SEM photo, sicula showing two rods instead of prosicula, note cortical bandages on metasicula (new); *3, Appendispinograptus supernus* ELLES & WOOD, 1906, sicula showing central origin of th1[1] foramen (Loxton & others, 2011, fig. 1J); *4, ?Pseudoclimacograptus scharenbergi stenostoma* (BULMAN, 1947), juvenile with central position of th1[1] foramen (Bulman, 1947, pl. X,*3*); *5, Appendispinograptus supernus*? (ELLES & WOOD, 1906), proximal end with parasiculae, NIGP 139881, Honghuanyuan section, Tongzi, Guizhou Province, China, *Dicellograptus complanatus* Biozone (new); *6, Styracograptus tubuliferus* (LAPWORTH, 1876a), proximal end showing only the presence of a virgellar spine (Goldman & others, 2011, fig. 1G); *7, Climacograptus cruciformis* VANDENBERG, 1990, showing mesial spines on first thecal pair, Viola Limestone (Maletz, 2017a, fig. 11,13F); *8, Appendispinograptus venustus* (HSÜ, 1959a), AFA 84 (NIGP material), Wangjiawan section, Wufeng Formation (Mitchell, Chen, & Finney, 2007, fig. 1,*4*); *9, Appendispinograptus longispinus* (T. S. HALL, 1902), AMNH 29267, Toquima Range, Nevada, USA (Riva, 1974a, fig. 4c). All scale bars, 1 mm.

mens. It is straight in early members but has a distinct curvature and twisting in the genus *Diplacanthograptus* (Fig. 237.1) and related taxa. *Climacograptus* and *Appendispinograptus* may have a short virgella curved or bent across the sicular aperture, but the sicula is not curved noticeably in these cases. The prosicula is poorly or incompletely preserved in many early members of the Climacograptidae (MITCHELL, 1987). In derived taxa, the prosicula is not preserved as a membrane but as one or two cortical rods, forming the outline of the prosicula (Fig. 237.2). These rods are homologous to the longitudinal rods in completely formed prosiculae of other Axonophora. Additional longitudinal rods on the prosicula are not present in the Climacograptidae. WILLIAMS and CLARKE (1999) described the rods in *Diplacanthograptus spiniferus* (RUEDEMANN, 1912) as secondary longitudinal ridges attached to the metasicula by radiating cortical bandages.

MITCHELL (1987, fig. 6A–B) figured specimens identified as *Pseudoclimacograptus scharenbergi* from the Balclatchie beds of Scotland lacking the prosicula, which is replaced by a single rod and possessing a distinctly twisted metasicula.

The position and exact development of the primary porus is unknown in most taxa of the Climacograptidae but is assumed to be of the resorption style, positioned on the right side of the virgella, as in *Diplacanthograptus spiniferus* (MITCHELL, 1987, fig. 7E–F). However, the resorption porus in *Appendispinograptus* is formed in a position directly on the virgellar axis (Fig. 237.3). The origination of virgella occurred late in this taxon and formed only at a point after the development of the porus (see LOXTON & others, 2011). BULMAN (1947) described a similar development in a juvenile of *Pseudoclimacograptus scharenbergi stenostoma* (Fig. 237.4).

A parasicula is commonly present in the Climacograptidae and can reach a considerable length. Some species of the genus *Appendispinograptus* developed a candle-like complex of secondary tubes on the proximal end, called parathecae (Fig. 237.5, Fig. 237.8). These have been identified as tubes only through the record of a single three-dimensionally preserved specimen of *Appendispinograptus supernus*? (ELLES & WOOD, 1906) (MITCHELL, CHEN, & FINNEY, 2007). The development of parasiculae and parathecae in *Appendispinograptus* is highly variable (Fig. 237.8–237.9) and unreliable for taxonomic identification (see LOXTON & others, 2011, p. 259). Parathecae are present in some mature specimens of *Climacograptus bicornis* (HALL, 1847) (BULMAN, 1947, fig. 30).

Thecal Development

All thecae, except for the first thecal pair, possess a distinct geniculum in the Climacograptidae. The geniculum may be provided with a genicular flange or be rounded without elaborations. The supragenicular wall may be vertical, inward- or outward-sloping or convexly curved. Also, the thecal apertures vary in their orientation from introverted through horizontal to everted. The strong zigzag shape of the median septum of *Pseudoclimacograptus scharenbergi* (Fig. 236; Fig. 238.7) has been regarded as typical of climacograptids, but is now known to be restricted to earlier taxa in which intrathecal folding is pronounced and strong crossbars are present.

The derivation of a pattern D astogeny from a pattern C astogeny (Fig. 238.1) is unknown. The pattern D astogeny is based on the presence of a robust, short and wide sicula with massive crossing canals. Most probably the crossing canal of $th2^1$ was aborted at an early stage and formed a list leaving a characteristic list scar on the ventral surface, easily visible in specimens of *Pseudoclimacograptus* (Fig. 238.8) and derived taxa with pattern D astogeny. The distal development of $th2^1$ and 2^2 started with an upward-growing flange on the dorsal side of the early part of $th1^2$ (Fig. 238.9). This flange grew as a wide construction upward across the aborted crossing canal of $th2^1$ and distally differentiated into the thecal tubes of $th2^1$ and $th2^2$ (Fig. 238.10). In the pattern E astogeny, a further reduction of the crossing canals occurred. The development of a flange as the last remains of the crossing canal of $th1^2$ was abandoned at an early stage. A new flange was secreted at the point where $th1^1$ began to grow upward and formed into the upward-growing $th1^2$ (Fig. 238.12). The differentiation of $th2^1$ is in the distal, upward-growing part of $th1^2$.

The Climacograptidae possessed a variable number of proximal end spines, and the virgella is the only consistent presence of a spine in the colonies. Subapertural to mesial spines can be present on $th1^1$ and $th1^2$ as in *Climacograptus,* but they often are present only on $th1^1$ as in *Diplacanthograptus* or may be lacking altogether as in *Styracograptus* (see Fig. 236). The spines are outward- or downward-directed, depending on their position in the colony and can reach a considerable length (VANDENBERG, 1990).

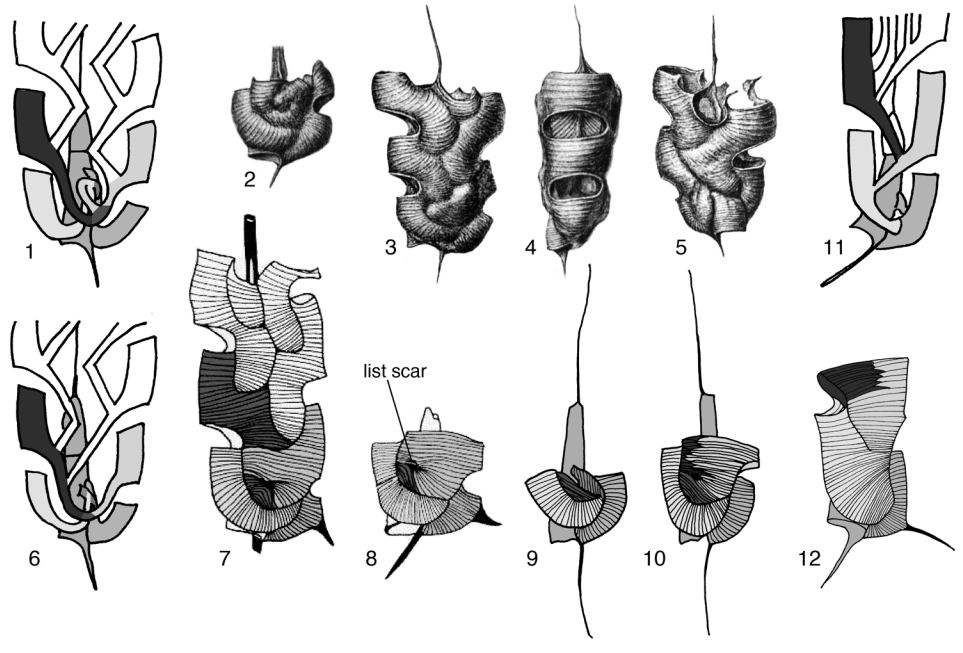


FIG. 238. Proximal development types in *Haddingograptus* MALETZ, 1997a and the Climacograptidae. *1, 6, 11,* pattern C, D, E astogenies (based on Mitchell, 1987); *2–5, Haddingograptus eurystoma* (JAANUSSON, 1960), pattern C astogeny (Bulman, 1932a, pl. 1); *7–8, Pseudoclimacograptus scharenbergi* (LAPWORTH, 1876), pattern D astogeny, reconstructions (adapted from Mitchell, 1987, fig. 6F, I); *9–10, Styracograptus tubuliferus* (LAPWORTH, 1876a) pattern D astogeny (specimens identified as *Climacograptus* (*Climacograptus*) sp. cf. *C.* (*C.*) *caudatus* by MITCHELL, 1987; GOLDMAN & WRIGHT, 2003); *12, Diplacanthograptus spiniferus* (RUEDEMANN, 1912), reverse view (adapted from Mitchell, 1987, fig. 7L). Specimens not to scale.

Torsion

The tubaria of many climacograptids (e.g., *Diplacanthograptus*, *Appendispinograptus*) appear to possess considerable torsion (VANDENBERG, 1990) that might be related to the torsion already visible in the sicular curvature (Fig. 237.1). A moderate torsion of the colonies may already be present in *Climacograptus bicornis, Climacograptus cruciformis* (VANDENBERG, 1990), and *Diplacanthograptus lanceolatus* (VANDENBERG, 1990), as described by VANDENBERG (1990). LOXTON and others (2011) suggested that the torsion is a taphonomic consequence of the presence of parasiculae and not an independent character of the colonies because torsion appears to be absent in specimens of *Appendispinograptus supernus* without parasiculae. However, the authors noted that the mesial spine on th1[1] in *A. supernus* is off-profile (LOXTON & others, 2011, p. 254). The strong torsion is also visible in specimens of *Appendispinograptus longispinus* (T. S. HALL, 1902) from Nevada (USA), which show the proximal spines in a symmetrical position, whereas the distal part of the colony attains a scalariform view (see RIVA, 1974a).

Climacograptus HALL, 1865, p. 111 [**Graptolithus bicornis* HALL, 1847, p. 268; OD] [=*Mendograptus* RUSCONI, 1948, p. 247 (type, *M. inversus*, M), syn. by TORO & BRUSSA, 2007, p. 233; =*Euclimacograptus* RIVA & KETNER, 1989, p. 82 (type, *Climacograptus hastata* T. S. HALL, 1902, p. 54, OD), syn. by ŠTORCH & others, 2011, p. 354]. Climacograptids with pattern D proximal astogeny; thecae sharply geniculate, with straight suprageniculare walls, simple deep semi-circular thecal excavations, and short thecal overlap; complete median septum weakly undulose to straight; subapertural to mesial spines on first pair of thecae; proximal membranes and parasiculae in mature specimens. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Paraorthograptus pacificus* Biozone):

worldwide.——Fig. 239,*1a–d*. **C. bicornis* (Hall), *1a,* lectotype, AMNH 1030a, Austin Glen Greywacke, left bank of Normans Kill, Kenwood, New York, USA (Riva, 1974a, pl. 1,*1*); *1b,* topotype, AMNH 29386, small specimen in obverse view (Riva, 1974a, fig. 1a); *1c,* topotype, AMNH 29390, proximal end with membranes (Riva, 1976, fig. 5f); *1d,* NMV P63487, showing torsion of tubarium, Warbisco Shale, east Gippsland, Victoria, Australia (VandenBerg, 1990, fig. 3a). Scale bars, 1 mm.——Fig. 239,*1e*. *Climacograptus hastatus* (T. S. Hall, 1902), lectotype, AMF46104, *Dicellograptus ornatus* Biozone, Stockyard Flat Creek, New South Wales, Australia, scale bar, 1 mm (Riva & Ketner, 1989, fig. 9a).

Alulagraptus Chen, Chen, Mitchell, Chen, & Zhang, 2019, p. 1189 [**Climacograptus uncinatus* Keble & Harris, 1934; OD]. Climacograptid with complete median septum; proximal development pattern unknown; proximal end rounded with virgella as only proximal end spine; single pair of scopuli branching from nema; scopuli may bear vane-like appendages. *Upper Ordovician* (*Katian, Dicellograptus complanatus* Biozone): Australia, China, North America.——Fig. 239,*3a*. **A. uncinatus* (Keble & Harris), lectotype, NMV P 14401A, Bolindian, *Alulagraptus uncinatus* Biozone, Yarra Track, between Matlock and Oaks, Victoria, Australia, scale bar, 1 mm (new; drawing by Jörg Maletz, based on photo provided by F. VandenBerg).——Fig. 239,*3b*. *A. ensiformis* (Mu & Zhang in Mu & others, 1963), holotype, NIGP 11749, *Appendispinograptus longispinus* Biozone, Xiehao Formation, East Qiqiaogou section, Chilianshan, northwest China, scale bar, 1 mm (new, redrawn from Chen & others, 2019, fig. 10,*4*).

Appendispinograptus Li & Li, 1985, p. 36, *ex Climacograptus* (*Appendispinograptus*) Li & Li, 1985, p. 36, Riva & Ketner, 1989, p. 77 [**Climacograptus venustus* Hsü, 1959, p. 346; OD] [=*Leptothecalograptus* Li in Mu & others, 2002, p. 677 (type, *Climacograptus leptothecalis* Mu & Geh in Fu, 1982, p. 456, OD), syn. herein]. Septate to aseptate climacograptids with distinct torsion of the tubarium and pattern E astogeny; th2[2] or later theca dicalycal in septate species; mesial spines arise from first thecal pair; secondary thecal parasicular outgrowths or webs common. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.——Fig. 239,*2*. **A. venustus* (Hsü), holotype, No 519, Wufeng Shale, Hubei Province, China, scale bar, 1 mm (adapted from Hsü, 1959a).

Diplacanthograptus Mitchell, 1987, p. 388 [**Climacograptus spiniferus* Ruedemann, 1912, p. 84; OD (=*Climacograptus typicalis* mut. *spinifer* Ruedemann, 1908, p. 411)] [=*Ensigraptus* Riva in Riva & Kettner, 1989, p. 89 (type, *Climacograptus caudatus* Lapworth, 1876a, OD), syn. by Goldman & Wright, 2003, p. 37]. Climacograptids with pattern E astogeny and narrow, asymmetrical proximal end with sicula lying almost entirely to right of tubarium midline in obverse view; sicular aperture oriented at ~70° from axis and bearing stout (but not necessarily long) virgella deflected across sicular aperture; virgella commonly matched by mesial spine on th1[1], such that they form pair which, in undeformed state, is symmetrical around tubarium axis; more rarely th1[2] also bears small mesial spine. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone–*Pleurograptus linearis* Biozone): worldwide.——Fig. 239,*4a–c*. **D. spiniferus* (Ruedemann); *4a–b,* lectotype, AMNH 1041/5a, Utica Shale, Balston Spa, New York, USA (Riva, 1974a, fig. 4); *4c,* NRM 1480 (Holm Collection), juvenile showing position of spines on proximal end and the two rods of the prosicula, Kurland, Estonia (Bulman, 1932a, pl. 3). Scale bars, 1 mm.

Pseudoclimacograptus Přibyl, 1947, p. 5 [**Climacograptus scharenbergi* Lapworth, 1876a, p. 6; OD]. Climacograptids with wide, rounded proximal end, strong zigzag median septum and distinct intrathecal folds; proximal end with virgellar spine and with or without subapertural spine on th1[1]; thecal apertures straight, horizontal; three-vaned nematularium in mature specimens; proximal end of pattern D astogeny. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Pleurograptus linearis* Biozone): China, Russia, Belgium, UK, Norway, Sweden, USA, Canada.——Fig. 240,*2a–c*. **P. scharenbergi* (Lapworth); *2a–b,* specimen in reverse (*a*) and obverse (*b*) views, PMO 118.047a,b, latex casts, Arnestad Formation, Oslo Region, Norway; *2c,* topotype, SM A19704, reverse view, Lower Hartfell Formation, Scotland, UK (see Williams, 1994, fig. 7g); scale bars, 1 mm (new).

Styracograptus Štorch & others, 2011, p. 356 [**Climacograptus tubuliferus* Lapworth, 1876a, p. 6; OD] [?=*Notograptus* Rusconi, 1948, p. 248 (type, *N. lanceolatus*, M), *nom. nud.,* Toro & Brussa, 2001, p. 362, based on scalariform climacograptid indet. with long nema, virgella, and parasicula, see Rusconi, 1950, fig. 46; Toro & Brussa, 2001 identified the type as *Climacograptus* sp. cf. *C. caudatus*]. Climacograptids with rounded proximal end and Pattern D proximal development that lacks spines on proximal thecae; prosicula represented by single prominent rod that is continuous with nema; virgella normally elongated; long nematularium may be present; tubarium septate or aseptate with median septum delayed in some septate species; thickened nemal crossbars at base of interthecal septum. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Hirnantian, Normalograptus extraordinarius* Biozone): worldwide.——Fig. 239,*5a–d*. **S. tubuliferus* (Lapworth); *5a,* lectotype, BU 1193g, *Pleurograptus linearis* Biozone, Hartfell Spa, Scotland, UK (Riva & Kettner, 1989, fig. 10H); *5b,* MCZ 9463/11, reverse view, somewhat reconstructed, showing origin of median septum; *5c,* MCZ 9463/10, juvenile showing single rod of prosicula grading into nema; *5d,* proximal end in obverse view (Mitchell, 1987, fig. 5R,K,Q; identified therein as *Climacograptus* sp. cf. *C. caudatus*). Scale bars, 1 mm.

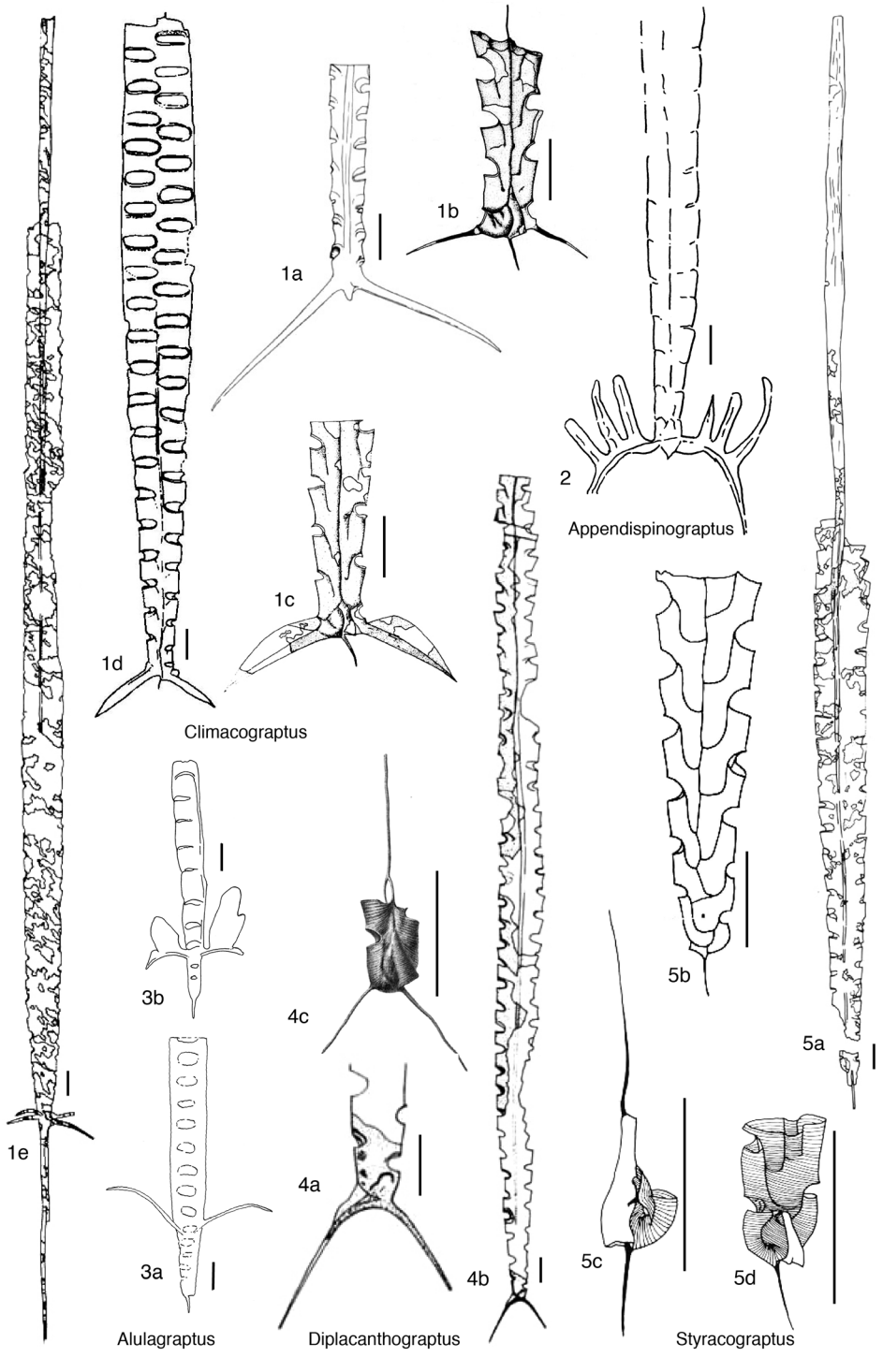


FIG. 239. Climacograptidae (p. 353–356).

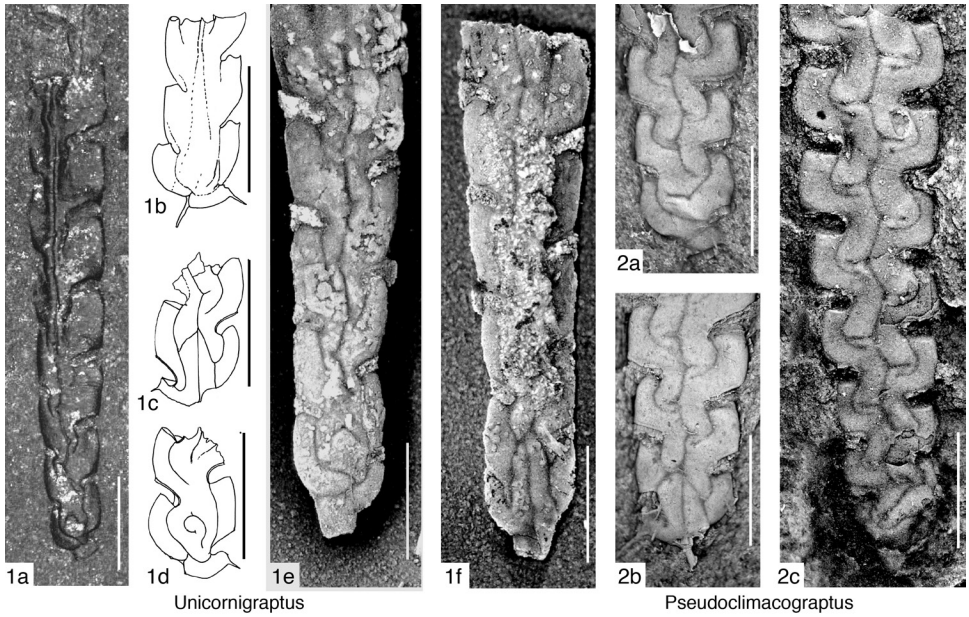


FIG. 240. Climacograptidae (p. 354–356).

Unicornigraptus CHEN & GOLDMAN, in CHEN & others, 2016, p. 311 [**U. xinjiangensis;* OD]. Proximal end of tubarium asymmetric with short first theca; th1[2] much longer than th1[1]; subapertural spine on th1[1] only; pattern C astogeny; virgella usually elongated; parasicula may be present; median septum complete, undulating, and with intrathecal folding; thecae with long and straight ventral side; with or without geniculum; thecal apertures with paired lobes or straight. *Middle Ordovician* (*Darriwilian, Levisograptus dentatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——FIG. 240,*1a*. **U. xinjiangensis,* holotype, NIGP 157509, reverse view, scale bar, 1 mm (Chen & others, 2016, fig. 6-97N).——FIG. 240,*1b*. *U. ambiguus* (MALETZ, 2011d), GSC 81805, flattened, isolated specimen, *Levisograptus dentatus* Biozone, St. Pauls Inlet, western Newfoundland, Canada, scale bar, 1 mm (Maletz, 2011d, fig. 4K).——FIG. 240,*1c–d*. *U. pungens* (RUEDEMANN, 1904), GSC 133528, isolated specimen in obverse (*c*) and reverse (*d*) views, scale bars, 1 mm (Maletz, 2011d, fig. 4I,fig. 4J).——FIG. 240,*1e–f*. *U. scandinavicus* CHEN & GOLDMAN, in CHEN & others, 2016, holotype, LO 2410t, in reverse (*e*) and obverse (*f*) views (specimen flaked out of slab, imprint bears a very long virgella and parasicula), Almelund Shale, Fågelsång, Scania, Sweden; scale bars, 1 mm (new).

Family DICRANOGRAPTIDAE Lapworth, 1873

[Dicranograptidae LAPWORTH, 1873b, table facing p. 555] [=superfamily Dicranograptacea LAPWORTH, 1873b, MITCHELL & others, 2007 (misspelled Dicranograptacae in fig. 1); =superfamily Dicranograptoidea LAPWORTH, 1873b, ŠTORCH & others, 2011); =Leptograptidae LAPWORTH, 1879c, p. 454; =Incumbograptidae GE in MU & others, 2002, p. 437; =Ningxiagraptidae GE in MU & others, 2002, p. 331; =Ordosograptidae LIN, 1980, p. 477]

Biserial, dipleural axonophorans, secondarily two-stiped or partly two-stiped, reclined, uniserial, or with cladial branching; proximal end with metasicular origin of th1[1]; proximal end provided with virgellar spine and additional apertural spines on at least first thecal pair; proximal development type dextral; pattern C astogeny or derived one; thecae variable, geniculate and with isolated, introverted apertures or simplified in derived taxa; intrathecal folds with crossbars present; complete median septum in biserial taxa; intrathecal folds lost in younger taxa with shortened thecal overlap and thecal simplification. *Middle Ordovician* (*Darriwilian, Nicholsonograptus fasciculatus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

MITCHELL (1987) and MITCHELL and others (2007) considered the Dicranograptidae to be a monophyletic clade with its members possessing quite variable colony

shapes from multiramous to one-stiped. The cladistic analysis of MITCHELL and others (2007, fig. 1) indicated that *Dicaulograptus* with a pattern C astogeny is the ancestral condition of the dicranograptid colony with all derived taxa possessing a pattern A astogeny or a derived one. MITCHELL (1987, fig. 17) interpreted the biserial, dipleural *Dicaulograptus hystrix* (BULMAN, 1932a) as derived from an archiclimacograptid ancestor. The interpretation gets more problematical with the recognition of two-stiped axonophorans with a generally dicellograptid tubarium construction during the early Darriwilian. MALETZ (1998b, 2014b) suggested a possible origin of the dicranograptids through *Levisograptus sinicus* (MU & LEE, 1958), based on the evidence from the earliest two-stiped taxa *Levisograptus dicellograptoides* (MALETZ, 1998b) and *Undulograptus* sp. (KRAFT & KRAFT, 2003) in the lower Darriwilian (MALETZ, 2014b). However, these taxa with a possible pattern U astogeny (Fig. 241.8) differ from the thecal construction in the younger species of *Dicellograptus,* and a considerable biostratigraphic gap in the presence of dicellograptid colony shapes during the Darriwilian renders the interpretation questionable.

MORPHOLOGY

Proximal Development

MITCHELL (1987) analyzed the proximal development of the Dicranograptidae in some detail and recognized several distinct astogenetic patterns (Fig. 241). MITCHELL and others (2007) identified the biserial axonophoran *Dicaulograptus* with a typical pattern C astogeny as the basal member of the Dicranograptidae. *Dicaulograptus hystrix* bears a simple sicula with multiple antivirgellar spines, but antivirgellar spines are lacking in *Dicaulograptus cumdiscus* FINNEY, 1985b.

BULMAN (1945) described the proximal development of *Dicranograptus nicholsoni* HOPKINSON, 1870 from isolated material and recognized the upward-growing flange connecting the initial part of th2^1 and forming the foramina for th2^1 and th2^2 and originating from the horizontally growing median part of th1^1 (Fig. 241.5–241.6). MITCHELL (1987) interpreted this development as pattern A′ (Fig. 241.2) in his analysis of the proximal development of Ordovician biserials. It differs from pattern A astogeny (Fig. 241.1) only through the presence of the lateral clefts at the virgella and a dorsal notch on the sicular aperture (Fig. 241.7). Derived dicranograptids have a dorsal notch and paired clefts on the side of the virgella, but these features are quite variable in the expression and may be lost in some taxa. Pattern A″ (Fig. 241.3) differs through the development of two separate stipes (the dicellograptid condition). Pattern N of MITCHELL (1987, fig. 1), the nemagraptid pattern (Fig. 241.4), bears a sicula that extends below the ventral sides of the stipes and should not be confused with the pattern N astogeny of MELCHIN and others (2011), referring to the development of a group of Silurian axonophorans. Recently, the genus *Dicellograptus* has been differentiated into a number of closely related genera, based on the growth direction of the proximal thecae and the orientation of the sicula (e.g., MU & others, 2002; CHEN & others, 2016). *Dicellograptus* bears a J-shaped first theca (th1^1) (Fig. 241.10–241.11), but it is more U-shaped in *Jiangxigraptus,* with its sicula usually leaning at least partly on stipe 2 (Fig. 241.9).

Cladia

BULMAN (1970, p. 106) expected that branching in the nemagraptids is cladial, and FINNEY (1985a) confirmed this based on isolated fragments of *Nemagraptus gracilis* (HALL, 1847) from the Athens Shale of Alabama, USA, in which the lateral branches originated from the thecal apertures of mature thecae. BATES and others (2011) described and illustrated the proximal end of a species of *Amphigraptus* with paired cladial branches originating from the apertures of the mother theca. The development of cladia in other Dicranograptidae has not been described in detail from isolated material, and details on the fusellar construction of these cladia are unknown. A dorsal rod

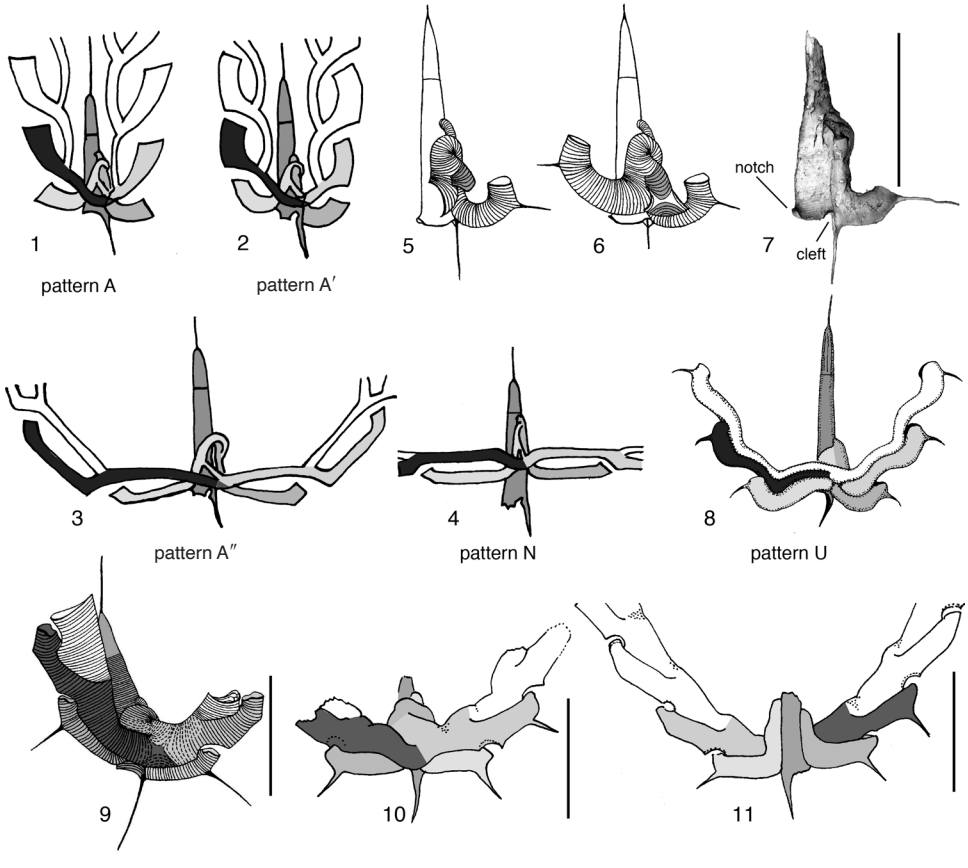


FIG. 241. Proximal development in the Dicranograptidae. *1–4,* Proximal development types (adapted from Mitchell, 1987, fig. 1). *5–6, Dicranograptus nicholsoni* HOPKINSON, 1870, initial part of th2[1] and upward-growing flange on th1[1] highlighted (adapted from Bulman, 1955, fig. 43); *7, Dicranograptus nicholsoni,* SMF 75811, juvenile, showing development of sicular aperture (new); *8,* inferred pattern U astogeny in *Levisograptus dicellograptoides* (MALETZ, 1998b), reconstruction (adapted from Maletz, 1998b, fig. 1A); *9, Jiangxigraptus salopiensis* (ELLES & WOOD, 1906) (adapted from reconstruction in Bulman, 1955, fig. 40; original specimen in STRACHAN, 1959, fig. 1); *10–11, Dicellograptus complanatus* LAPWORTH, 1880a in reverse (*10*) and obverse (*11*) views, PMU 35692, PMU 35691a, Koängen drill core, Scania, Sweden (new). Scale bars in *7, 9–11,* 1 mm.

similar to the secondary nema or pseudovirgula as in the monograptids (for example, *Cyrtograptus,* see THORSTEINSSON, 1955; URBANEK, 1963) has not been discovered in any dicranograptid, suggesting that the development is similar to that in the dichograptinid *Pterograptus* HOLM, 1881a (SKWARKO, 1974; MALETZ, 1994a).

The development of a colony with cladial distal branchings is considered a secondarily multiramous condition of the dicranograptid tubaria. Cladial branching appears in several genera and constructionally, most probably, these genera represent independent lineages. It is quite likely that the cladia-bearing nemagraptids (FINNEY, 1985a) are independently derived from a two-stiped nemagraptid such as *Nemagraptus subtilis* HADDING, 1913. Single cladia and even secondary cladia occur in the horizontal multiramous and fairly large colonies of *Amphigraptus* and *Pleurograptus* (see HALL, 1859c; NICHOLSON, 1867b) but also occur in the reclined *Tangyagraptus*.

Subfamily DICRANOGRAPTINAE Lapworth, 1873

[Dicranograptinae Lapworth, 1873b, table 1, facing p. 555] [=Dicellograptinae Ge in Mu & others, 2002, p. 412; =Leptograptinae Mu, 1950b, p. 181; =Tangyagraptinae Mu, 1963a, p. 368]

Biserial, dipleural axonophorans; secondarily two-stiped or partly two-stiped, reclined, uniserial, or with cladial branching; proximal end provided with virgellar spine and additional apertural to mesial spines on at least first thecal pair; proximal development type dextral; pattern C astogeny or derived one, excluding the Nemagraptinae with pattern N astogeny; thecae geniculate and with isolated, introverted apertures or simplified in derived taxa; complete median septum in biserial taxa; intrathecal folds and crossbars lost in younger taxa with shortened thecal overlap and apertural simplification. *Middle Ordovician* (*Darriwilian, Nicholsonograptus fasciculatus* Biozone)–*Upper Ordovician (Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

The subfamily Dicranograptinae is herein regarded as a paraphyletic group of taxa from which the Nemagraptinae originated through a number of changes in the proximal end of the colony. The biserial-uniserial tubarium shape of *Dicranograptus* could be interpreted as a secondary development due to the early appearance of the dicellograptids during the late Darriwilian. However, if the relationship to the genus *Dicaulograptus* can be substantiated, the two-stiped dicellograptid-type tubarium must be interpreted as the derived type.

TAXA WITHOUT CLADIAL BRANCHING

The grouping of the Dicranograptinae into taxa with and without cladia used herein is informal and does not suggest any taxonomic relevance. Cladial branching may have originated separately and independently in a number of lineages.

Dicranograptus Hall, 1865, p. 112 [**Graptolithus ramosus* Hall, 1847, p. 270; OD] [=*Cladograpsus* Emmons, 1855, p. 107 (type, *Cladograpsus dissimilaris* Emmons, 1855, pl. 1,*15*), SD Bulman, 1929, p. 173 (misspelled as *C. dissimilis*); *non Cladograpsus* Geinitz, 1852, syn. of *Didymograptus*]. Initiallly biserial and distally two-stiped dicranograptid with reclined, commonly spirally coiled stipes; proximal end of pattern A′ astogeny; thecae with intrathecal folds and geniculum; thecal apertures introverted and with apertural isolation; thecae with mesial to subapertural spines, at least in proximal end. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Katian, Paraorthograptus pacificus* Biozone): worldwide.——Fig. 242,*5a–b*. **D. ramosus* (Hall), *5a,* AMNH 30440, syntype (new; photo by Dan Goldman); *5b,* AMNH 30440, proximal end of syntype showing spines (new; drawing by John F. Riva). Scale bars, 1 mm.

Dicaulograptus Rickards & Bulman, 1965, p. 278 [**Lasiograptus hystrix* Bulman, 1932a, p. 29; OD]. Biserial dicranograptid with complex thecae with apertural introversion and mesial spines; thecae geniculate with strongly curved prothecae and metathecae, very convex free ventral wall, pleural spines, or pleural disks may be present; apertural excavations alternating and situated deep in tubarium, close to median septum; median septum slightly zigzag; proximal development of pattern A or pattern C astogeny. *Middle Ordovician* (*upper Darriwilian, Nicholsonograptus fasciculatus* Biozone–*Jiangxigraptus vagus* Biozone): China, Sweden, Norway, Canada, USA.——Fig. 242,*1a–c*. **D. hystrix* (Bulman); *1a,* holotype, NRM 48 (Holm collection), reverse view, scale bar 5 mm (Bulman, 1932a, pl. 9,*5*); *b–c,* paratypes, NRM Cn 59951, 59952, juveniles showing proximal development (Mitchell, 1988, fig. 11,*4,6*).——Fig. 242,*1d–e*. *D. cumdiscus* Finney, 1985b, holotype, USNM 377408, proximal (*d*) and distal (*e*) fragments of specimen, *Hustedograptus teretiusculus* Biozone, Pratts Ferry, Alabama, USA, scale bars, 1 mm (Finney, 1985b, fig. 2).

Dicellograptus Hopkinson, 1871, p. 20, original spelling as *Dicellograpsus* changed in ICZN Opinion 650, 1963][**Didymograpsus elegans* Carruthers, 1867b, p. 369; SD Gurley, 1896, p. 70] [=*Huayinograptus* Yu & Fang, 1981b; *nom. nud.,* herein (type, *Dicellograptus szechuanensis* Mu, 1950b, OD)] [=*Leptograptus* Lapworth, 1873b, p. 558 (type, *Graptolithus flaccidus* Hall, 1865, p. 143, OD), syn. by Chen & others, 2016, p. 162] [=*Leptograpsus* Ruedemann, 1908, p. 253 (misspelling of *Leptograptus*] [*non Leptograpsus* Milne Edwards, 1853, p. 171 (Crustacea, Decapoda, Grapsidae)]. Two-stiped dicranograptids with reclined, straight to spirally coiled stipes; proximal end of pattern A′ astogeny with sicula vertical and free between stipes; geniculate thecae with or without intrathecal folds and introverted and isolated apertures; at least first thecal pair with mesial to subapertural spines; J-shaped $th1^1$ and $th1^2$. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper*

Ordovician (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.——Fig. 242,*2a*. **D. elegans* (Carruthers), holotype, NHMUK Q850, Lower Hartfell Shale, *Pleurograptus linearis* Zone, Dob's Linn, Scotland, UK, scale bar, 10 mm (Elles & Wood, 1904, pl. 23,*2a*).——Fig. 242,*2b*. *D. flaccidus* (Hall), GSC 1957b, proximal end, Lake St. John's, east from Blue Point, Utica Shale, Canada, scale bar, 1 mm (new; drawing by John F. Riva).——Fig. 242,*2c–e*. *Dicellograptus complanatus* (Lapworth, 1880a); *2c,* PMU 22496, proximal end in reverse view; *2d,* PMU 22498, proximal thecae; *2e,* PMU 22499, distal thecae; Fjäcka Shale, Bestorp, Västergötland, Sweden, scale bars, 1 mm (Skoglund, 1963, fig. 10B–D).

Diceratograptus Mu, 1963a, p. 367 (p. 377, English text) [**D. mirus;* OD]. Two-stiped dicranograptids with heart-shaped axial cavity and distally separate stipes; supradorsal part of sicula visible between stipes; thecae strongly geniculate; number of spined proximal thecae and proximal development uncertain. *Upper Ordovician* (*Katian, Diceratograptus mirus* subzone of *Paraorthograptus pacificus* Biozone): China, Canada, USA.——Fig. 242,*3*. **D. mirus*, syntype, top of Wufeng Shale, Tangya, Yichang, China, scale bar, 1 mm (Mu, 1963a, fig. 13b).

Jiangxigraptus Yu & Fang, 1966, p. 93 [**J. mui;* OD] [=*Incumbograptus* Ge in Mu & others, 2002, p. 437 (type, *Jiangxigraptus inculus* Ge in Ge, Zheng, & Li, 1990, p. 89, OD), syn. herein] [=*Aclistograptus* Ge in Mu & others, 2002, p. 439 (type, *Graptolithus divaricatus* Hall, 1859c, p. 513, OD), syn. herein]. Two-stiped dicranograptids with reclined, commonly spirally coiled stipes; proximal end of pattern A′ astogeny with sicula partly or completely attached laterally to stipe two; thecae with strong prothecal folds; geniculum in proximal thecae; thecal apertures introverted and with apertural isolation; at least first thecal pair with mesial to subapertural spines; $th1^1$ and $th1^2$ generally U-shaped with upward-turned apertures. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone): worldwide.——Fig. 242,*6a*. **J. mui,* holotype, *Nemagraptus gracilis* Biozone, Hulo Formation, Xiushui drainage basin, Jiangxi Province, China, scale bar, 1 mm (Yu & Fang, 1966, fig. 2).——Fig. 242,*6b*. *J. inculus* (Ge in Ge, Zheng, & Li, 1990), holotype, NIGP 106213, proximal end, with strong tectonic deformation, *Nemagraptus gracilis* Biozone, China, scale bar, 1mm (new; photo by Zhang Yuandong).——Fig. 242,*6c*. *J. divaricatus* (Hall, 1859c), syntype, AMNH 35193, Kenwood, Normanskill, New York, USA, scale bar, 1 mm (new; photo by Dan Goldman).

Ningxiagraptus Ge in Mu & others, 2002, p. 331 [**Janograptus reclinatus* Ge in Ge, Zheng, & Li, 1990, p. 71; =*Ningxiagraptus yangtzensis* (Mu in Geh, 1963); Chen & others, 2016, p. 204; OD] [=*Deflexigraptus* Ge in Mu & others, 2002, p. 443 (type, *Leptograptus declinatus* Ge in Ge, Zheng, & Li, 1990, p. 81, OD), syn. herein]. Two-stiped dicranograptid with reclined stipes having wide angle of divergence; proximal end probably of pattern A′ astogeny; sicula connected laterally to stipe two; thecae with or without geniculum; apertures introverted or with straight apertures; mesial to subapertural spines on at least first thecal pair. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Climacograptus bicornis* Biozone): China, North America.——Fig. 242,*7a–b*. *N. yangtzensis; 7a,* syntype, NIGP 13010 (Geh, 1963, fig. 2d); *7b,* **N. reclinatus* (Ge in Ge, Zheng, & Li), holotype, NIGP 106102 (Mu & others, 2002, pl. 101,*6*). Scale bars, 1 mm.——Fig. 242,*7c*. *N. mensurans* (Ruedemann, 1908), AMNH 36147, proximal end, reverse view, J. Hall collection, Kenwood, New York, USA, scale bar, 1 mm (new; drawing by John F. Riva).

Pseudazygograptus Mu, Lee, & Geh, 1960, p. 37 [**Azygograptus incurvus* Ekström, 1937, p. 33; OD]. Single-stiped dicranograptid with variously oriented stipe, from horizontal to strongly reflexed; thecae slender, geniculate and frequently with genicular hoods; apertures with slight lateral lobes or straight. *Middle Ordovician* (*Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——Fig. 242,*4a–b*. **P. incurvus* (Ekström); *4a*, syntype, LO 3322T, fragment, Scania, Sweden (new); *4b,* OSU 32911, proximal end, Athens Shale, Alabama, USA (Finney, 1980, fig. 9B). Scale bars, 1 mm.

TAXA WITH CLADIAL BRANCHING

Taxa with single cladia, paired cladia, and even secondary cladia exist. The taxa may also be differentiated by their proximal developments. It is likely that the cladial-bearing taxa of the Dicranograptinae are not a monophyletic group. They are here assembled for easy access only.

Amphigraptus Lapworth, 1873b, p. 559 [**Graptolithus divergens* Hall, 1859c, p. 509; M] [=*Clematograptus* Hopkinson in Hopkinson & Lapworth, 1875, p. 652 (type, *Graptolithus multifasciatus* Hall, 1859c, p. 508, SD Gurley, 1896, p. 93), syn. by Bulman, 1970, p. 121]. Multiramous dicranograptids with paired primary cladia; secondary cladia may be present in mature specimens; stipes subhorizontal to moderately reclined; thecae geniculate and introverted; subapertural to mesial spines at least on first thecal pair; sicula slender and free or resorbed in larger specimens. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Dicranograptus clingani* Biozone): China, UK, USA.——Fig. 243,*1a–b*. **A. divergens* (Hall); *1a, A. multifasciatus,* holotype, NYSM 6840, *Nemagraptus gracilis* Biozone, Normanskill Shale, Kenwood, New York, USA, scale bar, 5 mm (Ruedemann, 1908, pl. 15,*4*); *1b,* holotype,

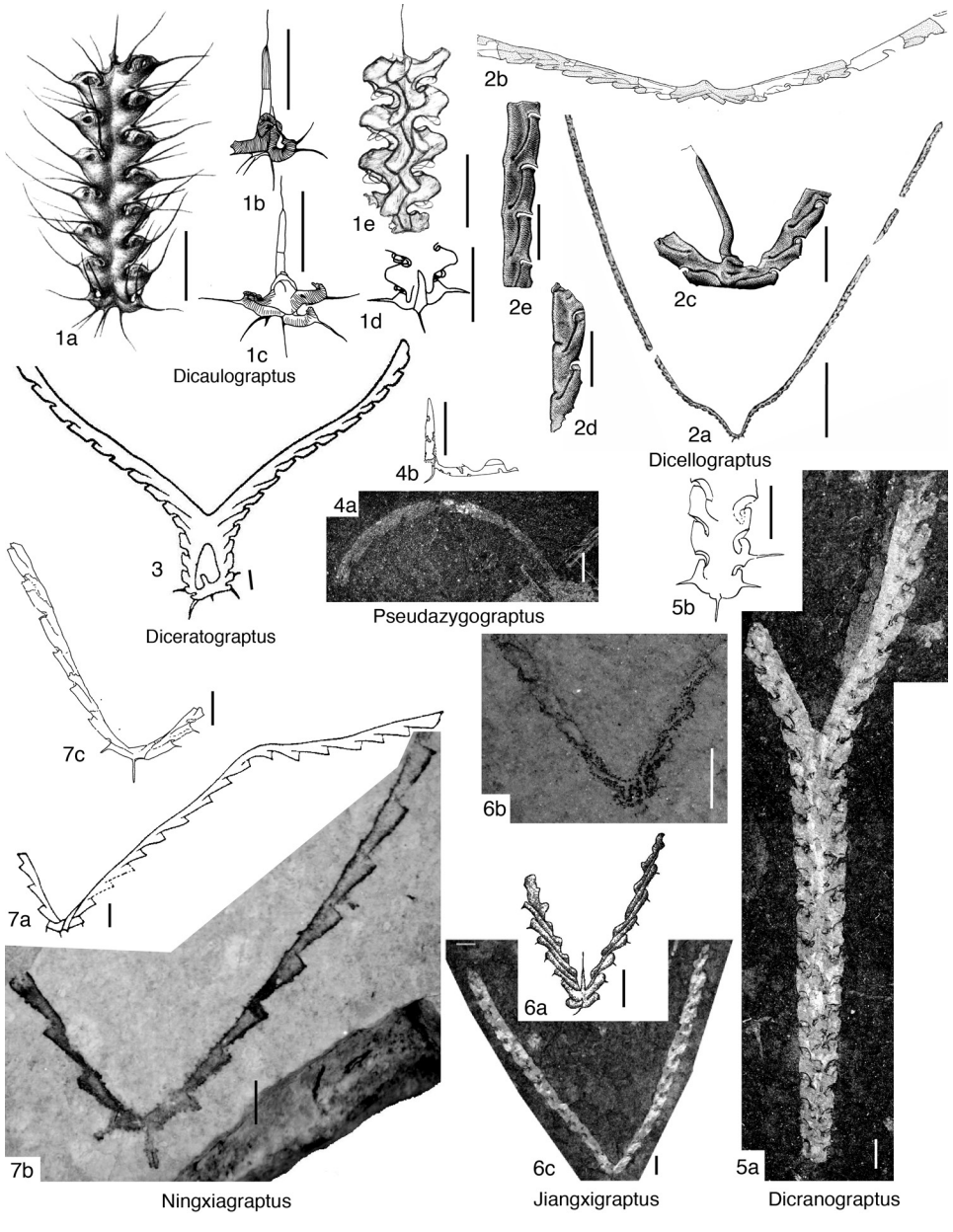


FIG. 242. Dicranograptinae without cladia (p. 359–360).

Nemagraptus gracilis Biozone, Normanskill Shale, Kenwood, New York, USA, scale bar, 5 mm (Hall, 1859c, fig. 9).

Pleurograptus NICHOLSON, 1867b, p. 257, original spelling as *Pleurograpsus* changed in ICZN Opinion 650, 1963 [**Cladograpsus linearis* CARRUTHERS, 1858, p. 467; OD]. Dicranograptid with cladial stipes of several orders; proximal development uncertain; sicula very slender and long, may be resorbed in mature specimens; thecae slender, ventral side parallel to dorsal side, with distinct geniculum. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Paraorthograptus pacificus* Biozone): UK, Canada, China, USA.——FIG. 243,*2a–b*. **P. linearis* (CARRUTHERS); *2a,* NHMUK PM Q848, large specimen, Hartfell Shale, Scotland, UK, scale

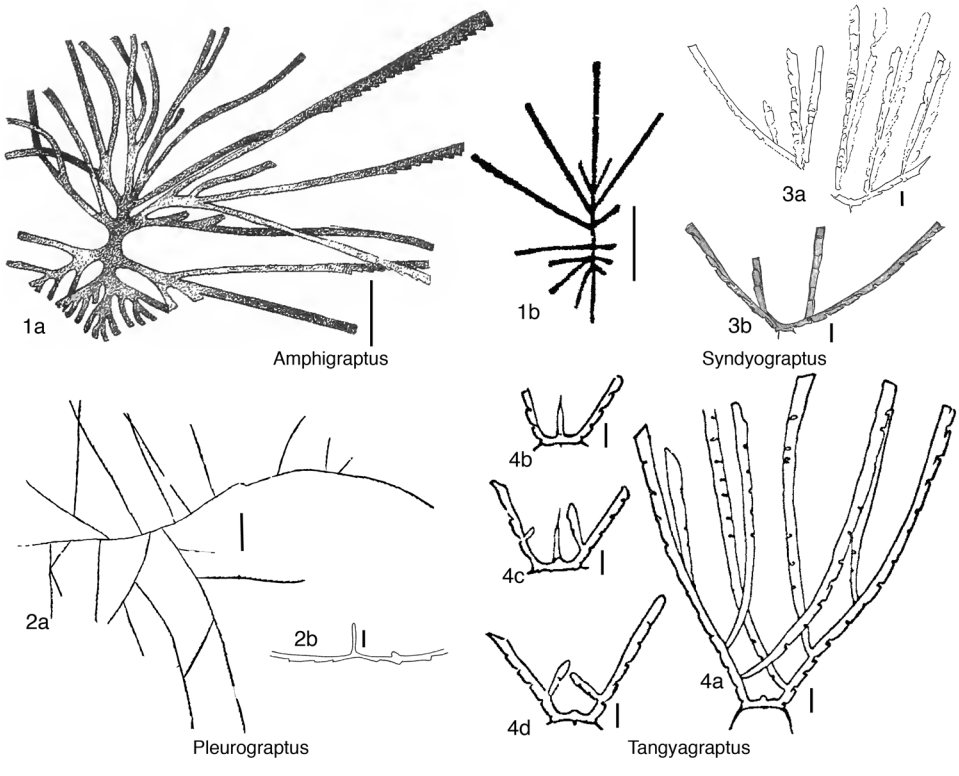


FIG. 243. Dicranograptinae with cladia (p. 360–362).

bar, 5 mm (Bulman, 1970, fig. 87,*1*); *2b,* NHMUK PM Q848, proximal end, scale bar, 1 mm (Strachan, 1969, fig. 1C).

Syndyograptus RUEDEMANN, 1908, p. 266 [**S. pecten;* OD]. Multiramous dicranograptids with paired primary cladia; stipes moderately reclined; thecae geniculate and introverted, with low inclination of ventral side; subapertural to mesial spines at least on first thecal pair; slender sicula connected laterally to stipe two. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Climacograptus bicornis* Biozone): China, USA.——FIG. 243,*3a–b*. **S. pecten; 3a,* syntype, NYSM 7363 (new); *3b,* syntype, NYSM 7364, proximal end showing inclined sicula; Glenmont, New York, USA (Ruedemann, 1908, fig. 185). Scale bars, 1 mm.

Tangyagraptus MU, 1963a, p. 359 (p. 377, English text)[**T. typicus;* OD]. Reclined, two-stiped dicranograptid with unpaired cladia originating on one side of both stipes; proximal development unknown; proximal end with prominent apertural spines on first thecal pair; prominent sicula may be resorbed in mature specimens. [Genus was misspelled as *Tangyograptus* MU, 1963a in FINNEY, 1985a, p. 1104.] *Upper Ordovician* (*Katian, Paraorthograptus pacificus* Biozone): China.——FIG. 243,*4a–d*. **T. typicus,* top of Wufeng Shale, Tangya, Yichang, China; *4a,* NIGP WM 185, holotype; *4b–d,* paratypes showing astogeny; scale bars, 1 mm (Mu, 1963a, fig. 10).

Subfamily NEMAGRAPTINAE Lapworth, 1873

[Nemagraptinae LAPWORTH, 1873b, p. 556, *ex* family Nemagraptidae LAPWORTH, 1873b]

Two-stiped dicranograptids with or without single or paired cladial branching; proximal end with high metasicular origin of th1[1]; proximal development type of pattern N astogeny with sicular aperture reaching beyond base of stipes; thecae variable, usually with strong, laterally expanded genicular flanges; apertures isolated and introverted, but simple and with low overlap in derived taxa; intrathecal folds may be present. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.

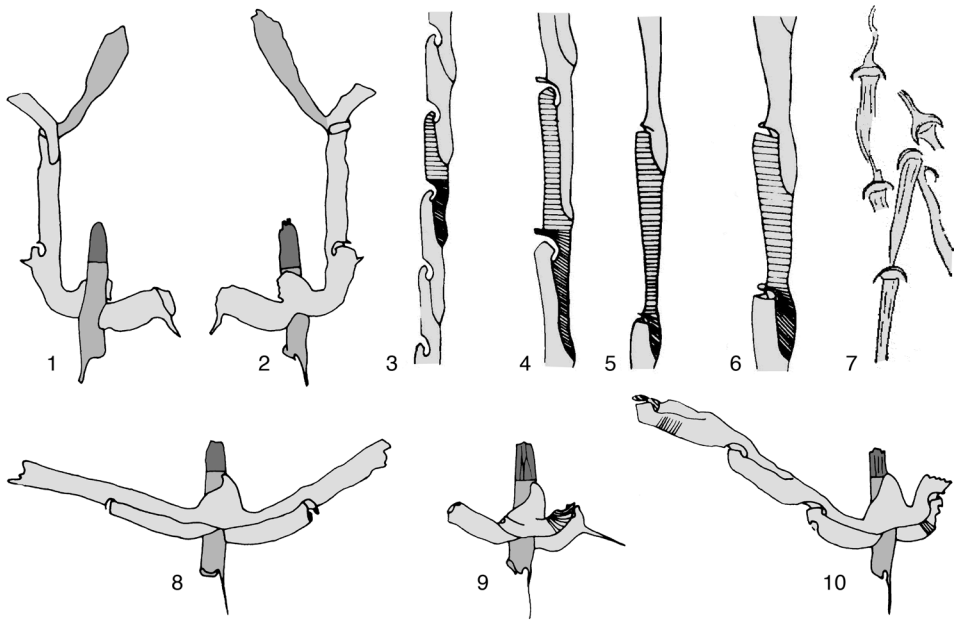


FIG. 244. Tubarium construction in *Nemagraptus*. *1–2, 5–6, 8, Nemagraptus gracilis* (HALL, 1847); *1–2,* proximal end showing cladium (Finney, 1985a, fig. 11–12); *5–6,* proximal (*5*) and distal (*6*) thecal style (Finney, 1985a, fig. 4,*6*–4,*7*); *7,* ventral view of stipes, holotype of *Ordosograptus delicatus* LIN, 1980 (Lin, 1980, fig. 1,*2*); *8,* proximal end in reverse view, slightly reclined stipes, see high metasicular origin of th1[1]; *3–4, 9–10, Nemagraptus linmassiae* FINNEY, 1985a; *3–4,* reconstruction of proximal (*4*) and distal (*3*) thecal style; *9–10,* proximal ends in reverse view (all adapted from Finney, 1985a). Illustrations not to scale.

The Nemagraptidae is a traditional name introduced by LAPWORTH (1873b) and consistently used to differentiate two-stiped to multiramous Upper Ordovician axonophorans. It was restricted by FINNEY (1985a) to taxa with a nemagraptid proximal end, that is to taxa in which the sicula extends downward beyond the stipes, excluding two-stiped to multiramous taxa with a dicellograptid proximal end in which the stipes diverge from close to the sicula (*Amphigraptus, Pleurograptus*). MALETZ (2014b, p. 515) revised the family and also included *Pleurograptus,* unaware of the dicellograptid proximal end of this genus illustrated in WILLIAMS (1982b, pl. 2).

Nemagraptidae has commonly been used as a taxonomic unit at the family level (e.g. BULMAN, 1970; MU & others, 2002), but is herein used as a subfamily to indicate its relationships to the dicranograptids. The Nemagraptinae originate from a dicellograptid ancestor in the late Darriwilian (see MITCHELL, 1987, fig. 13,*17*; MITCHELL & others, 2007), but the transition is poorly documented. *Nemagraptus linmassiae* FINNEY, 1985a still possesses the intrathecal folds (recognized as prothecal folds in FINNEY, 1985a) as a symplesiomorphic character retained from the dicellograptids, but already has the isolated metasicula (Fig. 244) as the main synapomorphy of the nemagraptids (FINNEY, 1985a, fig. 23,*1*). With the genera *Amphigraptus, Pleurograptus,* and *Tangyagraptus* now included in the Dicranograptinae, the Nemagraptinae comprises a single genus with a number of taxa having variable development of cladia. FINNEY (1985a) illustrated the development of cladia in *Nemagraptus* from chemically isolated material (Fig. 244.1–244.2). The thecae possess considerable overlap and indications of intrathecal folds in *Nemagraptus*

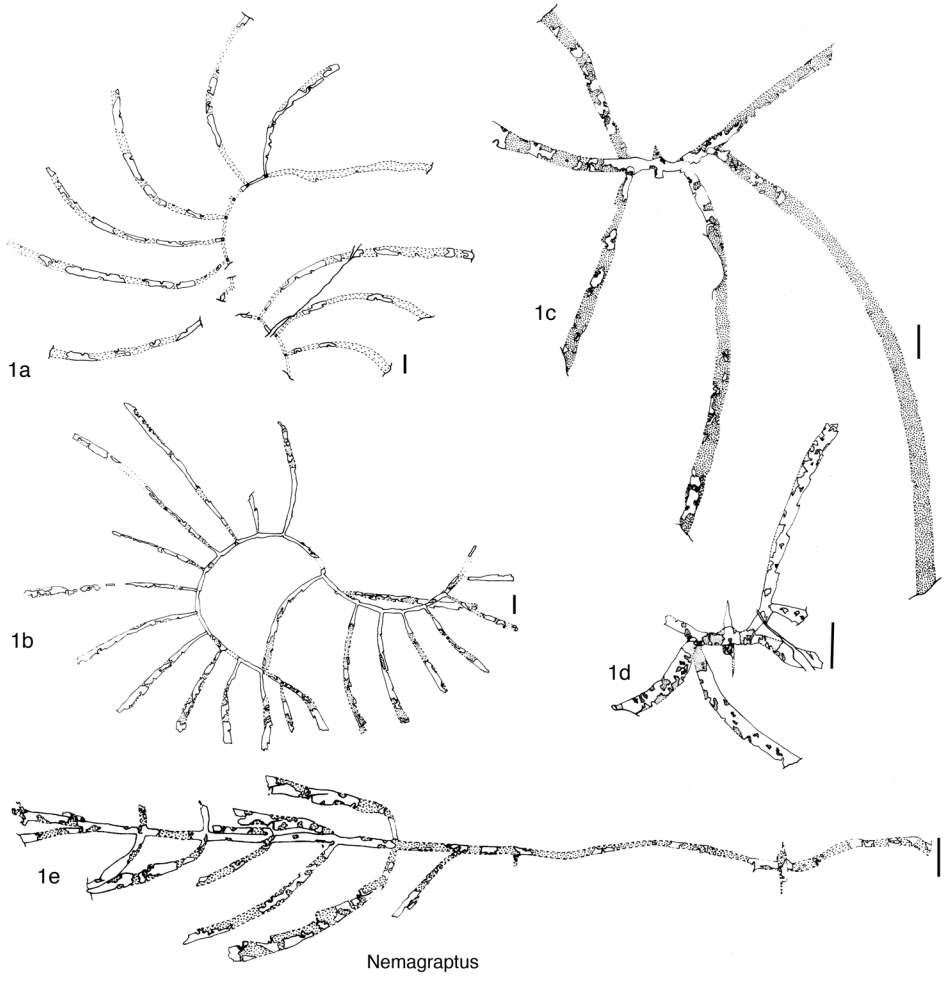


FIG. 245. Nemagraptinae (p. 364–365).

linmassiae (Fig. 244.3–244.4), whereas in *Nemagraptus gracilis* the thecae are shorter and lack introverted thecal apertures and lateral lappets (Fig. 244.5–244.6). Strong genicular lobes or flanges have been used to differentiate the genus *Ordosograptus* LIN, 1980 (Fig. 244.7), but is based on dorso-ventrally preserved *Nemagraptus* stipe fragments. Paired cladia were unknown from *Nemagraptus*, but the proximal ends of specimens described as *Amphigraptus* n. sp. A and *Amphigraptus* n. sp. B in FINNEY (1985a) clearly possess a nemagraptid proximal end and should be included in *Nemagraptus* (Fig. 245,*1c–e*).

Nemagraptus EMMONS, 1855, p. 109, original spelling as *Nemagrapsus* changed in ICZN Opinion 650, 1963 [**Graptolithus gracilis* HALL, 1847, p. 274; =*Nemagraptus elegans* EMMONS, 1855, p. 109; SD HALL, 1868, p. 211] [=*Coenograptus* HALL, 1868, p. 179 (type, *Graptolithus gracilis* HALL, 1847; SD BULMAN, 1929, p. 169, obj.)] [=*Geitonograptus* OBUT & ZUBTZOV, 1965, p. 24 (type, *G. suni,* OD), syn. by BULMAN, 1970, p. 120] [=*Helicograpsus* NICHOLSON, 1868e, p. 23 (type, *Grapolithus gracilis* HALL, 1847, p. 274, OD, obj.)] [=*Ordosograptus* LIN, 1980, p. 477 (type, *O. delicatus,* OD), syn. by FINNEY, 1985a, p. 1111] [=*Stephanograptus* GEINITZ, 1866, p. 124 (type, *Graptolithus gracilis* HALL, 1847, p. 274, OD, obj.)]. Two-stiped dicranograptids with or without single or paired cladial branching; proximal end with high metasicular origin of th1[1]; proximal development type

pattern N astogeny with sicular aperture reaching beyond base of stipes; thecae variable, usually with strong, laterally expanded genicular flanges; apertures isolated and introverted, but simple and with low overlap in derived taxa; intrathecal folds may be present. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——Fig. 245,*1a–b. *N. gracilis* (Hall); *1a,* AMNH 30458, lectotype; *1b,* AMNH 36766, more complete specimen; Normans Kill Shales, Kenwood, New York, USA; scale bars, 1 mm (Finney, 1985a, fig. 10,*1–2*).——Fig. 245,*1c–d*. *Nemagraptus* sp. B, Athens Shale, Calera, Alabama, USA; *1c,* OSU 32976, paired cladia on left stipe, scale bar, 1 mm; *1d,* OSU 32975, showing *Nemagraptus*-type proximal end; scale bar, 1 mm (Finney, 1985a, fig. 27,*1,3*; as *Amphigraptus* sp. B).——Fig. 245,*1e*. *Nemagraptus* sp. A, OSU 32973, paired cladia on distal part of stipe, Athens Shale, Pratt's syncline section, Alabama, USA, scale bar, 1 mm (Finney, 1985a, fig. 273; as *Amphigraptus* sp. A).

INFRAORDER NEOGRAPTINA

Jörg Maletz

Infraorder NEOGRAPTINA Štorch, Mitchell, Finney, & Melchin, 2011

[Neograptina Štorch, Mitchell, Finney, & Melchin, 2011, p. 368] [=family Monograptidae Lapworth, 1873b *sensu* Mitchell, 1987, p. 390; =suborder Monograptina of Mitchell & others, 2007]

Biserial, uni-biserial, and uniserial graptoloids lacking proximal spines except for the virgellar spine; proximal end in biserial taxa slender and usually pointed, asymmetrical; pattern A astogeny in early members and variable derived patterns in derived taxa; thecal style variable, from simple tubes with straight aperture to taxa with complex thecal apertures adorned with lappets, flanges, apertural and genicular hoods or hooks, or single or paired spines. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone)–*Lower Devonian* (*Pragian, Uncinatograptus yukonensis* Biozone): worldwide.

Mitchell (1987) emended the family Monograptidae to include all taxa that are now included in the Neograptina, thus extending the familiar term Monograptidae considerably. Mitchell and others (2007) used the name Monograptina for the same unit, but excluded the *Undulograptus* (now *Levisograptus*, see Maletz, 2011c) *austrodentatus* group as a stem group. The resulting confusion led Štorch and others (2011, p. 314) to introduce the term Neograptina for the same clade. Štorch and others (2011, p. 368) provided a cladistic definition (not a diagnosis; corrected in Melchin & others, 2011, p. 291) of the Neograptina, stating that "the Neograptina is the total clade comprising all species sharing a more recent common ancestor with *Monograptus priodon* than with *Diplograptus pristis* (i.e., the species on the branches arising from the right side of node 1 in fig. 6 [of Štorch & others, 2011] and all their descendents)." The definition was based on a specific diagram, but the authors noted that it would be difficult to provide a diagnosis due to the high variation of the included taxa. Typical biserial axonophorans and the derived uniserial taxa can be included in the Neograptina, following a similar concept to the one advocated first by Mitchell (1987) when redefining the Monograptidae.

Štorch and others (2011, p. 368) erected the monophyletic taxon Neograptina as a sister taxon to the Diplograptina, using the results of an analysis by Mitchell and others (2007) and identified *Undulograptus formosus* Mu & Lee, 1958 as the earliest member of the clade. Melchin and others (2011, fig. 3) separated three groups in the Neograptina (Fig. 246), the Normalograptidae, the Monograptoidea, and the Retiolitoidea and regarded the genus *Hirsutograptus* as *incertae sedis*. The authors considerably extended the concept of the Retiolitoidea and included a number of non-ancorate taxa.

The early (biserial) Neograptina possess a rounded to pointed proximal end without spines, except for the virgella, and a pattern A astogeny in the early members, modified to a pattern H astogeny or a derived one in later ones. According to Maletz (2011d), the precise phylogenetic relationship of the genus *Undulograptus* at the roots of the Climacograptidae and Normalograptidae (see Mitchell & others, 2007; Štorch & others, 2011) is uncertain, as the origin and early evolution of proximally spineless (except for the virgella) axonophorans is completely unresolved. Thus, a number of early Neograptina are herein regarded as stem group taxa and not included in the family Normalograptidae.

MORPHOLOGY

The description of the tubarium morphology focuses on the early taxa and their development (stem group taxa and Normalograptidae). Derived taxa (Retiolitoidea,

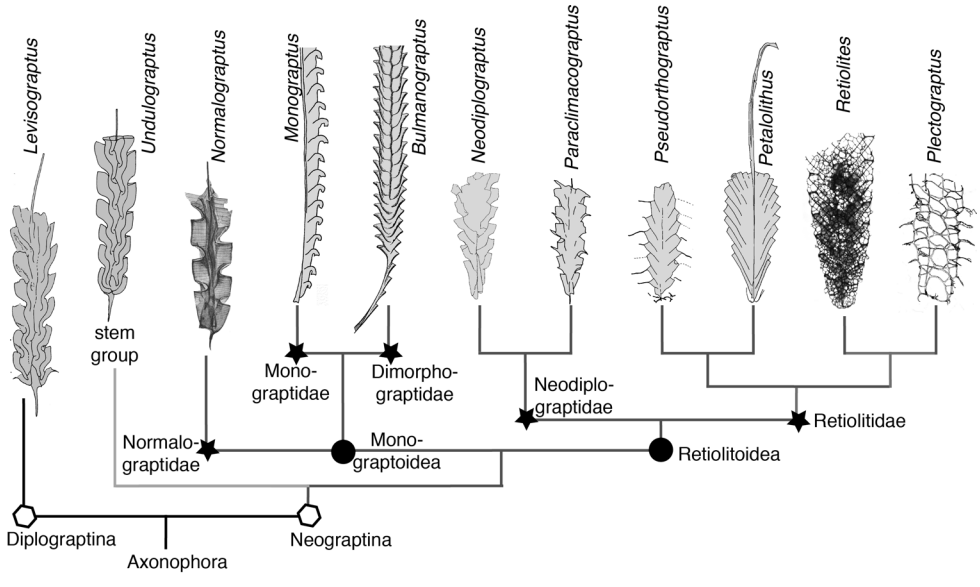


FIG. 246. Cladistic interpretation of origin of the Neograptina (new, based on data in MELCHIN & others, 2011, fig. 2 and ŠTORCH & others, 2011, fig. 6).

Monograptoidea) are covered in the following sections.

The proximal development types of early Neograptina are poorly understood. MITCHELL (1987) stated a pattern A astogeny (Fig. 247.2) for *Oelandograptus oelandicus* (BULMAN, 1963b) (Fig. 247.3–247.5) and a pattern B astogeny for the genus *Undulograptus* (Fig. 247.1). The pattern B astogeny of *Undulograptus* was based on *Proclimacograptus angustatus* (EKSTRÖM, 1937), as described by MALETZ (1997a). The species was erroneously regarded as the type species of *Undulograptus* by MITCHELL (1987, p. 397). The type of *Undulograptus*, however, is *Pseudoclimacograptus formosus* MU & LEE, 1958, a species for which the proximal development was unknown at the time, but MITCHELL (1992) identified a pattern C astogeny in *Undulograptus formosus* (Fig. 247.8) and some other species referred to *Undulograptus*. MALETZ and AHLBERG (2011b) discussed a group of *Undulograptus* species from the Krapperup drill core having a pattern C astogeny. A pattern C astogeny also appears in *Haddingograptus* species. MALETZ (2011d) discussed a possible origin of the derived climacograptids from these. Thus, a pattern C astogeny may be found in basal Neograptina, but the development of *Oelandograptus* and its inclusion in the Neograptina remains uncertain.

The proximal end of early Neograptina is evenly rounded to strongly asymmetrical. The first thecal pair is strongly upturned (Fig. 247) and the thecal apertures are oriented horizontally, but in *Oelandograptus* the apertures are outward inclined. The proximal development of pattern A astogeny in this taxon needs to be revised and verified. Depending on the position of the dicalycal theca, the proximal development of pattern C astogeny can be differentiated into two slightly different types. In taxa with a dicalycal theca $th3^1$, the obverse side has an arch connecting $th2^2$ and $th3^1$. This development appears in *Haddingograptus eurystoma* (JAANUSSON, 1960) and other *Haddingograptus* species (Fig. 247.6). In *Haddingograptus oliveri* (BOUČEK, 1973), with a dicalycal theca $th2^1$, the median septum is complete on both the obverse and reverse sides (see MALETZ, 1997a, fig. 7I–7J).

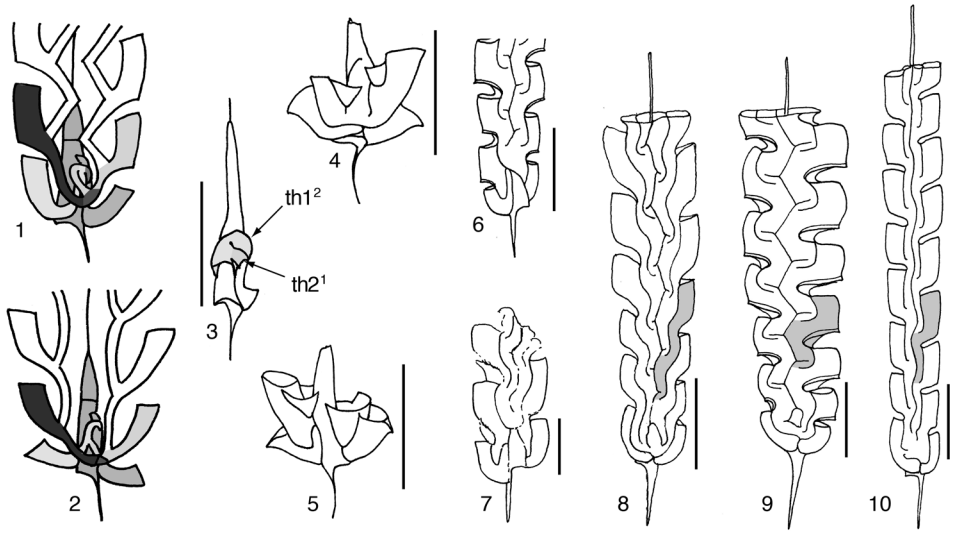


FIG. 247. Proximal development and tubarium shape of early Neograptina. *1,* Pattern B astogeny; *2,* pattern A astogeny; *3–5, Oelandograptus oelandicus* (BULMAN, 1963b), juveniles in reverse (*3–4*) and obverse (*5*) views; *6, Haddingograptus* MALETZ, 1997a sp., proximal end in obverse view, reconstruction (new); *7, Undulograptus novaki* (PERNER, 1895), OMR 54977, Drahous, Czech Republic, obverse view (new); *8, Undulograptus formosus* (MU & LEE, 1958), reconstruction of holotype, reverse view, showing long double sigmoidal thecae (adapted from Maletz, 2011c, fig. 1a); *9, Haddingograptus oliveri* (BOUČEK, 1973), short thecae with strong intrathecal folds (Maletz, 1997a, fig. 29c); *10, Proclimacograptus angustatus* (EKSTRÖM, 1937), short thecae, no intrathecal folds; (*1-5* adapted from Mitchell, 1987). All scale bars, 1 mm.

The sicula of most early Neograptina is short (less than 1.5 mm long) and widens rapidly in most members in which the sicula is known in isolated specimens, but elongated siculae exist in a number of derived taxa (e.g., *Cystograptus*, some *Petalolithus*, the monograptid *Lagarograptus* OBUT & SOBOLEVSKAYA in OBUT, SOLBOLEVSKAYA, & MERKUREVA, 1968, and *Coronograptus*). A number of members of the genera *Prolasiograptus* and *Haddingograptus* may have a short virgella curved or bent across the sicular aperture, but the sicula is not curved noticeably in these cases.

The thecal style varies considerably in the early Neograptina (Fig. 247.8–247.10) from simple straight tubes to strongly geniculate ones. The geniculum may be provided with a genicular flange or can be rounded without elaborations. The supragenicular wall may be vertical, inward or outward sloping, or convexly curved. The thecal apertures also can vary in their orientation from introverted through horizontal to everted. In biostratigraphically earlier taxa, the thecal overlap is high, and the thecae have a double sigmoidal curvature and a conspicuous presence of intrathecal septa and folds (Fig. 247.8). Subsequently, thecal overlap is reduced, and thecae may be short and show little curvature. In these, the intrathecal septa are missing and intrathecal folding does not exist (Fig. 247.10).

STEM GROUP NEOGRAPTINA

Biserial tubaria with rounded to pointed proximal end; primordial astogeny of pattern A (see MITCHELL, 1987) or a derived pattern; first two thecae generally U-shaped, initially closely adpressed to the sicula, lacking apertural spines; thecae with straight to undulate or geniculate ventral thecal walls; median septum straight to strongly sigmoidal, sometimes angular; intrathecal folding in many taxa. *Middle Ordovician* (*Darriwilian, Corymbograptus retroflexus* Biozone)*–Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.

The taxa discussed herein as stem group Neograptina are not included in any family group taxon herein. They may be combined by considering 1) their rounded proximal ends without apertural spines on the first thecal pair and 2) their initially long and doubly sigmoid thecae. In these taxa, the geniculum is rounded to strongly angular and may possess considerable genicular flanges or other modifications. The ventral thecal walls are either outward inclined or parallel to the tubarium midline. The unusual genus *Gymnograptus* may be related to the group, as it shares the proximal end lacking apertural spines on the first thecal pair and the short wide thecae comparable to those of *Haddingograptus* species. The proximal development, however, is derived and similar to a pattern H astogeny with th1[1] growing downward and upward again on its own protheca. Thecae widen rapidly, the supragenicular walls are reduced, and intrathecal folds are lacking. The genus *Reteograptus* is herein included due to the lack of proximal end spines and the thecal style of the early *Reteograptus speciosus* Harris, 1924, in which the fusellum is completely preserved (see Maletz, 1997a, pl. 6,*7*).

Gymnograptus Bulman, 1953 (*ex* Tullberg, manuscript), p. 514 [**Diplograptus linnarssoni* Moberg, 1896, p. 17; OD] [?=*Diplograptus* (*Idiograptus*) Lapworth, 1880a, p. 169 (type, *I.* (*Diplograptus*) *aculeatus* Lapworth, 1880a, p. 170, OD, *nom. dub.,* Strachan, 1996, p. 10)]. Neograptines with attenuated fusellum and thickened thecal lists; proximal end of pattern G astogeny; single antivirgellar spine and virgella bending outward from sicular aperture; distinct geniculum with short supragenicular wall and variably developed extensions developed as paired or multiple spines; median septum complete. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, Sweden, Norway, Spain.——Fig. 248,*3a–d.* **G. linnarssoni* (Moberg); *3a*, syntype, Fågelsång, Scania, Sweden (Moberg, 1896, fig. b); *3b–3d,* isolated specimens in reverse (*d*) and obverse (*b*) views, distal fragment (*c*), glacial boulder, Poland (Urbanek, 1959, fig. 4, 5, and 9, respectively). Scale bars, 1 mm.

Ekstroemograptus Maletz & Ahlberg, 2021, p. 377 (**E. inexpectatus;* OD). Robust neograptine with long overlapping, double sigmoid thecae with outward-inclined ventral thecal walls; proximal development similar to pattern B astogeny with strongly upturned thecal apertures of th1[1] and th1[2]; proximal end rounded with the virgella as the only proximal end spine; unusual U-shaped th1[2] seen in obverse view, whereas downward-growth of th1[1] is covered. *Middle Ordovician* (*middle Darriwilian, Holmograptus lentus–lower Nicholsonograptus fasciculatus* Biozone): Sweden, Belgium.——Fig. 249. **E. inexpectatus,* Krapperup drill core, Scania, Sweden; *a,* holotype, obverse view, LO 11201T; *b,* juvenile, obverse view, PMU 37430/1; *c,* PMU 37430/2, reverse view; *d–e,* PMU 37431, relief specimen in obverse (*d*) and reverse (*e*) views. Scale bars, 1 mm.

Haddingograptus Maletz, 1997a, p. 63 [**Pseudoclimacograptus* (*Pseudoclimacograptus*) *oliveri* Bouček, 1973, p. 121; OD]. Neograptines with broadly rounded, normally somewhat asymmetrical proximal end of pattern C astogeny; median septum usually sharply zigzag shaped; intrathecal folding conspicuous; strong genicular flanges or collar structures commonly with distinct ventral genicular notch; thecal apertures slit-like, horizontal. *Middle Ordovician* (*Darriwilian, Nicholsonograptus fasciculatus* Biozone–*Jiangxigraptus vagus* Biozone): China, Sweden, Norway, Spain, Canada, USA, Argentina.——Fig. 248,*6a–b.* **H. oliveri* (Bouček); *6a,* paratype, NRM Cn 2541, reverse view; *6b,* holotype, NRM Cn 2539, obverse view; Elnes Formation Rigshospitalet, Oslo, Norway; scale bars, 1 mm (adapted from Bulman, 1953, fig.1).——Fig. 248,*6c. Haddingograptus tarimensis* Chen in Chen & others, 2017, obverse view, reconstruction based on PMO 138.400, scale bar, 1 mm (based on Maletz, 1997a, fig. 31g).——Fig. 248,*6d–e. H. eurystoma* (Jaanusson, 1960), NRM 2345, 2352 (Holm collection), juvenile specimens in reverse (*d*) and obverse (*e*) views; scale bars, 1 mm (Bulman, 1932a, pl. 1,*12* and 1,*14*, respectively).

Oelandograptus Mitchell, 1987, p. 383 [**Glyptograptus austrodentatus oelandicus* Bulman, 1963b, p. 682; M]. Neograptines with undulatory median septum; thecae weakly sigmoidal with long, outwardly inclined infragenicular wall, sharply rounded geniculum, short, nearly vertical supragenicular wall; thecal apertures slightly everted, undulatory with concave ventral margin; proximal development of pattern A astogeny with evenly rounded to somewhat blunt, nearly symmetrical proximal end. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone–*Nicholsonograptus fasciculatus* Biozone): Norway, Sweden.——Fig. 248,*1a–b.* **O. oelandicus* (Bulman), holotype, NRM Cn 307 (Holm collection) in obverse (*a*) and reverse (*b*) views, lower Darriwilian, ?*Holmograptus lentus* Biozone, glauconithältig grå Vaginatumkalk, Hälludden, Öland, Sweden, scale bars, 1 mm (Bulman, 1936a, pl. 3,*5–6*).

Proclimacograptus Maletz, 1997a, p. 68 [**P. bulmani;* OD]. Neograptines with slender tubarium; th1[1] and th1[2] strongly upturned with horizontal apertures; median septum straight to moderately undulate; thecae short with straight, horizontal apertures; proximal development of pattern B astogeny. *Middle Ordovician* (*Darriwilian, Nicholsonograptus*

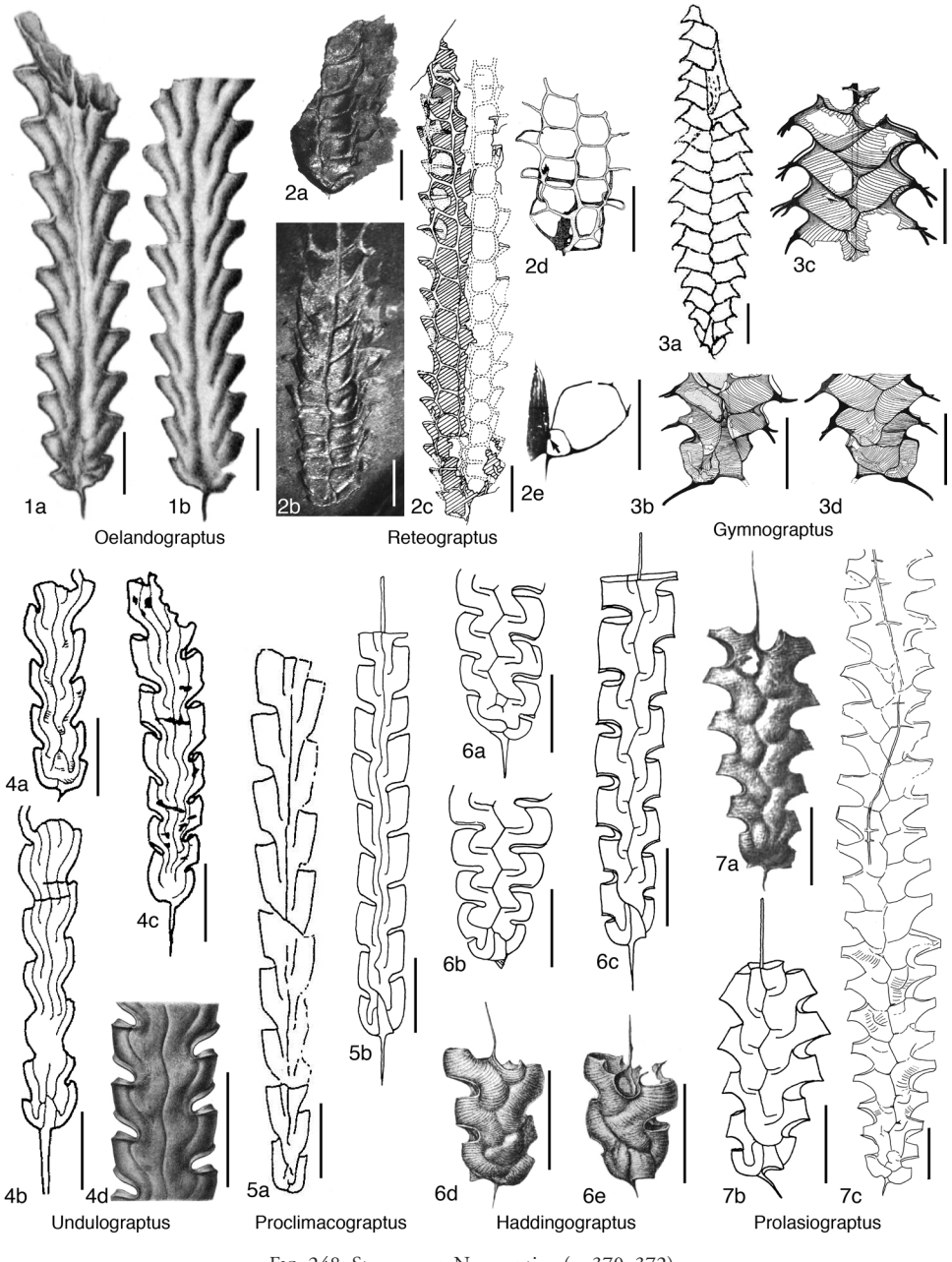


FIG. 248. Stem group Neograptina (p. 370–372).

fasciculatus Biozone–*Pterograptus elegans* Biozone): Czech Republic, Norway, Sweden, China.——FIG. 248,*5a. *P. bulmani,* holotype, PMO 138.711, reverse view, Almedalsveien, Slemmestad, Norway, scale bar, 1 mm (Maletz, 1997a, fig. 34C).——FIG. 248,*5b. P. angustatus* (EKSTRÖM, 1937), PMO 138.810, proximal end in obverse view, scale bar, 1 mm (Maletz, 1997a, fig. 33K).

Prolasiograptus LEE, 1963, p. 564 (p. 574, English text) [**Lasiograptus retusus* LAPWORTH, 1880a, p. 175; OD]. Neograptines with widely rounded proximal end, virgella as single proximal end spine; thecae with distinct geniculum, short, inward-inclined supragenicular walls; proximal development of pattern C astogeny. *Middle Ordovician* (*Darriwilian*, *Pseudamplexograptus distichus* Biozone):

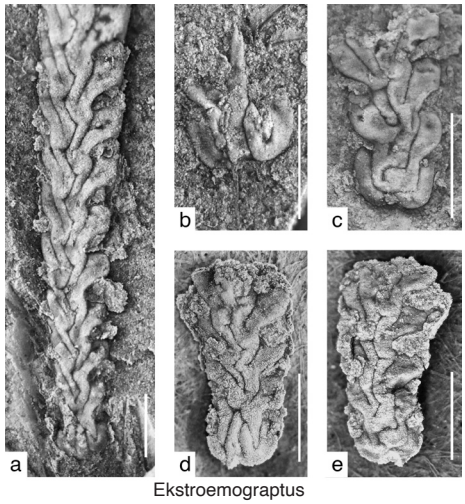


FIG. 249. Stem group Neograptina (p. 370).

Britain, Germany, Norway, Sweden, China.——FIG. 248,*7a–c. *P. retusus* (LAPWORTH); *7a,* NRM Cn 226 (Holm collection), Gärslösa, Öland, Sweden (illustrated as *Climacograptus scharenbergi* in Bulman, 1932a, pl. 1,*25–26*); *7b,* NRM 213 (Holm collection), Gärslösa, Öland, Sweden (Maletz, 1997a, fig. 29G); *7c,* holotype, BU 1349, Llandrindod Wells, Llandeilo, Wales, UK (new, drawing by C. E. Mitchell). Scale bars, 1 mm.

Reteograptus HALL, 1859b, p. 518 [**R. geinitzianus;* OD] [=*Retiograptus* HALL, 1865, p. 115 *nom. null.;* =*Clathrograptus* LAPWORTH, 1873b, table facing p. 555 (type, *C. cuneiformis,* OD), syn. by ELLES & WOOD, 1908, p. 315]. Proximally rounded, robust neograptines; fusellum strongly reduced, lacking in biostratigraphically younger taxa; preserved frequently as clathrial framework outlining tubarium; internal construction and proximal development unclear; sicula small, with complete prosicula, widening considerably toward aperture. *Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone)–*Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone): worldwide.——FIG. 248,*2a–b. R. speciosus* HARRIS, 1924, Darriwilian, Slemmestad, Oslo Region, Norway; *2a,* PMO 138.440, reverse view; *2b,* PMO 138.436, obverse view; scale bars, 1 mm (Maletz, 1997a, pl. 7l and pl. 6i, respectively).——FIG. 248,*2c–e. *R. geinitzianus; 2c,* lectotype, AMNH 37757, Austin Glen Graywacke (Normanskill Shale), Kenwood near Albany, New York, USA, scale bar, 1 mm; *2d,* OSU 32915, chemically isolated proximal end in reverse view, Pratt's Syncline, Athens Shale, Alabama, USA, scale bar, 1 mm; *2e,* OSU 32918, juvenile showing origin of th1[1] (*arrow*), Pratt's Syncline, Athens Shale, Alabama, USA, scale bar, 0.5 mm (*2c–e,* Finney, 1980, fig. 12c, 13f, and 14, respectively).

Undulograptus BOUČEK, 1973, p. 121 [**Pseudoclimacograptus formosus* MU & LEE, 1958, p. 406; OD; ?=*Climacograptus novaki* PERNER, 1895, pl. 7,*12a* (holotype, NM-L-7546, designated by BOUČEK, 1973, p. 114); ?=*Pseudoclimacograptus klabavensis* BOUČEK, 1973, p. 119, syn. by KRAFT & KRAFT, 2003, p. 136]. Neograptines with slender tubarium, with wide, rounded proximal end lacking spines except for commonly elongated virgella; geniculum rounded; proximal development of pattern C astogeny; median septum strongly undulate; thecae long, with double sigmoidal shape, without intrathecal folds, and with straight horizontal apertures. *Middle Ordovician* (*Darriwilian, Levisograptus dentatus* Biozone): Czech Republic, Sweden, Germany, Turkey, China.——FIG. 248,*4a–b. *U. formosus* (MU & LEE); *4a,* NIGP 9771b, specimen on slab with holotype, reverse view; *4b,* holotype, NIGP 9771, obverse view; scale bars, 1 mm (Mitchell, 1992, fig. 2c, 2e).——FIG. 248,*4c–d. U. camptochilus* (SKEVINGTON, 1965); *4c*, NRM Cn 59945, isolated specimen, scale bar, 1 mm (Mitchell, 1992, fig. 2a); *4d,* NRM Cn 59944, note unusual apertural flanges, scale bar, 1 mm (Bulman, 1936a, pl. 3,*30*).

Family NORMALOGRAPTIDAE Štorch & Serpagli, 1993

[Normalograptidae ŠTORCH & SERPAGLI, 1993, p. 14] [=superfamily Normalograptacea MITCHELL & others, 2007, p. 337] [=Metaclimacograptidae KOREN' & RICKARDS, 1996, p. 94]

Biserial tubaria with asymmetrical, usually narrow, rounded to pointed proximal end and short sicula; primordial astogeny of pattern H (see MITCHELL, 1987) or derived pattern; first two thecae closely adpressed to sicula, lacking spines; thecae with straight to undulate or geniculate ventral thecal walls; median septum straight to strongly sigmoidal, sometimes angular; median septum formed intermittently or lacking in some taxa. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone)–*Silurian* (*upper Telychian,* ?*Oktavites spiralis* Biozone): worldwide.

ŠTORCH and others (2011) discussed the family Normalograptidae as a paraphyletic taxon and extended it to include the basal Neograptina. The authors erroneously included all post-Hirnantian graptolites in the Normalograptidae in their cladistic diagram (ŠTORCH & others, 2011, fig. 6), even though they explicitly excluded them in the accompanying text. MELCHIN and others (2011, p. 293)

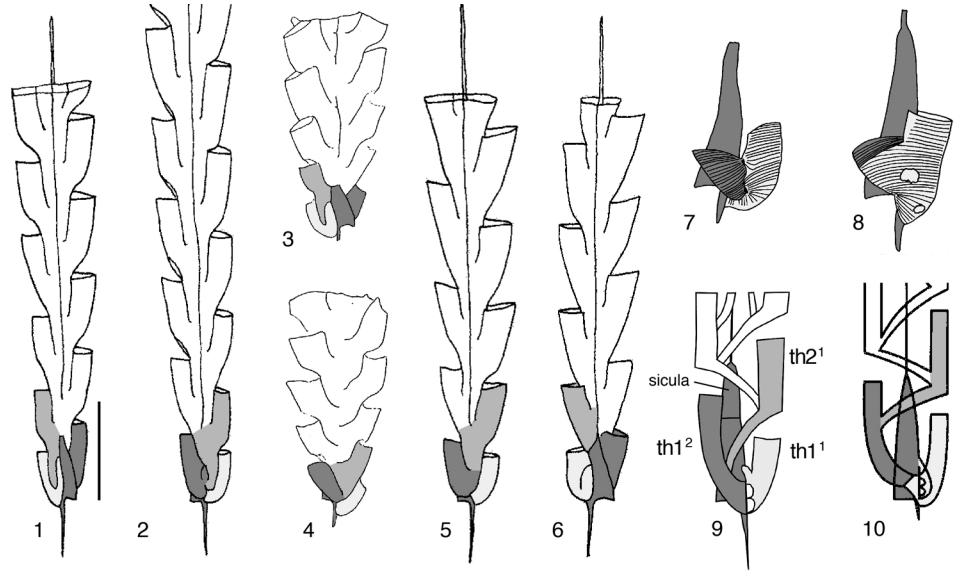


FIG. 250. Proximal development and colony shape of biserial Neograptina. *1–2, Proclimacograptus bulmani* MALETZ, 1997a in reverse (*2*) and obverse (*1*) views (new); *3–4, Skanegraptus janus* MALETZ, 2011b, in reverse (*4*) and obverse (*3*) views (adapted from Maletz, 2011b, fig. 2); *5–6, Pronormalograptus antiquus* (GE in GE, ZHENG, & LI, 1990) in reverse (*5*) and obverse (*6*) view (adapted from Maletz, 2011b, fig. 2); *7, Metaclimacograptus orientalis* (OBUT & SOBOLEVSKAYA, 1966), GSC 104912 (adapted from Melchin, 1998, fig. 4A); *8, Korenograptus nikolayevi* (OBUT, 1965), a neodiplograptid, GSC 104823, pattern H′ astogeny (adapted from Melchin, 1998, fig. 4B); *9*, diagram showing pattern H astogeny (adapted from Mitchell, 1987, fig. 1H); *10*, diagram showing pattern H′ astogeny (adapted from Melchin, 1998, fig. 2H). Sicula and thecae shading coded for easy comparison (*9*); scale bar, 1 mm (bar for *1* applies to *1–6*); *7–10* not to scale).

stated that "As a consequence of the variety of proximal and thecal morphologies found among taxa within this stem group, it is not currently possible to identify any morphologic criteria that can be used to uniquely characterize this taxon." The Normalograptidae represents a family with roots in the lower Darriwilian (Middle Ordovician). Both the precise origin of the Normalograptidae from a taxon of the early Neograptina *incertae sedis* and the relationship to the Climacograptidae are unclear (MALETZ, 2011b). The origin and subsequent differentiation of the Normalograptidae may need to be reevaluated, and it is herein preferred to base them on the origin of a pattern H astogeny instead of including 1) taxa with pattern A to pattern C astogenies and 2) lack of proximal spines except for the virgella (e.g., the taxa included in the stem group Neograptina). The first taxon with a proximal end pattern similar to proximal development type H is the genus *Skanegraptus,* but this taxon still has a number of characters similar to taxa with a pattern C astogeny (MALETZ, 2011b).

MORPHOLOGY

Normalograptidae contains a number of biserial, dipleural graptoloids with a rounded to pointed proximal end and a single proximal end spine, the virgella (Fig. 250.3–250.7). Their thecal style is simple—thecae with straight, outward-inclined to strongly geniculate ventral thecal walls. Geniculate thecae are prevalent and genicular elaborations are common. The thecal apertures are horizontal to everted and in geniculate taxa generally slit-like. A long nema is typical of many species and may be modified into an elongated nematularium.

MITCHELL (1987) introduced the proximal development pattern H based on the

investigation of *Normalograptus brevis* (Elles & Wood, 1906) and *Normalograptus kukersianus* (Wiman, 1895), a pattern that is considered characteristic of most Normalograptidae. In *Skanegraptus,* th1[1] grew downward along the ventral side of the sicula to a point below the sicular aperture and upward again in a U-shaped loop that left a space between the downward- and upward-growing parts on the obverse side (Fig. 250.3), in which the early part of th2[1] is visible. In derived taxa, the metathecal part of th1[1] grew attached to the dorsal side of its protheca (Fig. 250.6). There are two separate openings at the base of the downward growth of th1[1], one for the metatheca of th1[1] and the second for the origin of th1[2] (Fig. 250.9). An unconformity appears at the point of origin of th1[2] (Fig. 250.7) on the reverse side of the tubarium in pattern H species. In taxa of the derived pattern H′ in neodiplograptids, the unconformity was delayed (Fig. 250.8, Fig. 250.10), but otherwise the development was identical.

The thecae are fairly simple tubes in the Normalograptidae. The earliest known species, *Skanegraptus janus* Maletz, 2011b, has thecae with slightly convex ventral walls and moderate thecal overlap. The thecal apertures are straight and slightly everted. Most species, however, possess strongly geniculate thecae with a quite variable degree of genicular modification, mostly in the form of thickened genicular rims, but genicular flanges and even spines may exist. A considerable thickening may also be present around the thecal apertures, but other modifications have not been noted. Considerable genicular hoods developed in several *Metaclimacograptus* species. These were formed from the dorsal wall of the theca (not the ventral wall as stated by Loydell & Maletz, 2009, p. 279) before much of the succeeding theca was formed above it. These hoods display a distinct unconformity and, thus, may not be homologous to the genicular flanges in the diplograptids (e.g., *Archiclimacograptus*) and many neograptines in which the flanges or hoods are secondary constructions at the thecal geniculum.

The thecae (Fig. 250) have a short, straight, or slightly curved interthecal septum. An abrupt widening of the metatheca exists in many taxa at the aperture of the mother theca, after which the thecal tubes are nearly parallel sided (e.g., *Metaclimacograptus*). Apertural spines, except for the virgella, are extremely rare in the Normalograptidae, and chemically isolated material of such features does not exist. The genus *Hirsutograptus* bears multiple antivirgellar spines and paired genicular spines on the thecae. These spines may branch distally. Elongated basal spines appear in *Normalograptus trifilis* (Manck, 1923) and *Normalograptus longifilis* (Manck, 1924) and may be more common in the normalograptids.

The development of the median septum is quite variable in the Normalograptidae. The median septum appears to be lacking in part on the obverse side and is not developed on the reverse side in the only available relief specimen of *Skanegraptus janus* (Fig. 250.3–250.4). Early members of the Normalograptidae may bear a complete median septum on the obverse side, as in *Pronormalograptus antiquus* (Fig. 250.5–250.6). The median septum starts approximately at the base of th3[1] on the reverse side, and the first four thecae appear to be alternating in origin. In derived species, the median septum may be delayed considerably. The median septum is straight to considerably undulate, but intrathecal folding has not been recognized. It does not have the characteristic crossbars of the derived climacograptids (Goldman & others, 2011).

BIOGEOGRAPHY AND EXTINCTION

The Ordovician Normalograptidae are difficult to differentiate from the Climacograptidae. However, a number of constructional differences can be noted, and Goldman and others (2011) used these to recognize a distinct pattern of extinction and reinvasion of Upper Ordovician normalograptids in the palaeotropical regions (Fig. 251). The normalograptids apparently

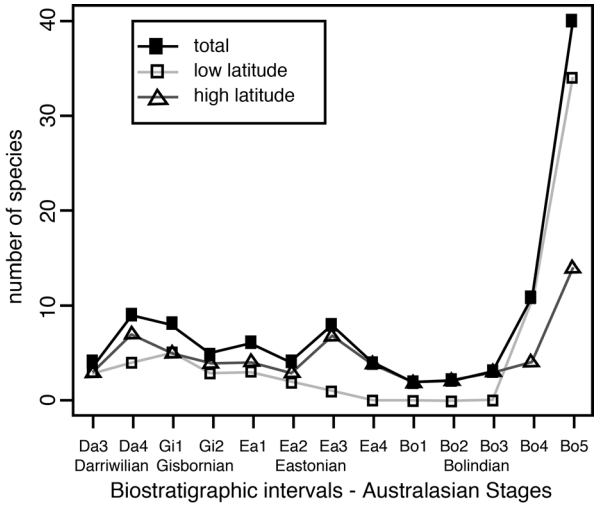


FIG. 251. Normalograptid diversity in the Upper Ordovician (redrawn from Goldman & others, 2011).

originated in high latitude regions during the early to middle Darriwilian and from there spread to the paleotropics. During the early Katian, the clade suddenly disappeared from low paleolatitudes, but reinvaded the regions during the late Katian to early Hirnantian.

The Normalograptidae formed one of the few axonophoran groups surviving the Hirnantian extinction and then quickly rediversified during the Llandovery. Actually, the Monograptoidea, Retiolitoidea, and Normalograptidae started to diversify during the Upper Ordovician (Katian to Hirnantian) time interval, while the Diplograptina went extinct at the end of the Hirnantian (BAPST & others, 2012). The Neograptina, especially the Monograptidae, apparently experienced one of the largest diversification events in graptolite history during the Llandovery, early Silurian (MELCHIN & others, 2011; SADLER, COOPER, & MELCHIN, 2011). However, a comparison of the diversity studies is difficult due to varying taxonomic concepts at the family level and higher taxonomical units in the analyses (see Retiolitoidea in BAPST & others, 2012; Retiolitidae and Petalolithidae in SADLER, COOPER, & MELCHIN, 2011). GOLDMAN and others (2011) indicated a total diversity of the Normalograptidae with 39 taxa in the Bo5 (upper Hirnantian, *Metabolograptus persculptus* Biozone), but BAPST and others (2012) indicated the presence of only five species in the interval. After the Hirnantian extinction event, the normalograptids rediversified and evolved during the Silurian to produce the Monograptidae as one of the most successful groups of planktic graptoloids. A number of diversity peaks and minor to major extinction events (e.g., ŠTORCH, 1995; SADLER, COOPER, & MELCHIN, 2011) also constituted the evolutionary pattern of the Silurian graptoloids and led to a bloom of the Normalograptidae, Petalolithinae, and Retiolitinae until the complete extinction of the biserial axonophorans in the late Silurian.

Normalograptus LEGRAND, 1987, p. 62 [**Climacograptus scalaris normalis* LAPWORTH, 1877, p. 138; OD] [=*Scalarigraptus* RIVA, 1988, p. 230 (type, *Climacograptus scalaris normalis* LAPWORTH, 1877, p. 138, OD), obj.]. Normalograptids with pattern H astogeny; unornamented geniculate thecae with straight or concave interthecal septa throughout tubarium; complete median septum, slightly undulate to straight, may be delayed; genicular hoods common. *Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone)–*Silurian, Llandovery (Telychian, Spirograptus turriculatus* Biozone): worldwide.——FIG. 252,*1a–b*. **N. normalis* (LAPWORTH); holotype, BU 1136, *Parakidograptus acuminatus* Biozone, Dob's Linn, Southern Uplands, Scotland, UK, scale bars, 1 mm (Blackett & Zalasiewicz, 2008, Atlas, Folio 2.61).

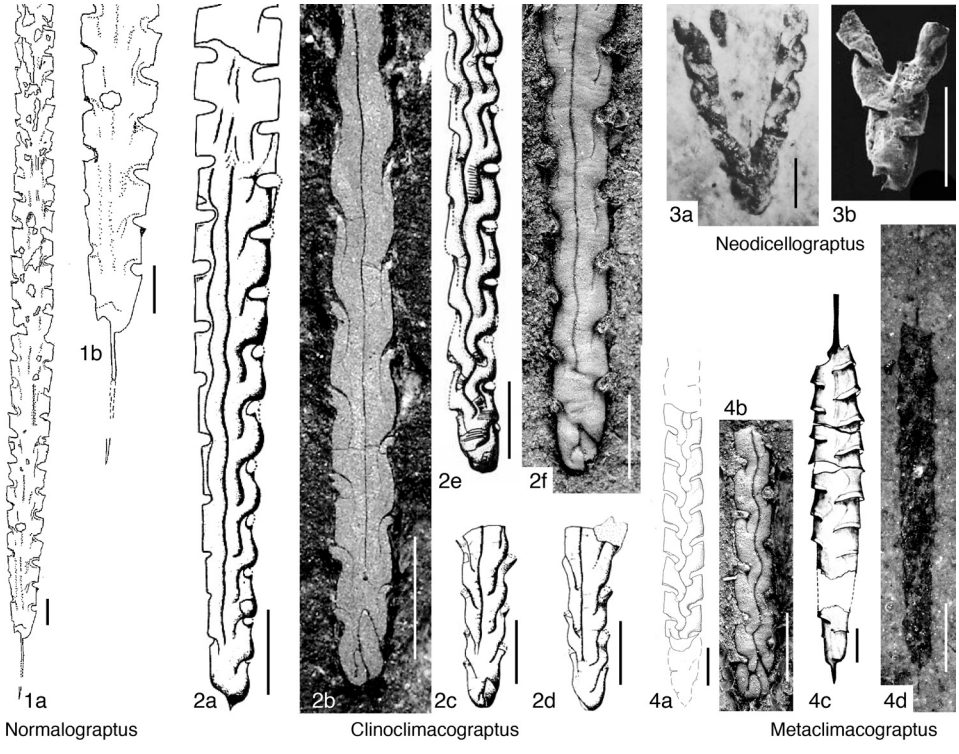


FIG. 252. Normalograptidae (p. 375–377).

Clinoclimacograptus BULMAN & RICKARDS, 1968, p. 8 [**Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus;* OD] [=*Pseudoglyptograptus* BULMAN & RICKARDS, 1968, p. 13 (type, *Pseudoglyptograptus vas* BULMAN & RICKARDS, 1968, p. 13, OD), syn. herein]. Normalograptid with proximally convex and distally concave supragenicular walls; thecal apertures strongly everted; median septum gently undulating proximally, distally straight; interthecal septae one-half the length of the supragenicular thecal walls proximally, ~two-thirds to three-fourths distally. [*Pseudoglyptograptus* is based on internal casts of *Clinoclimacograptus* as can be shown from the sectioned pyrite-filled material of TÖRNQUIST (see Fig. 252,*2b*)]. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Stimulograptus sedgwickii* Biozone): UK, Sweden, China.——FIG. 252,*2a–f*. **C. retroversus* (BULMAN & RICKARDS); *2a,* holotype, SM A52951, reverse view, ?*Stimulograptus sedgwickii* Biozone, Tomarp, Scania, Sweden (Bulman & Rickards, 1968, fig. 4b); *2b,* LO 1097t (identified as *Climacograptus scalaris* HISINGER, 1837 by TÖRNQUIST, 1893, pl. 1,*7–8*), Tomarp, Scania, Sweden (new); *2c–d,* GSM WEG 4058, holotype of *Pseudoglyptograptus vas* (BULMAN & RICKARDS) proximal end in obverse (*c*) and reverse (*d*) views, *Neodiplograptus magnus* Biozone, Cross Fell, northern England, UK (Bulman & Rickards, 1968, fig. 1K–L); *2e*, SM A23951, *Stimulograptus sedgwicki* Biozone, Spengill, Westmorland, UK (Bulman & Rickards, 1968, fig. 4a); *2f,* LO 11860t, obverse view, Röstånga drill core, 35.40–35.30 m, Scania, Sweden (Maletz, Ahlberg, & others, 2014, fig. 1K). Scale bars, 1 mm.

Hirsutograptus KOREN' & RICKARDS, 1996, p. 38 [**H. longispinosus;* OD]. Normalograptids with pattern H astogeny; geniculate thecae bearing laterally and ventrally directed genicular hoods, genicular spines, or both; full median septum. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus/Parakidograptus acuminatus* Biozone): Kazakhstan, Canada, China, UK (Scotland).——FIG. 253,*2a.* **H. longispinosus,* holotype, CNIGR 103/12879, Zhaksy-Kargala Valley, Kazakhstan, scale bar, 1 mm (Koren' & Rickards, 1996, fig. 8A).——FIG. 253,*2b–c*. *H. villosus* KOREN' & RICKARDS, 1996, Kos-Istek region, Kazakhstan; *2b,* juvenile, CNIGR 93A/12879 (Koren' & Rickards, 1996, fig. 7C); *2c,* holotype, CNIGR 90/12879, (Koren' & RICKARDS, 1996, fig. 8C). Scale bars, 1 mm.——FIG. 253,*2d*. *H. sinitzini* (KHALETZKAYA, 1960), Kurama Range, Uzbekistan, GSC 118401, scale bar, 1 mm (Koren' & Melchin, 2000, fig. 8,*16*).

Metaclimacograptus BULMAN & RICKARDS 1968, p. 3 [**Diplograpsus hughesi* NICHOLSON 1869, p. 235; OD] [=*Lithuanograptus* PAŠKEVIČIUS, 1976,

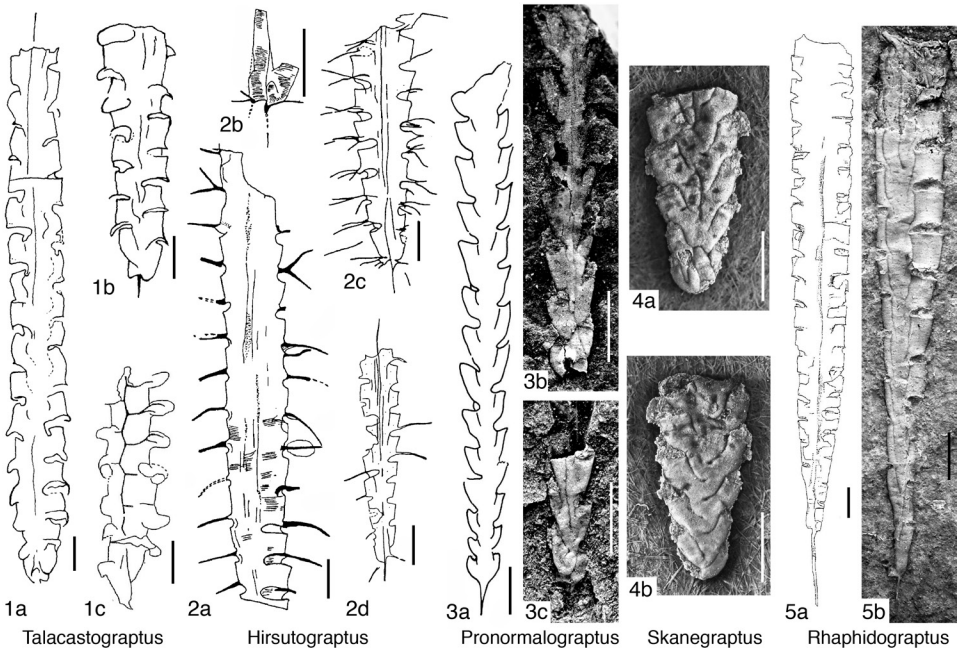


FIG. 253. Normalograptidae (p. 376–378).

p. 141 (type, *L. fusiformis* PAŠKEVIČIUS, 1976, p. 142, OD); syn. by LOYDELL, 1993, p. 55; =*Retioclimacis* Nanjing Institute of Geology and Palaeontology in MU & others, 1974, p. 215 (type, *R. typica,* OD, =*Metaclimacograptus undulatus* [KURCK, 1882]), *syn. by* LOYDELL, 1993, p. 55]. Normalograptid with pattern H astogeny and an undulose to zigzag median septum; convex or concavo-convex subapertural thecal walls and apertural introversion; very short thecal overlap; genicular thecal hoods formed from dorsal thecal wall, not as secondary genicular additions. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus* Biozone–*Telychian, Monoclimacis crenulata* Biozone): worldwide.——FIG. 252,*4a–b*. **M. hughesi* (NICHOLSON); *4a*, neotype (designated by PŘIBYL, 1948a, p. 18), NHMUK Q1360, ?*leptotheca* Biozone, Skelgill beds, Ambleside, England, UK (Zalasiewicz, 2000b, Atlas, Folio 1.42); *4b,* PMU 34438, obverse view, Röstånga drill core, 36.70–36.60 m, Scania, Sweden, scale bars, 1 mm (new).——FIG. 252,*4c*. *M. fusiformis* (PAŠKEVIČIUS, 1976), holotype, *Coronograptus cyphus* Biozone, Paroveja drill core, 721 m, Lithuania, scale bar, 1 mm (Paškevičius, 1979, pl. 2,*5*).——FIG. 252,*4d*. *M. undulatus* (KURCK, 1882), NIGP 45344, illustrated as *Retioclimacis typica* MU & LI, 1974 by NI (1978, pl. 2,*15*), scale bar, 1 mm (new).

Neodicellograptus MU & WANG, 1977, p. 313 [**N. dicranograptoides;* OD; ='*Dicellograptus*' *siluricus* MU & others, 1974, p. 211; syn. herein]. Normalograptid with pattern H astogeny; stipes diverging distally; thecae geniculate with introverted apertures; undulose dorsal stipe walls. *Silurian, Llandovery* (?*upper Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): China, Canada.——FIG. 252,*3a–b*. **N. siluricus* (MU & LI); *3a,* syntype, repository unknown, scale bar, 1 mm (Mu & others, 1974, pl. 99,*2;* photo provided by Xiao-feng Wang); *3b*, GSC 104837, Cape Manning section, Cornwallis Island, Arctic Canada, scale bar, 1 mm (Melchin, 1998, pl. 2,*12*).

Pronormalograptus CHEN in CHEN & others, 2017, p. 325 [**P. acicularis;* OD]. Normalograptids with pattern H proximal development; proximal end narrow, rounded, asymmetrical with short sicula; thecae with low angle of inclination to tubarium axis; thecae biform, commonly geniculate proximally, with curved to straight ventral thecal walls distally; medium septum complete or incomplete. *Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——FIG. 253,*3a*. **P. acicularis;* holotype, NIGP 157666, Dashimen section, Wuhai, Inner Mongolia, China, scale bar, 1 mm (Chen & others, 2017, fig. 6-102H).——FIG. 253,*3b–c*. *P. antiquus* GE in GE, ZHENG, & LI, 1990, *Pterograptus elegans* Biozone, Elnes Formation, Slemmestad, Norway; *3b,* PMO 234.255, obverse view; *3c,* PMO 234.061; scale bars, 1 mm (new).

Rhaphidograptus BULMAN, 1936b, p. 25 [**Climacograptus toernquisti* ELLES & WOOD, 1906, p.

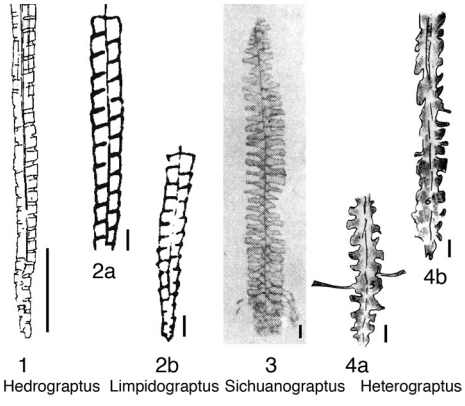


FIG. 254. Normalograptidae indet. (p. 378–379).

190; OD]. Normalograptids with pattern H astogeny modified by the presence of uniserial theca 1, produced by truncation of growth of th1[2]; thecae geniculate with genicular flanges, straight supragenicular walls; median septum complete on obverse side, considerably delayed on reverse side. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): UK, Czech Republic, Sweden, Germany, Poland, ?Canada.——FIG. 253,*5a–b*. **R. toernquisti* (ELLES & WOOD); *5a,* lectotype (designated by PŘIBYL, 1948a, p. 20), BU 1155, Birkhill Shale, Dob's Linn, Southern Uplands, Scotland, UK, scale bar, 1 mm (Zalasiewicz, 2008a, Atlas, Folio 2.91); *5b,* LO 1456t, latex cast in reverse view showing delay of median septum, specimen on slab with holotype of *Monograptus incommodus* TÖRNQUIST, 1899, scale bar, 1 mm (new).

Skanegraptus MALETZ, 2011b, p. 53 [* *S. janus;* OD]. Normalograptid with pointed, asymmetrical proximal end, lacking apertural spines on first thecal pair; proximal end with U-shaped th1[1]; paired early differentiation of th1[2] and th2[1] on reverse side; thecae with short overlap, straight outward-inclined apertures, lacking geniculum; median septum incomplete; thecal origins alternate. *Middle Ordovician, Darriwilian* (*Holmograptus lentus* Biozone): Sweden.——FIG. 253,*4a–b*. **S. janus,* holotype, LO 11196T, in obverse (*a*) and reverse (*b*) views, Krapperup drill core, Scania, Sweden, scale bars, 1 mm (Maletz, 2011b, fig. 1d and 1g).

Talacastograptus CUERDA, RICKARDS, & CINGOLANI, 1988, p. 753 [**T. leanzai;* OD] [=*Songxigraptus* FANG & others, 1990, p. 87 (English text, p. 135) (type, *S. elongatus*, OD); syn. herein]. Normalograptid with pronounced genicular hoods, which in profile views of tubarium, give thecae strongly hooked appearance, especially at proximal end; thecae strongly geniculate; ventral thecal margins introverted, strongly overgrown by genicular hoods; supragenicular wall convex; median septum complete, gently undulating to straight. *Lower Silurian* (*Llandovery, Rhuddanian, Atavograptus atavus* Biozone): Argentina, China.——FIG. 253,*1a–c*. **T. leanzai; 1a,* holotype, DPI 21883; *1b,* paratype, DPI 21884, proximal end in reverse view; both from La Chilca Formation, 16 km WNW of Talacasto station, San Juan Province, Argentina, scale bars, 1 mm (Cuerda, Rickards, & Cingolani, 1988, fig. 4a–b); *1c,* SM X. 28480, Lipéon Formation, Argentina, scale bar, 1 mm (Rickards & others, 2002, fig. 4e).

UNCERTAIN TAXA

A number of taxa listed here may be normalograptids, but are too poorly preserved or lack the proximal end for a more specific identification. They are listed and illustrated here in the interest of being complete, but these genera should not be considered available for further taxonomic purposes.

Hedrograptus OBUT, 1949, p. 13 [**H. janischewskyi;* OD]. *Silurian, Llandovery* (*Rhuddanian–?Aeronian*): Russia. [According to RIVA (1988, p. 225), "OBUT (1949) erected the genus *Hedrograptus* for early Silurian climacograptids with insignificant or incomplete apertural excavations on one side of the rhabdosome and complete on the other." RIVA (1988) provided a drawing of a latex cast of the type *H. janischewskyi*. According to this, the taxon does not bear any proximal spines except for the virgella and has a pointed proximal end, indicating a normalograptid relationship. The specimen is preserved in scalariform view and is indeterminate at the genus and species level.]——FIG. 254,*1*. **H. janischewskyi*, holotype, I.G.G.-COAH-SSSP No. 278/5, 1945, drawing from latex cast, scale bar, 10 mm (Riva, 1988, fig. 6).

Heterograptus HERNÁNDEZ SAMPELAYO, 1960, p. 33, *nom. dub.* [*type not designated]; *non Heterograptus* ZHAO & ZHANG in LIN, 1986, p. 241 (syn. of *Rhabdinopora*, Anisograptidae)]. *Silurian, Llandovery* (*Telychian*): Spain (Almadén). [Taxon is characterized by prolonged mesial spines and thecae, giving them an aspect of *Glossograptus;* possibly based on specimens of *Metaclimacograptus flamandi* (LEGRAND, 1993). Information provided by Juan Carlos Gutiérrez Marco.]——FIG. 254,*4a–b*. *Heterograptus* examples, scale bars 1 mm (Hernández Sampelayo, 1960, pl. 15,*5–6*).

Limpidograptus KHALETZKAYA, 1962, p. 72 [**L. posohovae;* OD]. *Silurian* (*Llandovery*): Uzbekistan (Tian-Shan). [This genus might be based on a scalariform biserial and is indeterminable at the genus and species level.]——FIG. 254,*2a–b*. **L. posohovae*, scale bars, 1 mm (Khaletzkaya, 1962, pl. 9,*11a–b*).

Sichuanograptus ZHAO in YE, 1978, p. 474 [**S. pennatus;* OD]. Axonophorans with biserial tubarium; proximally the periderm normal, but

thecae largely isolated, with common dissepiments, apertural spines, and floating vesicles, whereas distally the thecal walls are reduced and form clathria and reticula (diagnosis translated by Yuandong Zhang, 2017). *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone): China. [The taxon appears to be an indeterminable, strongly decayed or weathered normalograptid with thickened apertural rims.]——Fig. 254,*3*. **S. pennatus*, holotype, Qiaotang, Nanjiang, Sichuan Province, China, scale bar, 1 mm (Mu & others, 2002, p. 799, pl. 211,*3*).

SUPERFAMILY RETIOLITOIDEA

Jörg Maletz

Superfamily RETIOLITOIDEA Lapworth, 1873

[Retiolitoidea Lapworth, 1873b, table 1, facing p. 555, *nom. correct*. Kozłowska-Dawidziuk, Lenz, & Bates, 2003, p. 51, *ex* Retioloidea Lapworth, 1873b, table 1, facing p. 555] [=order Retiolitina Mikhaylova, 1970, p. 103, *partim*]

Neograptine axonophorans with scandent, biserial, dipleural, bistipular to unistipular tubarium; proximal development pattern supposedly of pattern H astogeny or a derived pattern, but development unknown in many taxa; thecae with straight to curved ventral walls; distinct geniculum present in some, with or without genicular additions; ancora, ancora umbrella, and ancora sleeve in derived Retiolitidae. *Upper Ordovician* (*Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.

Kozłowska-Dawidziuk, Lenz, and Bates (2003) regarded the presence of the ancora umbrella as the defining character for the Retiolitoidea and included the ancorate petalolithines in the clade. Melchin and others (2011) extended the concept of the Retiolitoidea by including the Neodiplograptidae (Fig. 255). No morphological diagnosis was provided for the taxon, but it was defined as "the most recent common ancestor of *Metabolograptus ojsuensis* and *Retiolites geinitzianus* and all of its descendants (Melchin & others, 2011, node 3, fig. 2–3)." The authors expanded the concept of the Retiolitoidea considerably from what was generally understood to be a retiolitid by adding a number of taxa that bear no indications of a true ancora. Melchin and others (2011, p. 296, node 3 in fig. 3) considered the presence of inclined, distal apertural thecal walls and inclined, interthecal septa as important synapomorphies of the Retiolitoidea, although there are no interthecal septa present in the derived retiolitines. The base of node 3 is collapsed into a polytomy in their figure 3, indicating the low bootstrap support of the nodes in this region of their cladogram (Melchin & others, 2011, fig. 2).

EVOLUTION

The Retiolitoidea originated in the Upper Ordovician through a normalograptid ancestor, but the precise biostratigraphic timing of the origin of the clade is uncertain (see Melchin & others, 2011, fig. 7). The oldest members of the Retiolitoidea appear to be *Neodiplograptus charis* (Mu & Ni, 1983) and *Metabolograptus ojsuensis* (Koren' & Mikhaylova in Koren', Mikhaylova, & Tzai, 1980) from the late Katian (Melchin & others, 2011).

The Retiolitoidea includes a basal paraphyletic family Neodiplograptidae with a number of very similar genera having an initial low disparity and low diversity in the uppermost Ordovician to lowermost Silurian. In the Llandovery, however, the diversification increased considerably with the evolution of the ancora sleeve and the following radiation of the Retiolitidae (see Lenz & others, 2018).

Family NEODIPLOGRAPTIDAE Melchin & others, 2011

[Neodiplograptidae Melchin, Mitchell, Naczk-Cameron, Fan, & Loxton, 2011, p. 296] [incl. Cameragraptidae Hundt, 1953b, p. 3, *nom. dub.*]

Biserial, dipleural neograptines with pattern H proximal development type or derived one; first thecal pair with outward-inclined apertures forming lip in derived taxa; thecae in many taxa having considerable biform development; ventral side of thecae rounded to geniculate, distally straight with outward-inclined straight apertures; medium septum complete, partial or lacking; interthecal septae outward inclined. *Upper Ordovician* (*upper Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Llandovery* (*Telychian, Monoclimacis griestoniensis* Biozone): worldwide.

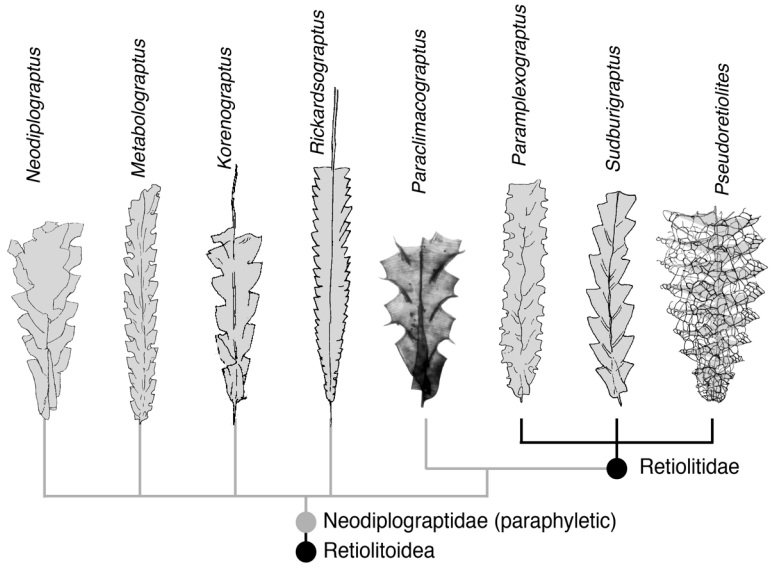


FIG. 255. Cladogram explaining the concept of the Retiolitoidea and the paraphyletic Neodiplograptidae; specimens from various sources, not to scale (new; based on data in MELCHIN & others, 2011).

MELCHIN and others (2011, p. 296) analyzed the early Silurian biserial axonophorans and erected the family Neodiplograptidae as "the partial clade that includes the most recent common ancestor of *Metabolograptus ojsuensis* and *Retiolites geinitzianus,*" and referred quite a number of taxa to the Retiolitoidea. MALETZ (2014b), however, identified only taxa with an ancora sleeve meshwork as the Retiolitoidea and preferred to include the non-ancorate Petalolithinae in the Neodiplograptidae.

The Neodiplograptidae, as defined by MELCHIN and others (2011), represents a poorly resolved clade with a basal polytomy (Fig. 255), indicating the difficulty of differentiating the individual taxa based on the largely flattened material available for investigation. As a paraphyletic taxon, the Neodiplograptidae led to the monophyletic Retiolitidae through a number of steps in the development of the ancora umbrella and ancora sleeve as an external, secondary development around the biserial tubarium. MELCHIN and others (2011) separated the retiolitid *Paramplexograptus* MELCHIN & others, 2011 from the neodiplograptid *Paraclimacograptus* through the lack of a median septum in *Paramplexograptus*. Otherwise the two genera are basically inseparable (Fig. 255).

MORPHOLOGY

The proximal development (Fig. 256) of the Neodiplograptidae ranges from a pattern H astogeny to a pattern H′ astogeny. The details of the proximal development of many of the taxa included in the analysis of MELCHIN and others (2011, Appendix 1) were listed as based on unpublished information. Thus, the proximal development types have to be regarded as uncertain until further material is published. The proximal development of *Neodiplograptus* and *Metabolograptus* has not been demonstrated from chemically isolated material or relief specimens showing growth lines. The proximal development of *Rickardsograptus tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967) is known from isolated material (MELCHIN 1998; MELCHIN & others, 2011). The species has a distal origin of $th1^2$ from a wide flange of $th1^1$ (Fig. 256.1–256.2), indicating a pattern H′ astogeny. A pattern H′ astogeny (Fig. 256.6) is also present in *Korenograptus*

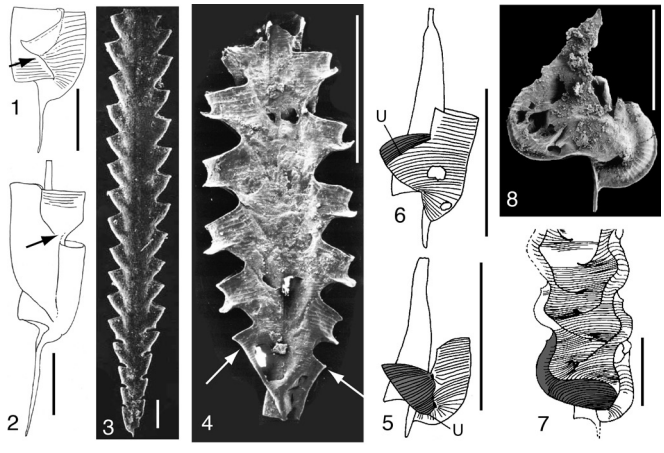


FIG. 256. Morphology and proximal development of the Neodiplograptidae. *1–3, Rickardsograptus tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967); *1,* juvenile showing late origin of th1[2] from large flange (new); *2,* origin of th2[1] from distal part of th1[2] (new); *3,* SEM photo of large specimen in relief showing geniculate proximal thecae and non-geniculate distal thecae (Melchin & others, 2011, fig. 4G); *4, Paraclimacograptus innotatus* (NICHOLSON, 1869), showing outward-inclined apertures with lip (*arrows*) on proximal end and geniculate thecae with strong genicular flanges (Koren' & Rickards, 2004, fig. 29); *5,* pattern H astogeny in the normalograptid *Metaclimacograptus orientalis* (OBUT & SOBOLEVSKAYA, 1966) showing unconformity (*u*) at origin of th1[2] tube; *6,* pattern H′ astogeny in *Korenograptus nikolayevi* (OBUT, 1965) with delayed unconformity (*5-6,* adapted from Melchin, 1998, fig. 4a–b) *7, Cystograptus penna* (HOPKINSON, 1869), reverse view (adapted from Jones & Rickards, 1967, fig. 2D); *8, Cystograptus vesiculosus* (NICHOLSON, 1868c), juvenile, obverse view (Koren' & Rickards, 2004, fig. 12). Scale bars, 1 mm.

nikolayevi (OBUT, 1965) as demonstrated by MELCHIN (1998, pl. 1,*4–9*) and LOYDELL and MALETZ (2009). The genus *Cystograptus,* with its extremely elongated sicula and long undulating thecae, is included preliminarily in the Neodiplograptidae following ŠTORCH (1985) and MELCHIN and others (2011, p. 296), who suggested a derivation from a species of *Neodiplograptus* or *Metabolograptus*. JONES and RICKARDS (1967) illustrated a possible pattern H astogeny for *Cystograptus penna* (HOPKINSON, 1869), which can also be supported by a single specimen of *Cystograptus vesiculosus* (NICHOLSON, 1868c) illustrated by KOREN' and RICKARDS (2004). In both taxa, the origin of th1[2] appears to be very low on the th1[1] at the point of change from downward to upward growth (Figs. 256.7–256.8) and not from an upward-growing flange on th1[1]. Details of the number and position of proximal foramina are not available.

The thecal style of the Neodiplograptidae ranges from simple outward-inclined thecae with straight ventral wall and aperture to strongly geniculate thecae with ventral thecal walls parallel to the tubarium midline. Many taxa are biform with the thecal style changing considerably from the proximal to the distal end. A number of geniculate proximal thecae are present in *Rickardsograptus* but the colony quite abruptly changes to nongeniculate thecae distally (Fig. 256.3). In other genera, the change in thecal style is more gradual and imperceptible and is difficult to see in poorly preserved, flattened specimens. MELCHIN and others (2011, p. 296) indicated that the most characteristic synapomorphies of their Neodiplograptidae include the presence of inclined distal thecal subapertural walls and inclined interthecal septa. Genicular elaborations largely include flanges (Fig. 256.4), but these may appear similar to spines in the typical lateral preservation of the tubaria.

Neodiplograptus LEGRAND, 1987, p. 62 [**Diplograptus magnus* LAPWORTH, 1900, p. 132; OD]. Neodiplograptids with pattern H proximal development type with rapidly widening proximal end; thecae sharply geniculate proximally and with slightly rounded, non-geniculate ventral side in distal

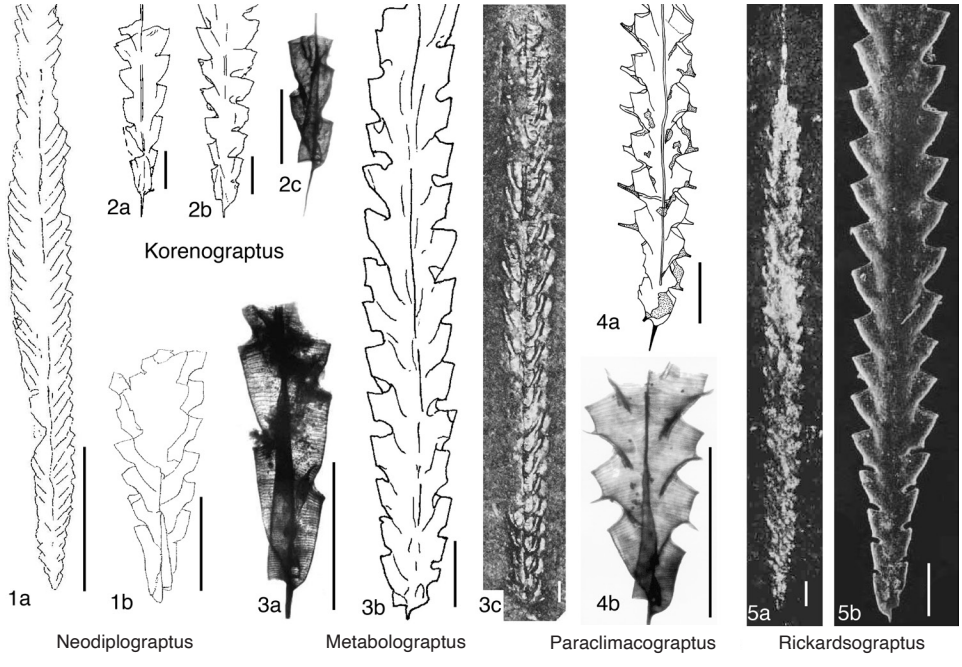


FIG. 257. Neodiplograptidae (p. 383–385).

thecae; thecal inclination increasing significantly through the proximal to mesial regions; full median septum distally. *Upper Ordovician* (*upper Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Llandovery* (*Aeronian, Neodiplograptus magnus* Biozone): worldwide.——FIG. 257,*1a–b*. **N. magnus* (LAPWORTH), River Wye, Rhayader, Wales, UK; *1a,* lectotype, BU 1295, poor external mold, scale bar 10 mm; *1b,* topotype, BU 1296, obverse view, scale bar, 1 mm (Zalasiewicz, 2000c, Atlas, Folio 1.68).

Korenograptus MELCHIN & others, 2011, p. 297 [**Glyptograptus gnomus* CHURKIN & CARTER, 1970, p. 24; OD]. Neodiplograptids with a pattern H proximal development type or derived type; colony parallel sided or widening slowly from the proximal end; thecae with slightly rounded to straight, nongeniculate ventral side; full median septum distally. *Upper Ordovician* (?*upper Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Llandovery* (*Rhuddanian, Neodiplograptus magnus* Biozone): worldwide.——FIG. 257, *2a–b*. **K. gnomus (*CHURKIN & CARTER), Alaska, USA; *2a,* USNM 161727; *2b,* holotype, USNM 161644; scale bars, 1 mm (Churkin & Carter, 1970, fig. 11f and 11e, respectively).——FIG. 257,*2c*. *K. magnus* (CHURKIN & CARTER, 1970), GSC 135126, Cape Manning, Nunavut, Canada, scale bar, 1 mm (Melchin & others, 2011, fig. 5i).

Metabolograptus OBUT & SENNIKOV, 1985, p. 55 [**Diplograptus modestus siberica* OBUT, 1955, p. 138; OD] [=*Persculptograptus* KOREN' & RICKARDS, 1996, p. 32 (type, *Diplograpsus persculptus* SALTER, 1873, p. 28, OD); syn. by MELCHIN & others, 2011, p. 296]. Neodiplograptids with pattern H proximal development type; colony parallel sided or widening gradually from proximal end; thecae with sharp to bluntly rounded genicula; full median septum, gently sinuous proximally; sinuous interthecal septa; subapertural walls parallel to moderately inclined. *Upper Ordovician* (?*upper Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Llandovery (Rhuddanian, Huttagraptus acinaces* Biozone): worldwide.——FIG. 257,*3a*. Possibly *Metabolograptus praecursor* (KOREN' & RICKARDS, 2004), GSC 135121, topotype (species unrecognizable, as based on distal fragments), scale bar, 1 mm (Melchin & others, 2011, fig. 5a).——FIG. 257,*3b*. **M. sibericus* (OBUT), holotype, CSGM211/6a, scale bar, 1 mm (Melchin & others, 2011, fig. 6a).——FIG. 257,*3c*. *M. persculptus* (ELLES & WOOD, 1907), lectotype, GSM 11782, scale bar, 1 mm (Williams, 1983, pl. 66,*3*).

Paraclimacograptus PŘIBYL, 1947, p. 4 [**Climacograpsus innotatus* NICHOLSON, 1869, p. 238; OD]. Neodiplograptids with a pattern H′ proximal development type; colony parallel sided or widening slowly from the proximal end; thecae with sharp to bluntly rounded genicula; genicula with ventrally projecting hood; thecae with wide apertural excavations, everted apertures, and slightly to moderately inclined supragenicular walls; median septum partial in proximal end, complete distally. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus*

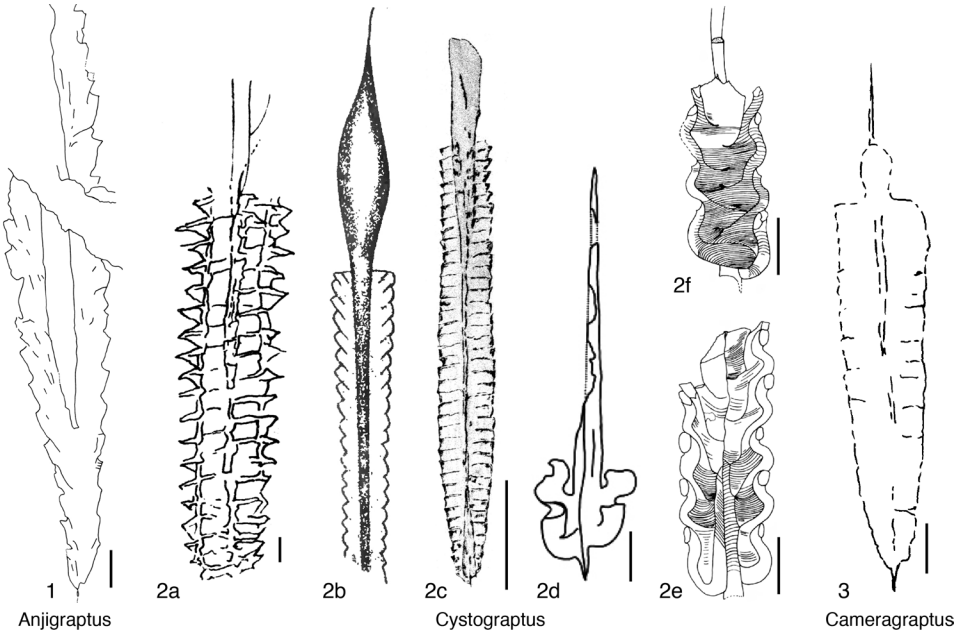


FIG. 258. Neodiplograptidae, uncertain status (p. 386).

Biozone)–*Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone): worldwide.——FIG. 257,*4a–b*. **P. innotatus* (NICHOLSON); *4a,* SM A20222, Dob's Linn, Scotland, topotype, 'typical specimen' of ELLES & WOOD (1906, pl. 27,*10a*) (Riva, 1988, fig. 5L); *4b,* GSC 104929, isolated specimen, Sakmara Formation, southern Urals, Russia (Russel, Melchin, & Koren' 2000, fig. 1,*9*). Scale bars, 1 mm.

Rickardsograptus MELCHIN & others, 2011, p. 297 [**Diplograptus* (?) *tcherskyi* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967, p. 59; OD]. Neodiplograptids with a pattern H′proximal development, or possibly pattern H astogeny in earlier taxa; thecae have pronounced widening mesially, which corresponds to change to more inclined and more gently sigmoidal to straight thecae. *Silurian, Llandovery* (*Rhuddanian, Atavograptus atavus* Biozone–*Neodiplograptus magnus* Biozone): worldwide.——FIG. 257,*5a–b*. **R. tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV); *5a,* holotype, flattened specimen, (Obut, Sobolevskaya, & Nikolaev, 1967, pl. 3,*1*); *5b,* isolated specimen in obverse view, GSC 135120, Arctic Canada (Melchin & others, 2011, fig. 4g). Scale bars, 1 mm.

UNCERTAIN STATUS

Genera listed here are either difficult to interpret and uncertain as to whether they belong to the family Neodiplograptidae, or poorly characterized and unrecognizable as valid. The genus *Cystograptus* has been considered to be related to *Neodiplograptus* (see ŠTORCH, 1985; MELCHIN & others, 2011); but because it possesses features not known from any other genus of the Neodiplograptidae, it cannot be reliably included here. The genus has an elongated sicula unlike any other neodiplograptid. The U-shaped initial thecae of the colony and the long sigmoidally curved thecae are reminiscent of an *Undulograptus* BOUČEK, 1973 species from the Middle Ordovician. A closer relationship, however, is unlikely. The proximal development type of *Cystograptus* appears to be a pattern H astogeny with a delayed dicalycal theca, indicated by the distal origin of the median septum. *Cystograptus* bears a conspicuously extended three-vaned nematularium that is overgrown by the advancing stipes in mature specimens (URBANEK, KOREN', & MIERZEJEWSKI, 1982).

Cameragraptus HUNDT, 1953b has been erected validly but is based on unrecognizable scalariform biserials. HUNDT (1953b) included a number of species in this genus, all based on the form of the nematularium.

Schauer (1971, p. 35) indicated that most specimens identified as *Cameragraptus* by Hundt (1953b) may belong to *Neodiplograptus thuringiacus* (Kirste, 1919), but this cannot be verified.

Anjigraptus Muir, Zhang, Botting, & Ma, 2021, p. 396 [**Anjigraptus wangi;* OD] Proximally biserial neodiplograptid with two uniserial stipes distally; proximal development probably of pattern H astogeny; proximal thecae geniculate, distally with straight, outwards inclined ventral sides, lacking a geniculum; apertures slightly extroverted. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): South China (Zhejiang Province).——Fig. 258,*1*. **A. wangi,* holotype, scale bar, 1 mm (Muir & others, 2021, fig. 2B).

Cystograptus Hundt, 1942, p. 205 [**C. speciosus;* SD Jones & Rickards, 1967, p. 181–182; =*Diplograpsus vesiculosus* Nicholson, 1868c, p. 61, syn. by Jones & Rickards, 1967, p. 181]. Neodiplograptids with elongated sicula and long, doubly sigmoid thecae; proximal development of modified pattern H astogeny; median septum straight to slightly undulate, delayed; robust three-vaned nematularium proximally overgrown in mature colonies. *Silurian, Llandovery* (*Rhuddanian, Parakidograptus acuminatus Biozone–Aeronian, Coronograptus cyphus* Biozone): Britain, Czech Republic, Denmark, Germany, Sweden, Kazakhstan, Canada, USA.——Fig. 258,*2a–d*. **C. vesiculosus* (Nicholson)*; 2a,* holotype of *C. speciosus,* repository unknown, scale bar, 1 mm (Münch, 1952, pl. 10,*8*); *2b,* holotype, original illustration, possibly NHMUK PM P.1880 (see Benton, 1979; Strachan, 1997), magnification unknown (Nicholson, 1868c, pl. 3,*11*); *2c,* BU 1231, typical specimen with nematularium, Dob's Linn, Scotland, UK, scale bar, 10 mm (Elles & Wood, 1907, pl. 28,8c); *2d,* juvenile showing long sicula, scale bar, 1 mm (Štorch, 2015, fig. 4g).——Fig. 258,*2e–f*. *C. penna* (Hopkinson, 1869), *Lagarograptus acinaces* Biozone, Rheidol Gorge, UK; *2e,* SM A57550, proximal end, reverse view; *2f,* SM A23952, proximal end, obverse view; scale bars, 1 mm (Jones & Rickards, 1967, fig. 1–2).

Cameragraptus Hundt, 1953b, p. 3 (no pagination in paper) [**C. cuneatus,* Hundt, 1953b, p. 4, fig. 7 (not fig. 4 as stated in the text); SD herein]. [Figure is a scalariform view of a biserial.] *Silurian, Llandovery* (*Rhuddanian–Aeronian*): Germany.——Fig. 258,*3*. *C. cuneatus,* holotype, BAF 186/4211, scale bar, 1 mm (Blumenstengel & others, 2006, pl. 1,*1B*).

FAMILY RETIOLITIDAE

Alfred C. Lenz, Denis E. B. Bates, Anna Kozłowska, and Jörg Maletz

Family RETIOLITIDAE Lapworth, 1873

[Retiolitidae Lapworth, 1873b, table 1, facing p. 555]

Axonophorans (Neograptina) with scandent, biserial, dipleural, bistipular to unistipular tubarium; mostly pattern I astogeny or derived pattern, but development unknown in most taxa with poorly preserved fusellum; ancora umbrella and ancora sleeve weakly developed in derived petalolithines, well developed in all retiolitines; sicula and fusellum fully preserved in petalolithines, rarely in retiolitines. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian, Ludlow* (*lower Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.

Melchin and others (2011) revised the family Retiolitidae based on a cladistic analysis and extended the concept considerably to include a number of non-ancorate taxa previously not referred to the Retiolitidae, although Melchin (1998) already combined the ancorate and non-ancorate taxa. They defined the Retiolitidae as "the first species that acquired a unistipular (aseptate) biserial rhabdosome in the clade that contains *Paramplexograptus madernii* and *Retiolites geinitzianus* and all its descendants" (Melchin & others, 2011, p. 298 node 4, fig. 2–3). Melchin, Lenz, and Kozłowska (2017) followed this usage, even though Maletz (2014b) preferred a more restricted definition of the superfamily Retiolitoidea and the family Retiolitidae. He differentiated the family Retiolitidae into two subfamilies, the paraphyletic Petalolithinae and the derived, monophyletic Retiolitinae, based on the presence or absense of the fusellum of the thecate part of the tubarium, respectively.

Even though the absence of the fusellum has to be regarded as a preservational aspect, it most easily separates the two groups in the fossil record. The recognition of tubarium characters, especially in the Retiolitinae, is based on chemically isolated material, which may differ considerably in preservation from shale specimens (Fig. 259.3–259.4). Specimens of *Pseudoretiolites perlatus* (Nicholson, 1868a) sometimes show the preservation of the fusellum in shale material (e.g., Elles & Wood, 1908; Bouček & Münch, 1944; Obut, Sobolevskaya, & Merkureva, 1968). By comparison, the chemically isolated material provides a full three-dimensional view of the lists, whereas fusellar structures are recognized only in a relatively few taxa (Bates & Kirk, 1992, 1997; Lenz, 1994a, Lenz & Kozłowska-Dawidziuk, 2002b; Kozłowska-Dawidziuk, 1997, Kozłowska, Dobrowolska, & Bates, 2013). Bouček and Münch (1944) commented on the preservation of an outer (ancora sleeve) membrane covering the list structure in *Retiolites*. Holm (1890, pl. 2,*5*) described and illustrated the preservation of thecae inside the lists of the ancora sleeve in this genus.

MORPHOLOGY

The Ancora

The ancora is a branched virgellar spine that bears four lateral branches, from which an ancora umbrella and the ancora sleeve may develop (Fig. 260.2–260.4). Early growth stages can be readily recognized by the initially four-pronged construction of the ancora. Bates and Kirk (1992) described the ancora umbrella for three species of *Pseudorthograptus* and *Petalolithus* and compared the construction with that of the derived retiolitines. The ancora and ancora umbrella form a generally saucer- or umbrella-shaped construction below the aperture of the sicula (Fig. 260.4–260.6), with the addition of spiral or polygonal cortical lists (Bates & Kirk, 1992, 1997). In addition, the ancora sleeve may form, originating from the upward-growing ancora umbrella lists and connecting with the lateral

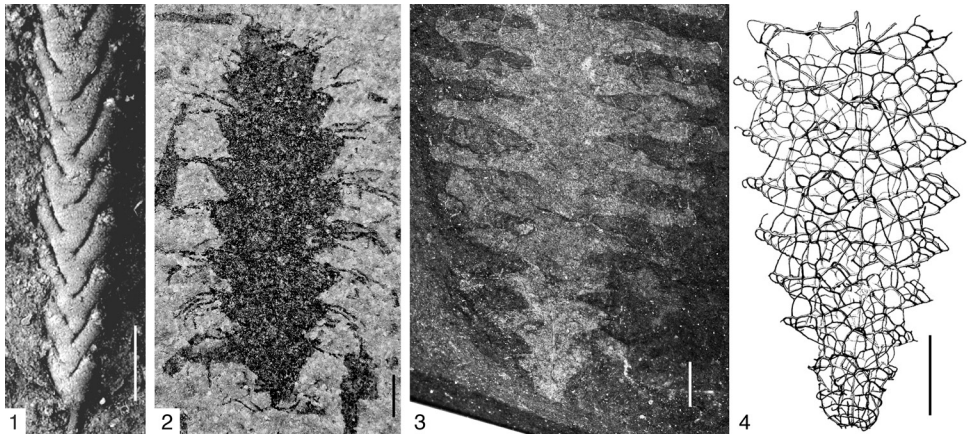


FIG. 259. *1, Rivagraptus bellulus* (TÖRNQUIST, 1890), PMU 31873, proximal end in reverse view and full relief, showing preserved thecae, Tomarp, Scania, Sweden (new); *2, Spinadiplograptus inopinatus* (BOUČEK, 1944), PŠ 3632b, flattened specimen showing fusellum of the thecae, ancora umbrella, and thecal spines, *Demirastrites triangulatus* Biozone, Czech Republic (Štorch, 2015, fig. 9A); *3–4, Pseudoretiolites perlatus* (NICHOLSON, 1868a); *3,* NIGP 168459, flattened specimen in shale showing fusellum and ancora sleeve mesh, Yesanguan, Badong County, Hubei, China (new; specimen provided by Wang Chuanshang, Wuhan, China); *4,* GSC 137613, chemically isolated specimen in three dimensions showing ancora sleeve meshes, Llandovery, upper Aeronian, *Lituigraptus convolutus* Biozone, Arctic Canada (inverted SEM photo, Melchin, Lenz, & Kozłowska, 2017, fig. 3,*1*). Scale bars, 1 mm.

thecal walls at the lateral apertural lists. In *Pseudorthograptus* (Fig. 260.8) and *Spinadiplograptus,* in addition to the ancora umbrella, lateral thecal apertural spines may be formed, but there is no evidence of a fully developed ancora sleeve. Extremely long spines connect to a possible ancora sleeve in *Victorograptus,* but the poor preservation prevents recognition of such details.

The construction is clear in derived retiolitids, the Retiolitinae: The ancora sleeve attaches to the thecal framework mainly to the lateral apertural lists (see BATES, KOZŁOWSKA, & LENZ, 2005) and apertural spines are present in *Pseudoplegmatograptus* and *Giganteograptus*. The ancora sleeve forms the secondary, lateral tubarium walls in the Retiolitinae (Fig. 260.9), although the lateral thecal walls of the tubarium are seldom preserved. The reason for the evolution of the ancora is unclear, although a number of other taxa, considered to be unrelated to the Retiolitidae, independently developed a branched virgella (e.g., *Akidograptus* DAVIES, 1929; *Parakidograptus* LI & GE, 1981).

Fusellum Reduction

The Petalolithinae bear complete thecal walls made of fusellar tissue (Fig. 260.4–260.8). The thecal walls appear to have become reduced in thickness during the evolution of the Retiolitidae and are rarely preserved in the Retiolitinae, although shards and seams in the clathrium and reticulum are interpreted as remains of fusellar walls. A few Retiolitinae specimens have preserved thecal walls and ancora sleeve walls, e.g., *Pseudoretiolites, Spinograptus praerobustus* (LENZ & KOZŁOWSKA-DAWIDZIUK, 2002a), but in general, the walls are not preserved. In early Retiolitinae, the prosicula is routinely fully preserved, whereas the metasicula may be fully to partially preserved or absent. In younger taxa, the prosicula may or may not be present, and a construction of clathrial and reticular lists is all that remains of the tubarium. A thickened apertural list is common in *Pseudorthograptus* specimens in which the thecal walls are complete, whereas further tubarial lists, including a mid-ventral list on the thecae, appear in *Hercograptus,* in addition to the ancora sleeve lists (ŠTORCH, 2015).

Thecal Framework and Ancora Sleeve

The thecal framework consists of lists of nema, virga, virgella, transverse lists, lateral apertural lists, thecal lips, connecting lists,

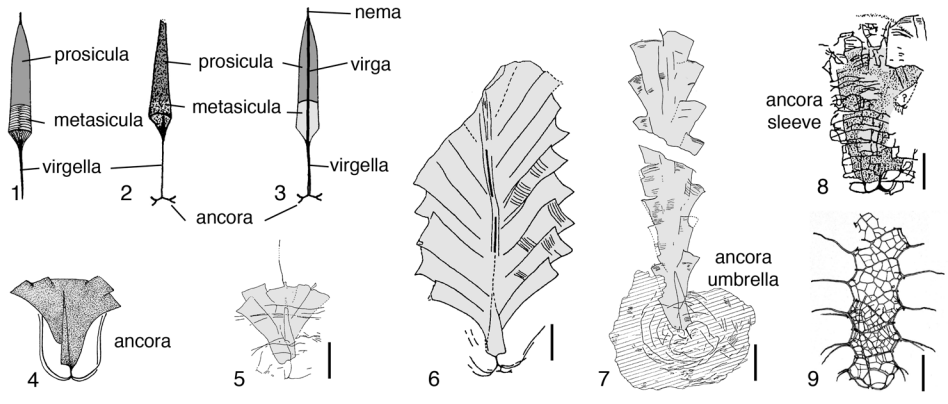


FIG. 260. The ancora and ancora sleeve. *1,* Axonophoran sicula with ventral virgella (Bulman, 1970, fig. 48); *2,* retiolitid sicula with ancora on ventral virgella (Bates & Kirk, 1986, fig. 28); *3,* retiolitine sicula from virgellar side showing virga as connection between virgella and nema (new); *4, Petalolithus* SUESS, 1851 sp., juvenile showing ancora with long extensions (Bates & Kirk, 1986, fig. 28); *5, Petalolithus ovatoelongatus* (KURCK, 1882) with possible ancora sleeve development (Koren' & Rickards, 1996, fig. 11D); *6, Petalolithus ovatoelongatus* (KURCK, 1882) showing extension of ancora (Koren' & Rickards, 1996, fig. 10J); *7, Dimorphograptoides physophora* (NICHOLSON, 1868a) showing extensive ancora umbrella development (Koren' & Rickards, 1996, fig. 19A); *8, Pseudorthograptus* LEGRAND, 1987 sp. showing ancora umbrella and ancora sleeve lists (Koren' & Rickards, 1996, fig. 18F); *9, Spinograptus spinosus* (WOOD, 1900) with thecal and ancora sleeve lists, lacking fusellar membranes (Maletz, 2010b, fig. 5A). Sicula and thecate tubarium in gray; scale bars in *5–9*, 1 mm.

mid-ventral lists, and zigzag lists (BATES, KOZŁOWSKA, & LENZ, 2005). The ancora sleeve consists of lists developing from the ancora umbrella and connects to the thecal framework, generally the first thecal pair. The thecal framework lists are more robust than those of the ancora sleeve, although both may vary in width. However, it appears that only the seams of thecal framework lists commonly bear shards, interpreted as remnants of fusellar walls; whereas ancora sleeve lists yield no evidence of a fusellar covering, although varying amounts of bandaging may occur at localized sites. Not all taxa possess ancora sleeve lists. By way of explanation, the terms clathrium and reticulum (ELLES & WOOD, 1908, p. 334; BOUČEK & MÜNCH, 1944, 1952), used to differentiate tubarium lists, are informal, subjective terms and mostly correspond to more robust and narrower lists, respectively.

EVOLUTION

According to MELCHIN and others (2011), the Retiolitidae originated from a neodiplograptid ancestor close to *Paraclimacograptus* PŘIBYL 1947. The early petalolithines—*Glyptograptus*, *Sudburigraptus,* and *Paramplexograptus*—appeared during the Late Ordovician (Hirnantian) and diversified during the early Silurian (Rhuddanian) into a number of genera. Ancorate taxa appeared during the mid-Rhuddanian with the genus *Pseudorthograptus*. It is clear that the development of the ancora umbrella and ancora sleeve of the Retiolitidae originated during the Rhuddanian from a simple branching of the virgella at a point close to the sicular aperture. Similar developments occurred independently in a number of taxa during the Late Ordovician and early Silurian. *Climacograptus baragwanathi* (T. S. HALL, 1906), from the Eastonian 2 (middle Katian) of Victoria, Australia, appears to be the earliest taxon producing a meshwork of bars at the end of the virgella (VANDENBERG & COOPER, 1992, fig. 9D). However, it is very unlikely that a phylogenetic relationship existed between the Late Ordovician graptoloids bearing a virgellar meshwork and the ancorate Retiolitidae.

Taxa with branching at the virgella but not considered to be closely related to the retiolitoids appeared in the earliest Silurian

Akidograptus ascensus Biozone. Stein (1965), Koren' and Rickards (1996), and Štorch and Feist (2008) illustrated juvenile specimens of *Akidograptus ascensus* (Davies, 1929) with at least three branching divisions of the virgella. A short virgella with two horizontal branches is also present in *Avitograptus avitus* (Davies, 1929), but it is unlikely to be a homologous structure of the ancora of the Retiolitidae (Melchin & others, 2011). *Normalograptus minor* (Huang, 1982) from the *Metabolograptus persculptus* Biozone (Hirnantian, Upper Ordovician) also bears multiple branching divisions of the virgella. Thus, the addition of further constructional complexities from the virgella was common in the early Silurian, but only in the retiolitoid clade did they become a standard, with a long and successful period of development.

Subfamily PETALOLITHINAE Bulman, 1955

[Petalolithinae Bulman, 1955, p. 87, *nom. correct*. Melchin & others, 2011, p. 298, *ex* Petalograptinae Bulman, 1955, p. 87]

Axonophorans (Neograptina) with long, nearly straight thecae, often with gentle ventral curvature and variable thecal overlap; thecal apertures straight, outward inclined, sometimes with variable number of apertural spines; pattern I astogeny or derived pattern; tubarium commonly tabular, exaggeratedly rectangular in cross section; incomplete median septum on obverse side in many taxa; ancora development in derived taxa present, sometimes with poorly developed, unattached ancora sleeve. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone): worldwide.

Bulman (1970) did not refer to the Petalolithinae but included *Petalograptus* (now *Petalolithus;* see Loydell, 1992, p. 36) in the Diplograptidae, even though he had earlier erected the subfamily Petalograptinae for the genera *Petalolithus* and *Cephalograptus* (see Bulman, 1955). Štorch and Serpagli (1993) extended the Petalolithinae to include the genus *Glyptograptus*.

Melchin and others (2011, p. 298) defined the Petalolithinae as the "partial clade that includes the first species that acquired a unistipular (aseptate) biserial rhabdosome in the clade that contains *Paramplexograptus madernii* and *Retiolites geinitzianus* and its descendants, but excluding the taxa included in the subfamily Retiolitinae." Thus, the authors defined the Petalolithinae as a paraphyletic taxon, referring to the genus *Petalolithus* but also revised and enlarged the taxon considerably.

The Median Septum

The existence of a partial median septum in some petalolithines has been known for a long time. Törnquist (1893) noted this in his material of *Diplograptus palmeus* Barrande, 1850 (=*Petalolithus minor* Elles, 1897, see Maletz, 2014b, fig. 23), and it was recognized in the same species by Bates and Kirk (1992, fig. 41) (Fig. 261.2–261.4). The median septum is visible on the obverse side but not on the reverse side. *Petalolithus folium* (Hisinger, 1837) also has a median septum on the obverse side, but on the reverse side only a fine line is visible in partially collapsed specimens, possibly indicating breakage of the thecal wall due to the presence of the nema and partial median septum (Fig. 261.1). Bulman (1955, fig. 63,*7a*) indicated the presence of a partial median septum in *Cephalograptus.*

ANCORATE TAXA

Petalolithus Suess, 1851, p. 100, *nom. nov. pro Diprion* Barrande, 1850, p. 14, homonym of *Diprion* Schrank, 1802, p. 209 (Hymenoptera) [**Prionotus folium* Hisinger, 1837, p. 114; SD Lapworth, 1873b, table 1, facing p. 555] [=*Petalograptus* Suess, 1851, *sensu* Lapworth, 1873b, table 1, facing p. 555 (type, *P. folium,* OD); =*Corbograptus* Koren' & Rickards, 1996, p. 86 (type, *C. enigmatica,* OD), syn. herein]. Robust petalolithine with pattern I astogeny, possessing rectangular thecae with either straight or concave ventral sides; cross section of tubarium rectangular to oval; ancora present, sometimes also partial ancora sleeve with lists; partial median septum on obverse side. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Telychian, Spirograptus guerichi* Biozone): worldwide.——Fig. 262,*2a–c.* **P. folium* (Hisinger); *2a,* NRM-PZ Cn 69037, (new); *2b,* lectotype (designated by Bouček & Příbyl, 1942, p. 8), NRM-PZ Cn 69040 (new); *2c,* PŠ 821, showing ancora and long, slender nematu-

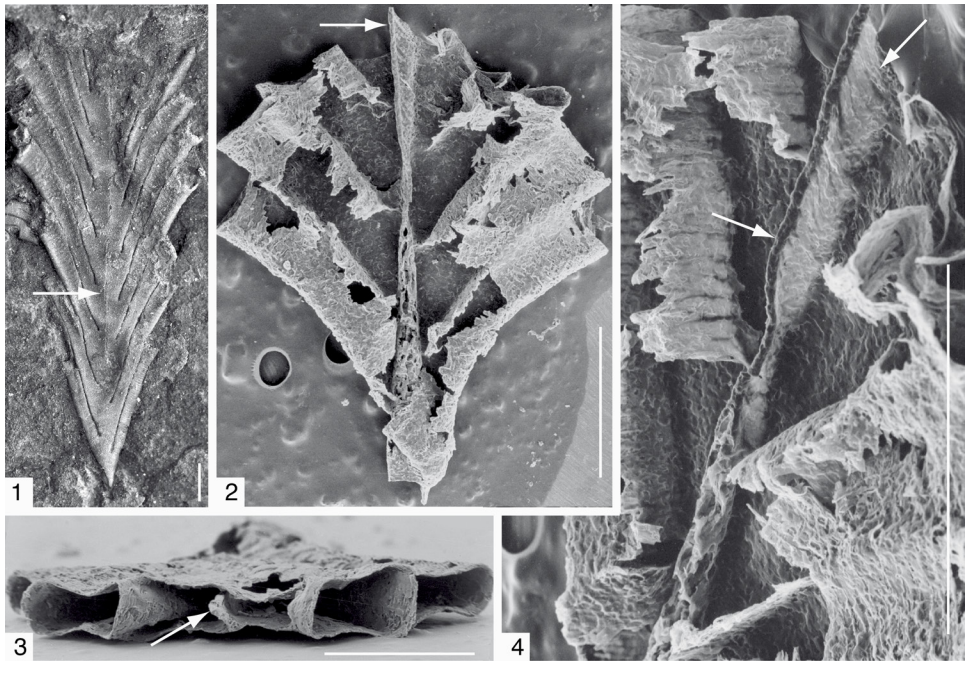


FIG. 261. The median septum. *1, Petalolithus folium* (HISINGER, 1837), LO 11863t, Röstånga, Sweden, reverse view, showing break (*arrow*) due to collapsed lateral wall (Maletz, Ahlberg, & others, 2014, fig. 1N); *2–4, Petalolithus minor* ELLES, 1897, Kallholn, Sweden; *2, 4,* NMW 91.52G.448A, broken specimen showing partial median septum on obverse side and bound by nema (*lower arrow*), fuselli are visible in the partial median septum (*upper arrow*) (new); *3,* NMW 91.52G.505, distal end of small tubarium showing partially collapsed wall and median septum with nema (new). Scale bars, 1 mm in *1–3;* 100 µm in *4*.

larium, Tmaň, Czech Republic (Štorch, 1998a, fig. 5,*2c*). Scale bars, 1 mm.——FIG. 262,*2d*. *Petalolithus* sp., holotype of *Corbograptus enigmatica* KOREN' & RICKARDS, 1996, CNIGR 197/12879, southern Urals, Russia, scale bar, 1 mm (Koren' & Rickards, 1996, fig. 20i).

Cephalograptus HOPKINSON, 1869, p. 159, original spelling as *Cephalograpsus* changed in ICZN, Opinion 650, 1963 [**Diplograpsus cometa* GEINITZ, 1852, p. 26; OD]. Petalolithine with pattern I astogeny and strongly elongated thecae but short sicula; thecae with fairly straight ventral sides; number of thecae often reduced; ancora present in some; partial median septum on obverse side. *Silurian, Llandovery* (*Aeronian*, *Lituigraptus convolutus* Biozone–*Stimulograptus halli* Biozone): worldwide.——FIG. 262,*1a–d*. **C. cometa* (GEINITZ); *1a,* type specimen, not preserved, scale unclear (Geinitz, 1852, pl. 1,*28a*); *1b,* LO 1120t, reverse view, latex cast; *1c,* LO 1121t, obverse view showing median septum, latex cast; *1d,* LO 1124t, proximal end in obverse view; *1b–1d,* Tommarp, Scania, Sweden, scale bars, 1 mm (new).

Dischidograptus NI, 1978, p. 399 [**Petalolithus mirabilis* MU & others, 1974, p. 213; OD]. Robust petalolithine with pattern I astogeny, possessing square thecae with concave ventral sides; ancora present; tubarium splitting into two separate stipes, following the first branching division of the nema; nema branching several times dichotomously at regular distances, eventually forming tangled mesh of rods. [Inclusion of *D.* (?) *regius* (HUNDT, 1957a) in *Dischidograptus* uncertain due to lack of ancora]. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus Biozone–?Telychian, Spirograptus turriculatus* Biozone): China, ?Germany.——FIG. 262,*3a–b*. **D. mirabilis* (MU & others); *3a,* holotype, NIGP 121427, showing branched nema but lacking proximal end, Hubei, China, scale bar, 1 mm (Melchin, 1998, fig. 6U); *3b,* NIGP 168329, YD-1, drill core, proximal end with ancora and branched nema, scale bar, 1 mm (new).——FIG. 262,*3c. D.*(?) *regius,* holotype, BAF H4217, Thuringia, Germany, scale bar, 1 mm (Schauer, 1971, pl. 13,*8*).

Dimorphograptoides KOREN' & RICKARDS, 1996, p. 85, *ex Pseudorthograptus* (*Dimorphograptoides*) KOREN' & RICKARDS, 1996, p. 85, herein [**Diplograpsus physophora* NICHOLSON, 1868c, p. 56; OD]. Petalolithine with short uniserial part; proximal pattern unknown; thecae with thickened apertural rims; ventral thecal walls straight to concave; ancora umbrella with four prongs and additional spiral lists and with probable ancora sleeve. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Coronograptus cyphus* Biozone): UK, Czech Republic, Germany, Russia.——FIG. 263,*1a–b*. **D.*

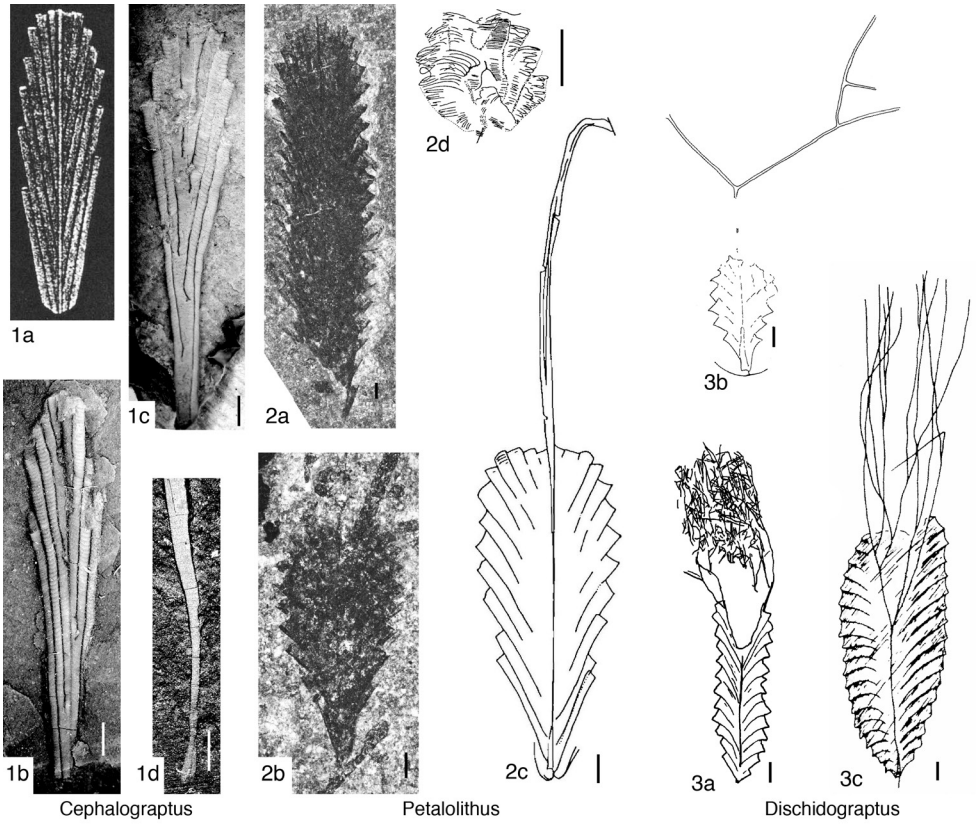


FIG. 262. Retiolitidae (Petalolithinae) (p. 390–391).

physophora (NICHOLSON); *1a,* holotype, NHMUK PM 1891(4), Garpol Linn, Birkhill Shale, Moffat area, Scotland, UK (Nicholson, 1868c, fig. 7); *1b,* SM A210464a, Dob's Linn, Birkhill Shale, Scotland, UK, scale bar, 1 mm (Koren' & Rickards, 1996, fig. 19D).

Dittograptus OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 69 [**D. fortuitus;* OD]. Petalolithine with pronounced ancora and extensive scopular membranes, reaching distally to at least 29th thecal pair; proximal development of pattern I astogeny; thecae simple, possibly with ventral apertural spines. *Silurian, Llandovery* (*lower Aeronian, Demirastrites triangulatus* Biozone–*Pribylograptus leptotheca* Biozone): Czech Republic, Germany, Russia.——FIG. 263,*5a–b.* **D. fortuitus; 5a,* holotype, CNIGR 61/9765, proximal end in lateral view; *5b,* CNIGR 64/9765, adult specimen in scalariform view; scale bars, 1 mm (Koren' & Rickards, 1996, fig. 20G–H; for photos of complete specimen, see Obut, Sobolevskaya, & Merkureva, 1968, pl. 6,*1,* pl. 6,*4*).

Hercograptus MELCHIN, 1999, p. 263 [**H. introversus;* OD]. Petalolithine with partly attenuated fusellum; proximal development pattern I astogeny; ancora umbrella with spiral lists extending to form ancora sleeve connected to lateral thecal apertural margins; thecal apertures considerably widened laterally; fusellum at thecal apertures reduced to conspicuous list structure; nema free. *Silurian, Llandovery* (*upper Rhuddanian, Coronograptus cyphus* Biozone–*lower Aeronian, Campograptus curtus* Biozone): Czech Republic, Canada (Arctic).——FIG. 264,*a–b.* **H. introversus; a,* holotype, GSC 104935, Cape Manning section, Arctic Canada, scale bar, 1 mm (new; provided by M. Melchin); *b,* paratype, GSC 14936, proximal end with ancora umbrella, showing lateral widening close to thecal aperture, Cape Manning section, Arctic Canada, scale bar, 1 mm (Melchin, 1999, fig. 1B).

Pseudorthograptus LEGRAND, 1987, p. 62 [**Diplograpsus insectiformis* NICHOLSON, 1869, p. 236; OD]. Petalolithine with concave first thecal pair and pattern I astogeny; partial median septum present; thecal apertures with ventrolateral processes developed as gentle lateral cusps to paired spines; ventral thecal walls straight to concave; ancora with four prongs and additional spiral lists. *Silurian, Llandovery* (*Rhuddanian, Coronograptus gregarius* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): world-

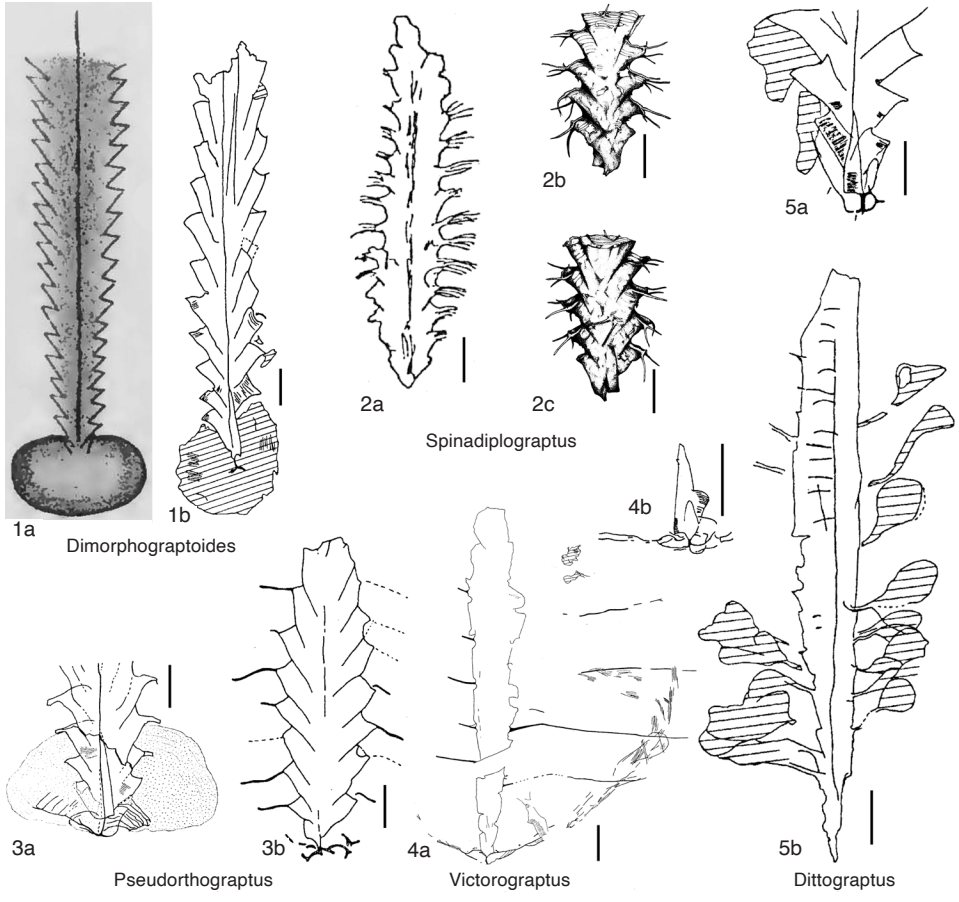


FIG. 263. Retiolitidae (Petalolithinae) (p. 391–393).

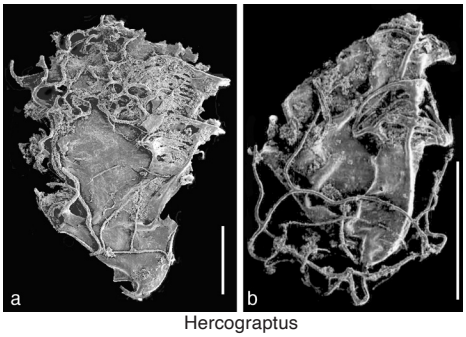
wide.——FIG. 263,*3a*. *P. obuti* (RICKARDS & KOREN', 1974), SVEGEI material, no number, Alimbet Creek, South Urals, Russia, scale bar, 1 mm (Rickards & Koren', 1974, fig. 9).——FIG. 263,*3b*. **P. insectiformis* (NICHOLSON); NHMUK PM Q3112, specimen from holotype slab, scale bar, 1 mm (Rickards & Koren', 1974, fig. 4).

Spinadiplograptus HUNDT, 1965, p. 21 [**Orthograptus* (?) *inopinatus* BOUČEK, 1944, p. 2; SD herein]. Petalolithine with concave first thecal pair and pattern I astogeny; median septum lacking; thecal apertures with paired lateral spines at the thecal apertures; ventral thecal walls straight to concave; small, shallow ancora umbrella; no ancora sleeve. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Lituigraptus convolutus* Biozone): Canada (Arctic); Czech Republic; Germany; Sweden.——FIG. 263,*2a–c*. **S. inopinatus* (BOUČEK); *2a,* holotype, NMP L2732, Velká Chuchle, Czech Republic (Bouček, 1944, fig. 1b); *2b–c,* SM X.25935, chemically isolated specimen in reverse (*b*) and obverse (*c*) views, Cape Phillips Formation, Arctic Canada, scale bars, 1 mm (Koren' & Rickards, 1996, fig. 17).

Victorograptus KOREN' & RICKARDS, 1996, p. 45 [**V. morosus;* OD]. Petalolithine with long genicular thecal spines; proximal development and thecal style incompletely known; wide and shallow ancora umbrella with extremely wide possible ancora sleeve possibly connected to genicular spines. *Silurian, Llandovery* (*Aeronian, Coronograptus gregarius* Biozone): Russia.——FIG. 263,*4a–b*. **V. morosus; 4a*, holotype, CNIGR 106/12879; *4b,* paratype, CNIGR 107/12879; southern Urals, Russia, scale bars, 1 mm (Koren' & Rickards, 1996, fig. 9a and 9b, respectively).

NON-ANCORATE TAXA

Agetograptus OBUT & SOBOLEVSKAYA, in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 78 [**A. secundus;* OD] Petalolithine with pattern I′ proximal development type; tubarium aseptate with free central nema; thecae with straight outward-inclined or



Hercograptus

FIG. 264. Retiolitidae (Petalolithinae) (p. 392).

slightly curved ventral thecal wall without geniculum; uniserial first theca by redirection of growth of second theca; thecal apertures straight, outward inclined; paired apertural spines may be present; virgella strongly elongated. *Silurian, Llandovery,* (*upper Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Pribylograptus leptotheca* Biozone): Canada, China, Russia, Sweden.——FIG. 265,*1a–c*. **A. secundus; 1a–b,* holotype, CNIGR 91/9765; *1c,* paratype, CNIGR 91/9766, showing long virgella; scale bars, 1 mm (Obut, Sobolevskaya, & Merkureva, 1968, pl. 8).——FIG. 265,*1d. A. spiniferus* OBUT & SOBOLEVSKAYA, in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, GSC 104885, Arctic Canada, scale bar, 1 mm (Melchin, 1998, pl. 7,*1*).

Comograptus OBUT and SOBOLEVSKAYA, in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 60 [**C. comatus;* OD]. Petalolithine with a pattern I proximal development type; thecae sharply geniculate; no median septum; nema free and central; sicular aperture with at least three spines projecting outward from sicula; additional sicular and thecal spines produced during maturation of colony. *Silurian, Llandovery* (*upper Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Stimulograptus sedgwickii* Biozone): Canada, China, UK, Czech Republic, Germany, Russia.——FIG. 265,*2a–c*. **C. comatus; 2a,* holotype, CNIGR 27/9765, proximal and distal part of tubarium, lower *Demirastrites triangulatus* Biozone, Norilsk region, Siberia, Russia (Koren' & Rickards, 1996, fig. 6g); *2b,* specimen from Arctic Canada (Russel-Houston, 2001, pl. 2h); *2c,* juvenile with three proximal spines (Russel-Houston, 2001, pl. 2j). All scale bars, 1 mm.

Rivagraptus KOREN' & RICKARDS, 1996, p. 62 [**Diplograptus bellulus* TÖRNQUIST, 1890, p. 28; OD]. Petalolithine with Pattern I or N proximal development and curved to straight ventral thecal walls; tubarium aseptate with free, central nema; sicular length reduced. *Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): worldwide.——FIG. 265,*3a–d*. **R. bellulus* (TÖRNQUIST); *3a,* lectotype, selected herein (lectotype selection by PŘÍBYL, [1948a, p. 11] of specimen in TÖRNQUIST, 1890, pl. 1,*25* is based on missing specimen), LO 948t, flattened proximal end in reverse view, showing thecal spines (new); *3b,* lectotype, LO 948t, original illustration showing long virgella (Törnquist, 1890, pl. 1,*27*); *3c,* GSC 135129, reverse view, infrared photo, Arctic Canada (Melchin & others, 2011, fig. 5l); *3d,* LO 11859t, proximal end in obverse view, Röstånga drill core at 33.65-33.55 m (new). Scale bars, 1 mm.——FIG. 265,*3e*. **R. kayi* (CHURKIN & CARTER, 1970), GSC 135128, isolated proximal end in reverse view, infrared photo, Arctic Canada, scale bar, 1 mm (Melchin & others, 2011, fig. 5j).

Glyptograptus LAPWORTH, 1873b, table 1, facing p. 555 [**Diplograpsus tamariscus* NICHOLSON, 1868a, p. 526; OD] Petalolithine with pattern I proximal development type; nema embedded in obverse wall of tubarium or with narrow, obverse partial median septum; thecae with rounded to flowing geniculum. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian, Llandovery* (*Telychian, Streptograptus crispus* Biozone): worldwide.——FIG. 266,*1a–c*. **G. tamariscus* (NICHOLSON); *1a,* paralectotype, NHMUK PM Q.578, Birkhill Shale, Wamphray, Dumfries, Scotland, UK (Zalasiewicz, 2008b, Atlas, Folio 2.88); *1b,* lectotype (selected by PŘÍBYL, 1948a, p. 10), NHMUK PM Q.579, Birkhill Shale, Wamphray, Dumfries, Scotland, UK (Zalasiewicz, 2008b, Atlas, Folio 2.88); *1c,* GSC 104864, proximal end in reverse view, Arctic Canada (Melchin, 1998, pl. 5,*2*). Scale bars, 1 mm.——FIG. 266,*1d*. **G. tamariscus,* ssp. GSC 104874, long specimen in reverse view, broken into three pieces, scale bar, 1 mm (Melchin, 1998, pl. 6,*1*).

Paramplexograptus MELCHIN, MITCHELL, NACZK-CAMERON, FAN, & LOXTON. 2011, p. 298 [**Paraorthograptus paucispinus* LI in Anhui Geological Survey Team, 1982; OD]. Petalolithine with pattern H′ proximal development type or derived one; colony parallel-sided or widening gradually from proximal end; sicular aperture with slight dorsal flare; median septum lacking; nema attached to bases of the interthecal septa; thecae with sharp genicular thickenings or ventral flanges, slightly to moderately inclined, usually concave subapertural walls; apertures everted. *Upper Ordovician* (*upper Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian, Llandovery* (*lower Rhuddanian, Atavograptus atavus B*iozone): Canada, China, Russia.——FIG. 266,*2a–b*. **P. paucispinus* (LI in Anhui Geological Survey Team), southern Anhui, China (Melchin & others, 2011, fig. 6h–i). *2a,* lectotype, NIGP 67260; *2b,* topotype, NIGP 1540281; scale bars, 1 mm.——FIG. 266,*2c*. **P. madernii* (KOREN' & MIKHAILOVA, in KOREN', MIKHAYLOVA, & TZAJ, 1980), GSC 135122, Cape Manning, Nunavut, Canada, scale bar, 1 mm (Melchin & others, 2011, fig. 5b).

Parapetalolithus KOREN' & RICKARDS, 1996, p. 57 [**P. dignus;* OD] [=*Parapetalolithograptus* RICKARDS, WRIGHT, & THOMAS, 2009, p. 71; misspelling of *Parapetalolithus*]. Petalolithine with pattern I proximal development type; first thecal pair straight, V-shaped; no median septum; nema free

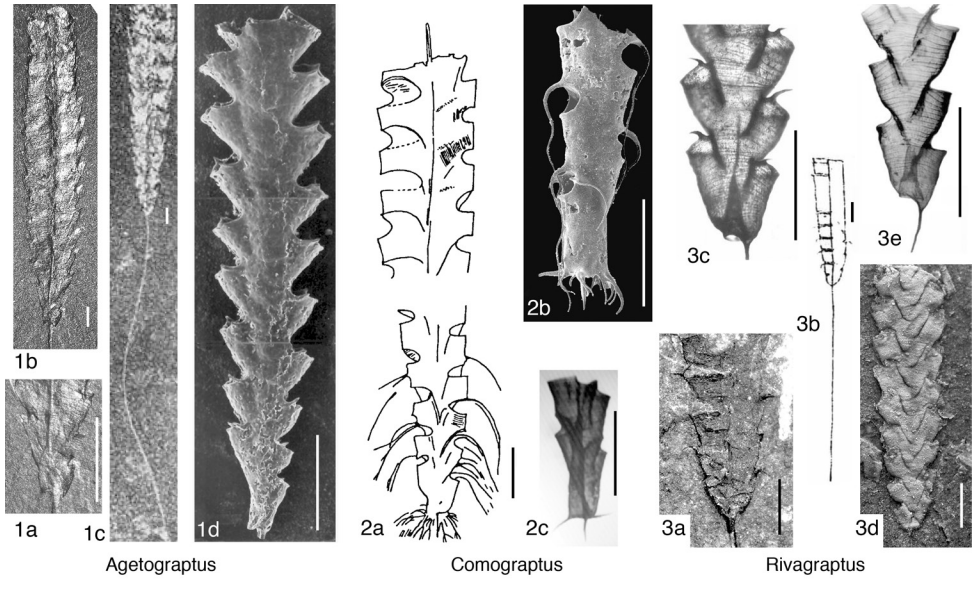


FIG. 265. Retiolitidae (Petalolithinae) (p. 393–394).

and central or embedded in obverse wall, typically with extended nematularium; moderately inclined thecae with nearly straight ventral side and outward-inclined, straight thecal apertures. *Silurian, Llandovery* (*upper Aeronian, Stimulograptus halli* Biozone–*Telychian, Monoclimacis griestoniensis* Biozone): worldwide.——FIG. 266,*3a–b*. **P. dignus; 3a,* holotype, CNIGR 124/12879, obverse view, Zhaksy-Kargala Valley, southern Urals, Russia; *3b,* CNIGR 123/12879, Kos-Istek region, southern Urals, Russia; scale bars, 1 mm (Koren' & Rickards, 1996, fig. 11j and 11k, respectively).——FIG. 266,*3c. P. conicus* (BOUČEK, 1932), lectotype, NMP L 25043, Zelkovice, Bohemia, Czech Republic, scale bar, 1 mm (Štorch, 2000a).

Sudburigraptus KOREN' & RICKARDS, 1996, p. 47 [**Orthograptus eberleini* CHURKIN & CARTER, 1970, p. 29; OD]. Petalolithine with pattern H′ and possibly pattern I astogeny; tubarium aseptate with non-geniculate thecae; colonies with slight dorsal curvature of proximal end and slightly flared dorsal sicular margin. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Coronograptus cyphus* Biozone): Canada, USA, UK.——FIG. 266,*4a*. **S. eberleini* (CHURKIN & CARTER), holotype, USNM 161783, Alaska, USA, scale bar, 1 mm (Melchin & others, 2011, fig. 6n).——FIG. 266,*4b*. *Sudburigraptus* sp. 1, GSC 135127, infrared photo, reverse view, southern Urals, Russia, scale bar, 1 mm (Melchin & others, 2011, fig. 5h).

Subfamily RETIOLITINAE Lapworth, 1873

[Retiolitinae LAPWORTH, 1873b, table 1, facing p. 555] [incl. Plectograptinae BOUČEK & MÜNCH, 1952, p. 10 (Czech text), p. 110 (English text); Pseudoretiolitinae OBUT & ZASLAVSKAYA, 1974, p. 159 (English version, 1976, p. 123); Gothograptinae OBUT & ZASLAVSKAYA, 1983, p. 112 (English version, 1986, p. 218); Pseudoplegmatograptinae OBUT & ZASLAVSKAYA, 1983, p. 105 (English version, 1986, p. 209); Cometograptinae, Neogothograptinae, Paraplectograptinae, Rotaretiolitinae, Sokolovograptinae, and Spinograptinae KOZŁOWSKA-DAWIDZIUK, LENZ, & BATES, 2003, p. 51]

Tubarium generally preserved as framework of lists formed of cortical bandages surrounding highly attenuated and rarely preserved fusellar walls; proximal development of pattern R astogeny; thecal framework lists joined by ancora sleeve, a distal development of the ancora umbrella; fragments of fuselli generally preserved as shards remaining in thecal framework list seams; sicula typically preserved in stratigraphically earlier taxa, but reduced or not preserved in later forms, with the rare exception of some occurrences in *Spinograptus* spp. (LENZ, 1994a; KOZŁOWSKA-DAWIDZIUK, 1997); thecae with variable inclination, lacking interthecal septa and thecal overlap; thecal apertures generally considerably enlarged; ancora sleeve list surfaces seamed inside or outside, indicating presence of ancora sleeve membrane; bandages smooth, longitudinally striated or pustulose; virgella and nema connected by virga, a

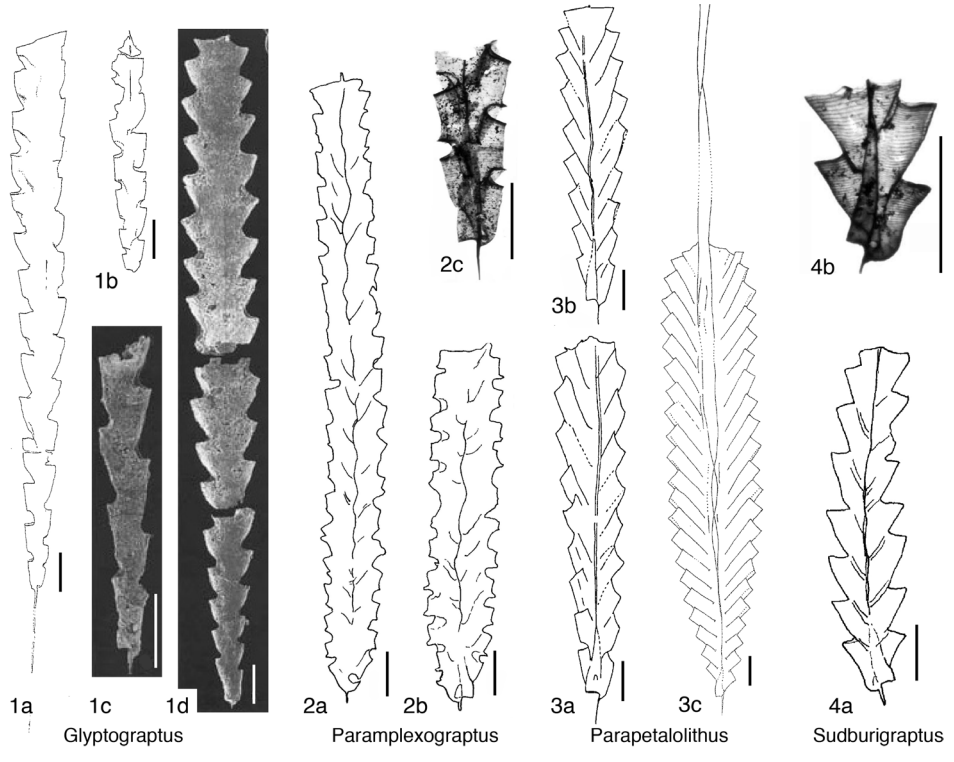


FIG. 266. Retiolitidae (Petalolithinae) (p. 394–395).

thickened longitudinal rod on prosicula. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus/Demirastrites pectinatus* Biozone)–*Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.

MELCHIN and others (2011, p. 300) emended the Retiolitinae as "the first ancora-bearing graptolite species within the clade that includes *Retiolites geinitzianus* that acquired thecae constructed of a full framework of lists and reduced or absent fusellar walls, and all of its descendents."

The retiolitines have been misunderstood for a long time, in part because of the tacit assumption that their immediate ancestors were axonophorans with a fully developed fusellum that had simply lost their continuous fusellar coverings, retaining only a meshwork of lists (e.g., BULMAN, 1955, 1970). A second reason was the lack of recognition of the unique double-layer nature of the retiolitid tubarium construction with its internal thecal framework and the external ancora umbrella and ancora sleeve (Fig. 267–Fig. 268). It is only since the advent of scanning electron microscopy (SEM) that this has come fully to light. Three-dimensional specimens showing the dual construction had been recovered and illustrated by TÖRNQUIST (1880, 1890) and HOLM (1890), but these apparently were subsequently overlooked or forgotten. The detailed SEM studies instituted by BATES and KIRK (e.g., 1978, 1984, 1987, 1991, 1992, 1997), working with isolated, three-dimensionally preserved material, clearly showed that retiolitines possess a framework unlike that of any other neograptines (Fig. 268). The Late Ordovician Lasiograptidae (see ŠTORCH & others, 2011) mirrored some features found in the Retiolitinae, but their external meshwork (lacinia) is based on

growth and branching of thecal spines and does not bear indications of the presence of membranes (Bates & Kirk, 1991).

MORPHOLOGY

In the vast majority of instances, retiolitine tubaria are preserved with only cable-like lists arranged in a meshwork pattern. However, originally there were also two membrane-based constructions: the thecal framework inside, formed from the fusellum (Fig. 267.1), and a second layer, the ancora sleeve, on the outside (Fig. 267.2, 267.5–267.6). The retiolitine membranes are very thin and usually not preserved, but their presence was already noted on flattened and relief material (e.g., Tullberg, 1883; Törnquist, 1890; Perner, 1897; Elles & Wood, 1908; Lenz & Thorsteinsson, 1997). The incrementally deposited fusellar membrane, predominantly the thecal framework, is present in only a very few taxa, e.g., *Retiolites, Pseudoretiolites* (Fig. 259.3), *Stomatograptus* (Fig. 267.1), and a number of *Spinograptus* species (Kozłowska-Dawidziuk, 1997, Kozłowska, Dobrowolska, & Bates, 2013).

The ancora sleeve consists of meshes made of lists formed of cortical bandages derived from the ancora umbrella. The lists of the thecal framework have seams, which are U-shaped in cross section (Fig. 269.3). Very commonly, the seams demonstrate evenly spaced, U-shaped increments or shards (Fig. 269.5) that Bates and Kirk (1992) interpreted as remnants of fusellar sheets. The ancora sleeve consists of meshes made of lists formed of cortical bandages derived from the ancora umbrella. It is not clear, however, whether fuselli or cortical bandages fully or partially covered these membranes.

The first theca of retiolitines emerged through a sicular resorption foramen (Fig. 270), from which was derived a column of successively developed thecae, forming the thecal framework. Further development of the retiolitine tubarium is difficult to ascertain. The proximal development type probably is comparable to the pattern I astogeny, but details are not preserved, and Melchin (1998) defined the pattern as pattern R, differentiated from pattern I astogeny by the presence of the ancora and its incorporation into the framework of the first thecal pair. The thecae of the Retiolitinae do not show any thecal overlap and, thus, lack an interthecal septum.

The ancora umbrella was constructed before the thecae of the tubarium appeared. It was followed by the upward extension of the ancora umbrella, constituting the ancora sleeve (Bates, 1990), which in turn linked up with the thecal framework, giving rise to the outermost lateral walls of the tubarium. The ancora sleeve is, therefore, exclusively the product of the distal extension from the ancora umbrella that partially envelops and laterally and ventrally joins with the underlying thecal framework (Fig. 267). The retiolitines are thus unique among the graptolites in that most possess double lateral walls: an inner one being the homologue of the normal neograptid (or axonophoran) thecal walls within which the nema is present, and an outer wall (ancora sleeve) derived entirely from the distal extension of the ancora (Fig. 267.2).

The early growth stages of the ancora-derived structures in both the retiolitines and the petalolithines are basically identical at the level of the ancora and ancora umbrella (Fig. 271). As a consequence of the great similarities between the ancoras and ancora umbrellas of the petalolithines and retiolitines, these structures are regarded as homologous (Mitchell, 1987; Bates, 1990). The petalolithines are thus widely accepted as being ancestral to the retiolitines (Bates & Kirk, 1984, 1987, 1991, 1992; Mitchell, 1987; Lenz, 1993b, 1994a, 1994b; Lenz & Melchin, 1997; Melchin, 1998, 1999; Lenz & Kozłowska-Dawidziuk, 2001; Melchin & others, 2011, fig. 3). Further support for concluding that the retiolitine and the petalolithine subgroups share a common origin is that both are part of the group that shares

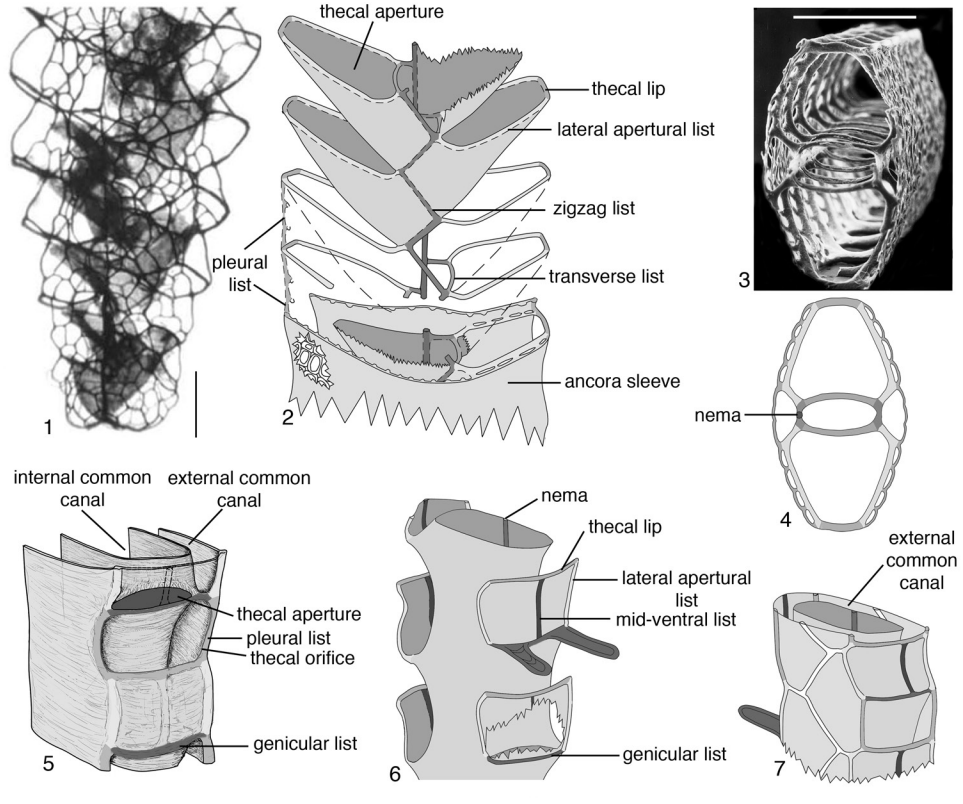


FIG. 267. Morphology and morphological terminology. *1, Stomatograptus* TULLBERG, 1883, showing preservation of thecal walls comprised of sheetlike fusellar bands, scale bar,1 mm (Lenz & Thorsteinsson, 1997, fig. 1); *2, Retiolites* BARRANDE, 1850, reconstruction of median part, showing thecal framework and connection to ancora sleeve (*gray*); *3, Retiolites*, cross section showing strong transverse lists and nema, scale bar, 1 mm (Bates, 1989, fig. 11); *4, Retiolites*, cross section showing thecal framework; ancora sleeve (*light gray*) (adapted from Bates & Kirk, 1997, fig. 127b); *5–7, Spinograptus praerobustus* (LENZ & KOZŁOWSKA–DAWIDZIUK, 2002a), reconstruction of median part of colony showing thecate part, ancora sleeve, and list development (*2, 5–7,* adapted from Bates & others, 2006, fig. 1–2).

the astogenetic pattern I (BATES, KOZŁOWSKA, & LENZ, 2005). One of the differences in early growth stages is the presence of the virga, a thickened longitudinal cortical list on the prosicula connecting the virgella with the nema in the Retiolitinae but not in the Petalolithinae.

Ancora umbrellas of the retiolitines range from very simple, comprised of a few branches (e.g., *Paraplectograptus*) (Fig. 271.3) with some smoothly bounded by a rim (e.g., *Rotaretiolites*) (Fig. 268.1), to very complex, comprised of many meshes, to those with numerous radial and spiral lists (e.g., *Pseudoretiolites*) (Fig. 271.5), and range from a shallow saucer-shape to a deep cup-shape in profile (Fig. 271.5–271.6).

In general, the ancora umbrella structures are more complex, including a spiral structure, during the Llandovery (Fig. 271.2), and generally simpler structures during the Wenlock and Ludlow taxa (Fig. 271.3, Fig. 271.6). In some retiolitines there is an outer ancora situated outside of the main ancora. In these, the seams of the ancora membranes are outward facing on the inner ancora, and inward facing on the outer ancora (Fig. 272).

The earlier retiolitines possess ancora sleeve seams on the outside of the ancora sleeve, as was demonstrated for *Retiolites angustidens*

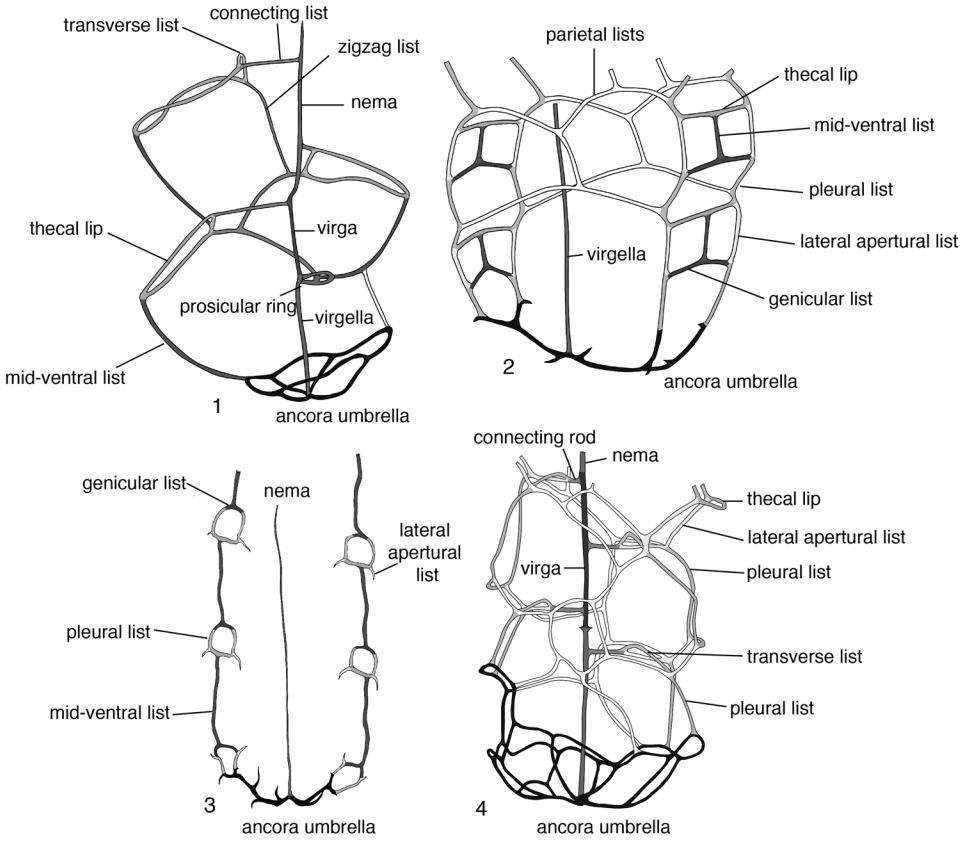


FIG. 268. Terminology of thecal lists in the Retiolitinae. *1, Rotaretiolites* BATES & KIRK, 1992, possessing only thecal framework, prosicular ring, and simple ancora umbrella; *2, Plectograptus* MOBERG & TÖRNQUIST, 1909, showing very simple ancora umbrella and large lateral and ventral orifices; *3, Plectodinemagraptus* KOZŁOWSKA-DAWIDZIUK, 1995, showing strongly reduced framework; *4, Paraplectograptus* PŘÍBYL, 1948a, tubarium with strong ancora umbrella, lacking reticulum (all adapted from Bates, Kozłowska, & Lenz, 2005, fig. 5). Color version of illustrations available in *Treatise Online* 114.

ELLES & WOOD, 1908 by BATES and KIRK (1997, fig. 118). In most derived retiolitines, the seams of the ancora sleeve are facing inward, except for the ancora umbrella, and the lists are pustulose (KOZŁOWSKA-DAWIDZIUK & LENZ, 2001).

The retiolitine girder-like structures, the cortical lists, are the mainstays for retiolitine preservation and have three styles of surface micro-ornamentation built up concentrically, layer by layer: pustulate, parallel ridges, and smooth to finely striated. Taxa with smooth to finely striated surfaces (Fig. 269.1) appeared during the early Aeronian, extended through the Telychian, and in a more limited way into the Wenlock, then disappeared at the end of the early Homerian. Strong parallel ridges occurred only in *Rotaretiolites* during the Telychian (Fig. 269.4).

Taxa with pustule ornamentation and finely striated lists (Fig. 269.2) appeared during the middle Telychian and continued until the extinction of the retiolitids during the middle Ludlow. Thus, two forms of micro-ornamentation were present from the late Llandovery to early Wenlock, whereas only pustular ornamentation remained following the late Wenlock graptolite extinction. In reference to smooth cortical lists, however, it should be kept in mind that at least some of the list

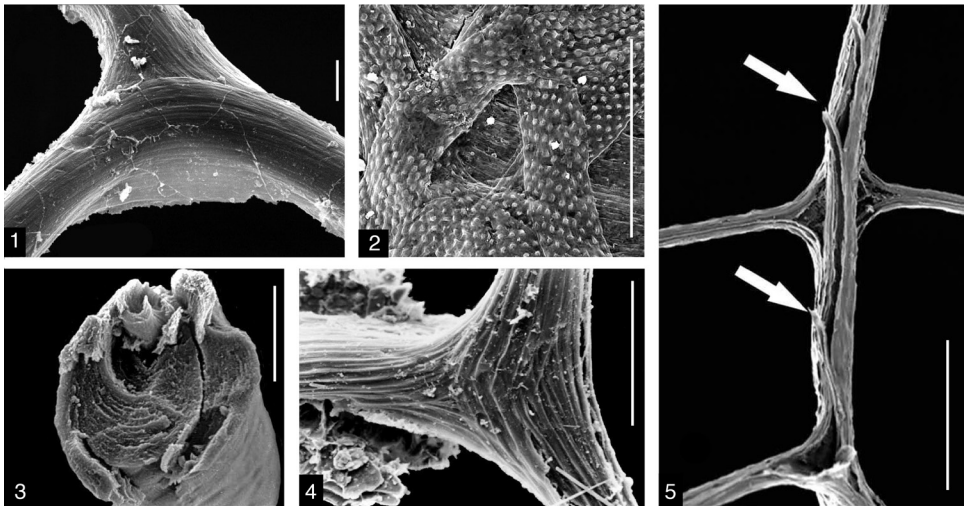


Fig. 269. General morphology and micromorphology of retiolitines. *1, Eorograptus spirifer* Melchin, Lenz, & Kozłowska, 2017, lists showing fine striation (Melchin, Lenz, & Kozłowska, 2017, fig. 9,*4*); *2, Gothograptus nassa* (Holm, 1890), ZPAL G.54.6, cortical bandages on genicular hood showing well-developed pustules (Kozłowska, Lenz, & Melchin, 2009, fig. 3); *3,* NMW 91.52G.95, cross section of a list of *Retiolites* Barrande, 1850, showing concentric cortical bandage layers and insertion seam (new); *4, Rotaretiolites* Bates & Kirk, 1992, NMW 91.52G.52, with robust parallel striae (new); *5, Gothograptus nassa,* ZPAL G.66/2, seams with shards indicated by *white arrows* (new). Scale bars, 10 µm in *1, 3–4;* 100 µm in *2,5*.

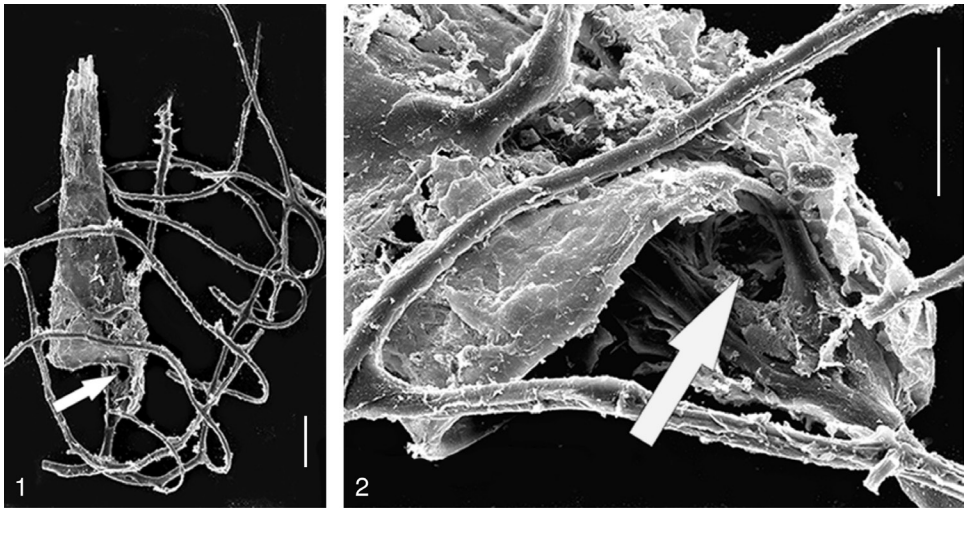


Fig. 270. Resorption foramen. *Pseudoretiolites* Bouček & Münch, 1944 sp., GSC 137638, distal end of metasicula, showing downward curvature of theca 1^1 and well rounded foramen (*arrows*), Llandovery, middle Aeronian, upper *Campograptus curtus* Biozone, Arctic Canada; *1,* complete distal end of sicula, ancora, and four spiral lists, scale bar, 0.5 mm; *2,* enlargement showing well-rounded porus, scale bar 50 µm (Melchin, Lenz, & Kozłowska, 2017, fig. 11,*2*).

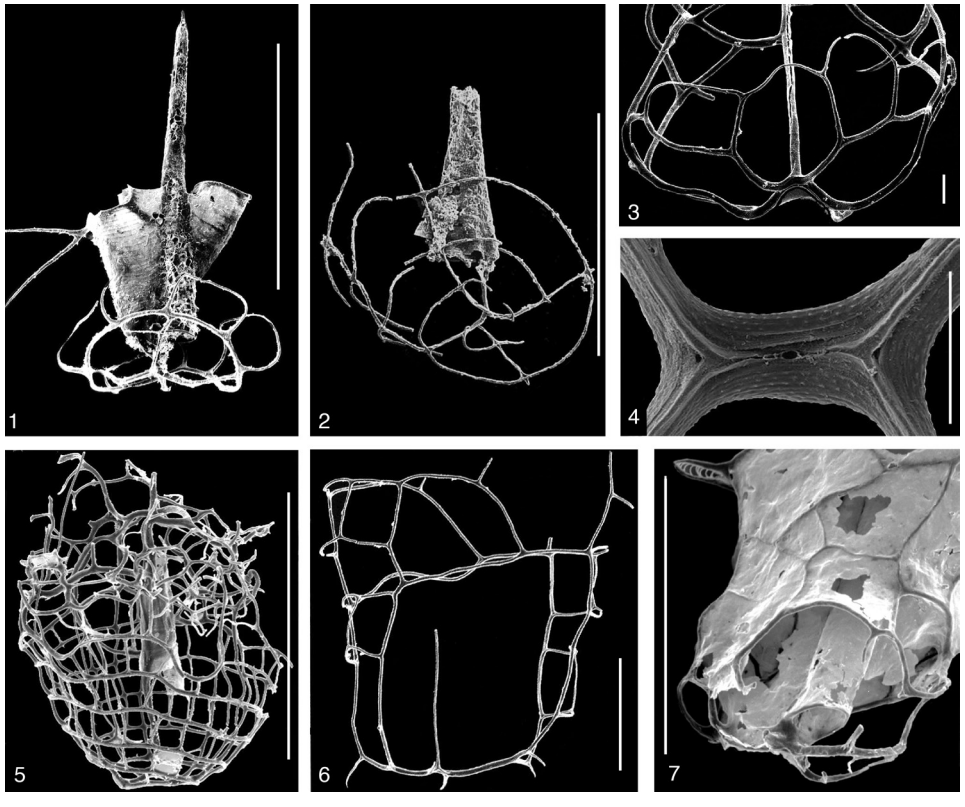


FIG. 271. Ancoras and ancora umbrellas. *1, Spinadiplograptus inopinatus* (BOUČEK, 1944) (petalolithine), GSC 9819, complete ancora umbrella, Arctic Canada (Bates, Kozłowska, & Lenz, 2005, fig. 3F); *2,* ancora umbrella of *Pseudorthograptus* sp. cf. *P. obuti* RICKARDS & KOREN', 1974 (petalolithine) with spiral and radial lists (Bates & Kirk, 1992, fig. 44); *3,* simple ancora umbrella of *Paraplectograptus* PŘÍBYL, 1948a (retiolitine), Arctic Canada; *4, Spinograptus* BOUČEK & MÜNCH, 1952, (retiolitine) ancora, showing pustules and seams on outside (Bates, Kozłowska, & Lenz, 2005, fig. 3D); *5,* complex, spiraled ancora umbrella of *Pseudoretiolites hyrichus* (Melchin, Lenz, & Kozłowska, 2017, fig. 10,*2*) (retiolitine); *6,* very simple ancora umbrella of *Plectograptus* MOBERG & TÖRNQUIST, 1909 (retiolitine) (Bates, Kozłowska, & Lenz, 2005, fig. 1E); *7, Spinograptus praerobustus* LENZ & KOZŁOWSKA-DAWIDZIUK, 2002a, proximal end showing rarely preserved, complete fusellar walls between cortical lists and fully preserved sicula (Bates, Kozłowska, & Lenz, 2005, fig. 2A). Scale bars, 1mm in *1–2, 5–7;* 0.1 mm in *3–4.*

smoothness might be attributable to abrasion rather than biological origin. The function of the micro-ornamentations is unknown.

More than one type of ornamentation can be present in a single taxon. In *Eisenackograptus,* for example, the external bandaging on the ancora sleeve is pustular, but the ornamentation on the inside of the ancora umbrella, sleeve, and thecal framework is striated.

Retiolitine distal ends fall into two groups. One group has an open distal end (e.g., *Retiolites* and *Stomatograptus*) and was universal during the Llandovery and early Wenlock, with a very few ranging as high as the early Ludlow (e.g., some species of *Plectograptus* and *Spinograptus*). The other group includes those with a finite tubarium, most of which possessed a tubular appendix (e.g., *Eisenackograptus, Gothograptus, Neogothograptus;* see KOZŁOWSKA, DOBROWOLSKA, & BATES, 2013, p. 88), which is generally regarded as a single final theca. Alternatively, a few taxa had a closed end with no appendix and only a nema projecting beyond the distal end of the tubarium, for instance, *Spinograptus praerobustus; Spinograptus tubothecalis* KOZŁOWSKA,

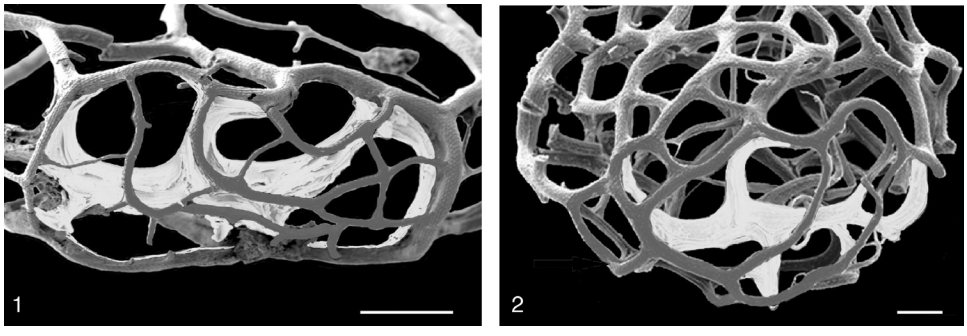


FIG. 272. The outer ancora. *1, Neogothograptus* sp., ZPAL G.66/3, specimen with well-developed ancora umbrella with seams facing outward (*light gray*) (new); *2, Baculograptus chainos* (Lenz, 1993b), GSC 120711, showing well-developed outer ancora with seams facing inward (*dark gray*); Arctic Canada; scale bars, 100 µm (new).

DOBROWOLSKA, & BATES, 2013; and *Cometograptus marsupium* (LENZ, 1993b). A special development occurred in *Cometograptus bicladis* (LENZ, 1993a), in which the tubarium split distally into two uniserial stipes.

PHYLOGENETIC ANALYSIS AND SYSTEMATICS

Cladistic studies of retiolitids began with LENZ and MELCHIN (1997), in which all of the then-known genera were included. It was followed by the studies of BATES, KOZŁOWSKA, and LENZ (2005) and KOZŁOWSKA, LENZ, and MELCHIN (2009), the last being a study of only those with pustular micro-ornamentation. The most recent study by MELCHIN, LENZ, and KOZŁOWSKA (2017) (Fig. 273) is of taxa that originated during the Aeronian and early Telychian (Llandovery) and was of special importance because it showed the roots of the subgroups of the retiolitines and the links to the petalolithines.

There are four major clade groups in the cladogram (Fig. 273): (A) a paraphyletic stem group, *Pseudoretiolites,* being ancestral to all subsequent taxa; (B) the monophyletic *Pseudoplegmatograptus* clade, typical of traditional retiolitines with fine, parallel striation to smooth surfaces of the cortical bandages and, normally, complex morphology—these became extinct at the end of the lower Homerian (upper Wenlock); (C) a monophyletic group with *Aeroretiolites, Rotaretiolites,* and other members of this subclade that ranged from the *Lituigraptus convolutus* Biozone (Aeronian, Llandovery) to the *Spirograptus guerichi* Biozone (Telychian, Llandovery); and (D) a monophyletic group with *Eorograptus, Paraplectograptus,* and *Sokolovograptus,* in which the earlier taxa *Eorograptus* and *Paraplectograptus* have parallel micro-ornamentation, and the somewhat later occurring taxa (*Sokolovograptus* and *Paraplectograptus*) have pustular bandages. As such, in this subclade, some taxa have parallel micro-ornamentation and others have a pustulose ornamentation, which developed somewhat later. *Sokolovograptus* and/or *Paraplectograptus* are considered ancestral to all of the stratigraphically higher taxa and can be directly linked to the cladogram in KOZŁOWSKA, LENZ, and MELCHIN (2009), where the earliest taxon is shown as *Pseudoplectograptus* (synonym of *Paraplectograptus,* herein). The result is that all taxa previously recognizable as Silurian retiolitids are now considered to be members of a single subfamily Retiolitinae.

Retiolites BARRANDE, 1850, p. 68, *nom. conserv.,* ICZN, Opinion 199, 1954 [**Gladiolites geinitzianus* BARRANDE, 1850; M] [=*Gladiolites* BARRANDE, 1850, *nom. suppr.,* ICZN, Opinion 199, 1954c; =*Gladiograptus* HOPKINSON & LAPWORTH, 1875, p. 633 (type, *G. geinitzianus* BARRANDE, 1850, p. 68, M); =*Dimykterograptus* HABERFELNER, 1936, p. 92 (type, *D. bončevi,* M), syn. by BOUČEK & MÜNCH, 1944, p. 31)]. Robust, initially widening tubarium; ancora umbrella shallow, saucer-

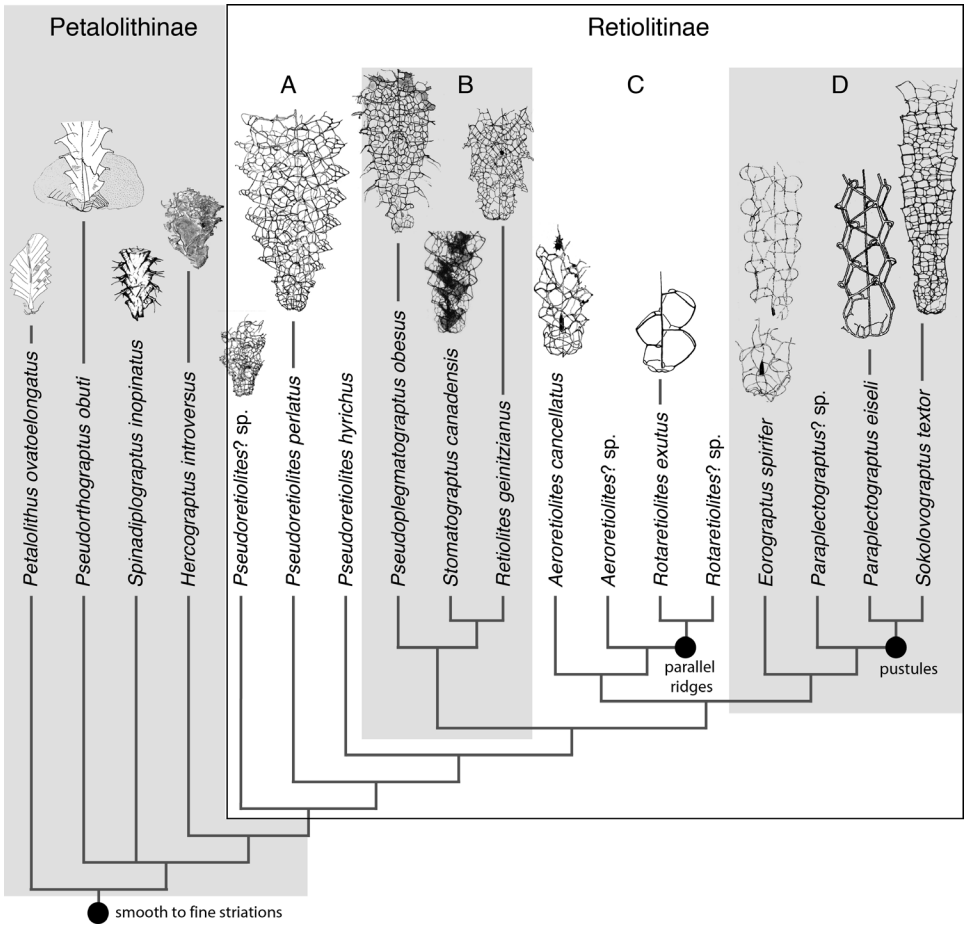


FIG. 273. Cladogram resulting from the analyses that included all taxa in the study of MELCHIN, LENZ, and KOZŁOWSKA (new; based on Melchin, Lenz, & Kozłowska, 2017, fig. 5).

shaped with few polygonal meshes; nema with connecting lists; triangular proximal lateral orifices and small subcircular proximal ventral orifices; reverse side thecal walls with zigzag list; ventral sides defined by horizontal thecal lips and vertical pleural lists; lateral apertural lists inclined at 45° to 60° to tubarium axis; proximal thecal orifices occasionally with reticular hoods formed from the ancora sleeve; unornamented thecal membrane; ancora sleeve with dense and robust reticulum; narrow external common canals without stomata; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus/Streptograptus crispus* Biozone)–*Wenlock (Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 274,*1a*. **R. geinitzianus* (BARRANDE), neotype (selected by LOYDELL & ŠTORCH, 1996 and accepted by ICZN, Opinion 1901, 1998), NM L31612, Llandovery, *Cyrtograptus murchisoni* Biozone, Vyskočilka, Czech Republic, scale bar, 10 mm (new).——FIG. 274,*1b*. *R. australis* M'COY, 1875, GSC137748, ?lower Wenlock, Arctic Canada, scale bar, 1 mm (new).——FIG. 274,*1c*. *Retiolites* sp., GSC 114221, with proximal thecal hoods, Llandovery, Upper Telychian, *Cyrtograptus sakmaricus* Biozone, Arctic Canada, scale bar, 1 mm (Kozłowska-Dawidziuk & Lenz, 2001, fig. 2,*2*).

Aeroretiolites MELCHIN, LENZ, & KOZŁOWSKA, 2017, p. 139 [**A. cancellatus;* OD]. Slender tubarium with few lists; prosicula present; ancora umbrella with spiral lists and continuous undulating rim; ventral side bears pleural lists, looped apertural lists and inclined mid-ventral lists connected to transverse lists; nema with connecting lists on obverse side; pleural lists joined to middle of lateral apertural lists; ancora sleeve weakly developed; ancora sleeve lists with seams facing outward; bandages finely

striated. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone): Arctic Canada.——Fig. 274,*3a–b*. **A. cancellatus; 3a,* holotype, GSC 137651, proximal end; *3b,* paratype, GSC 137653, distal fragment; Arctic Canada; scale bars, 1 mm (Melchin, Lenz, & Kozłowska, 2017, fig. 14).

Baculograptus Lenz & Kozłowska-Dawidziuk, 2002a, p. 329 [**Gothograptus chainos* Lenz, 1993a, p. 17; OD]. Tubarium with appendix; ancora umbrella strongly asymmetrical, with paired ventral lobes; nema distally incorporated into lateral wall and in appendix; kidney-shaped ventral orifices; ventral walls with thecal lips, geniculum, long lateral apertural lists, short pleural lists, and mid-ventral lists; parietal lists initially zigzag, distally oblique; reticulum present; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli–Colonograptus ludensis* Biozones): Arctic Canada; UK, ?Australia (New South Wales).——Fig. 274,*2a–c*. **B. chainos* (Lenz); *2a,* holotype, GSC 104004, ventrolateral view (Lenz, 1993b, pl. 7,*6*); *2b,* GSC 120709, lateral view (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 10,*1*); *2c,* GSC120717, distal end with appendix; Wenlock, upper Homerian, *Colonograptus ludensis* Biozone, Arctic Canada, scale bars, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 10,*6*).

Cometograptus Kozłowska-Dawidziuk, 2001, p. 84 [**C. tomczyki;* OD]. Robust, variably shaped tubarium; shallow ancora umbrella with six meshes; nema free; large proximo-lateral orifices more than half width of tubarium; ventral sides with thecal lips, pleural lists, and lateral thecal lists; mid-ventral lists may be partially developed; genicular structures lacking or developed as spines, loops, or hoods; stomata may be present; long mid-lateral spines with seams on ancora sleeve wall in some species; lists of ventral walls with seams inside; ancora sleeve seams outside; bandages with pustules. *Silurian, Wenlock* (*lower Homerian, Cyrtograptus lundgreni* Biozone): Kazakhstan, Czech Republic, Germany, Poland, USA (Nevada); Canada (Arctic).——Fig. 275,*2a*. **C. tomczyki*, holotype, ZPAL G.24/8, Bartoszyce core, northeastern Poland, scale bar, 1 mm (Kozłowska-Dawidziuk, 2001, fig. 5b).——Fig. 275,*2b*. *C. apsis* Lenz & Kozłowska-Dawidziuk, 2001, GSC 126935, with portions of bandages on lateral wall of theca, Arctic Canada, scale bar, 1 mm (Lenz & Kozłowska, 2006, fig. 8,*6*).

Dabashanograptus Ge, 1990, p. 82 [**D. chengkouensis;* OD]. Robust and distinctly widening tubarium; prosicula preserved; ancora umbrella unknown; nema with connecting lists; reticulum with coarse polygonal meshes of more or less equal size. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone): China (Sichuan).——Fig. 274,*4a–b*. **D. chengkouensis,* holotype, NIGP 21147a–b (part and counterpart), Chengkou, Sichuan, China; scale bars, 1 mm (Ge, 1990, pl. 10).

Doliograptus Lenz & Kozłowska-Dawidziuk, 2002a, p. 331 [**D. latus;* M]. Ovate tubarium; shallow ancora umbrella with undulate rim; nema free; kidney-shaped lateral proximal orifices; ventral walls with thecal lips, genicular lists, pleural lists, lateral thecal and mid-ventral lists; ancora sleeve walls with vague zigzag pattern; dense reticulum; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli* Biozone): Canada (Arctic).——Fig. 275,*3a–b*. **D. latus; 3a,* holotype, GSC 104678, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2001, fig. 10.6); *3b,* GSC 104679, large, fairly complete specimen, note glue covering thecal outer walls; scale bar, 1 mm (Lenz, 1994b, fig. 6,*7*).

Eiseligraptus Hundt, 1959, p. 15 [**Plegmatograptus eisenacki* Hundt, 1951a, p. 56, fig. 13; OD]. Robust, largely parallel-sided tubarium; free nema with branched nematularium emanating from a single point; ancora umbrella incompletely known; ancora sleeve with regular hexagonal meshes. *Silurian, Llandovery* (*Telychian Spirograptus turriculatus* Biozone): Germany.——Fig. 275,*1a*. **E. eisenacki* (Hundt), holotype, BAF H4667, Weinberg bei Hohenleuben, Germany, scale bar, 1 mm (new).——Fig. 275,*1b*. *E. cystifer* Hundt, 1959, holotype, BAF 67 H4104, Weinberg bei Hohenleuben, Germany, scale bar, 1 mm (new).

Eisenackograptus Kozłowska-Dawidziuk, 1990, p. 203, *ex Gothograptus* (*Eisenackograptus*) Kozłowska-Dawidziuk, 1990, p. 203, Kozłowska-Dawidziuk, 1995, p. 272 [**Gothograptus eisenacki* Obut & Sobolevskaya, 1965, p. 41; OD]. Finite tubarium with prominent appendix; shallow, asymmetrically developed ancora umbrella; proximal lateral orifices kidney-shaped; nema incorporated into wall at base of appendix; thecal orifices directed distally; ventral thecal walls undulose, formed from thecal lips, short pleural lists, long lateral apertural lists, and partial mid-ventral lists; transverse lists present; reticulated ventral thecal walls extending downward into tubarium; irregular reticulum with indistinctly developed oblique parietal lists; outer ancora may be present; ancora sleeve lists with seams facing outward; bandages pustulose to almost smooth and occasionally striate. *Silurian, Wenlock* (*upper Sheinwoodian, Cyrtograptus perneri* Biozone–*lower Homerian, Cyrtograptus lundgreni* Biozone): Russia (Taimyr), Poland, Canada (Arctic), Latvia.——Fig. 275,*4a–b*. **E. eisenacki* (Obut & Sobolevskaya); *4a,* holotype, CINGR 33/8783, 1087a/24 *Testograptus testis* Biozone, central Taimyr, Russia, scale bar, 1 mm (Sobolevskaya, 2011, p. 259; specimen lost); *4b,* GSC 104017, very well-preserved specimen, Wenlock, Lower Homerian, *Cyrtograptus lundgreni* Biozone, Arctic Canada, scale bar, 1 mm (new).

Eorograptus Sennikov, 1984, p. 54 [**Pseudoplegmatograptus singularis* Sennikov, 1976, p. 160; OD]. Tubarium parallel sided; prosicula without virga; nema with connecting lists; ancora umbrella shallow, bowl-shaped, with spiral threads; ventral side formed by vertical pleural lists and looping horizontal thecal lips; zigzag lists on reverse side;

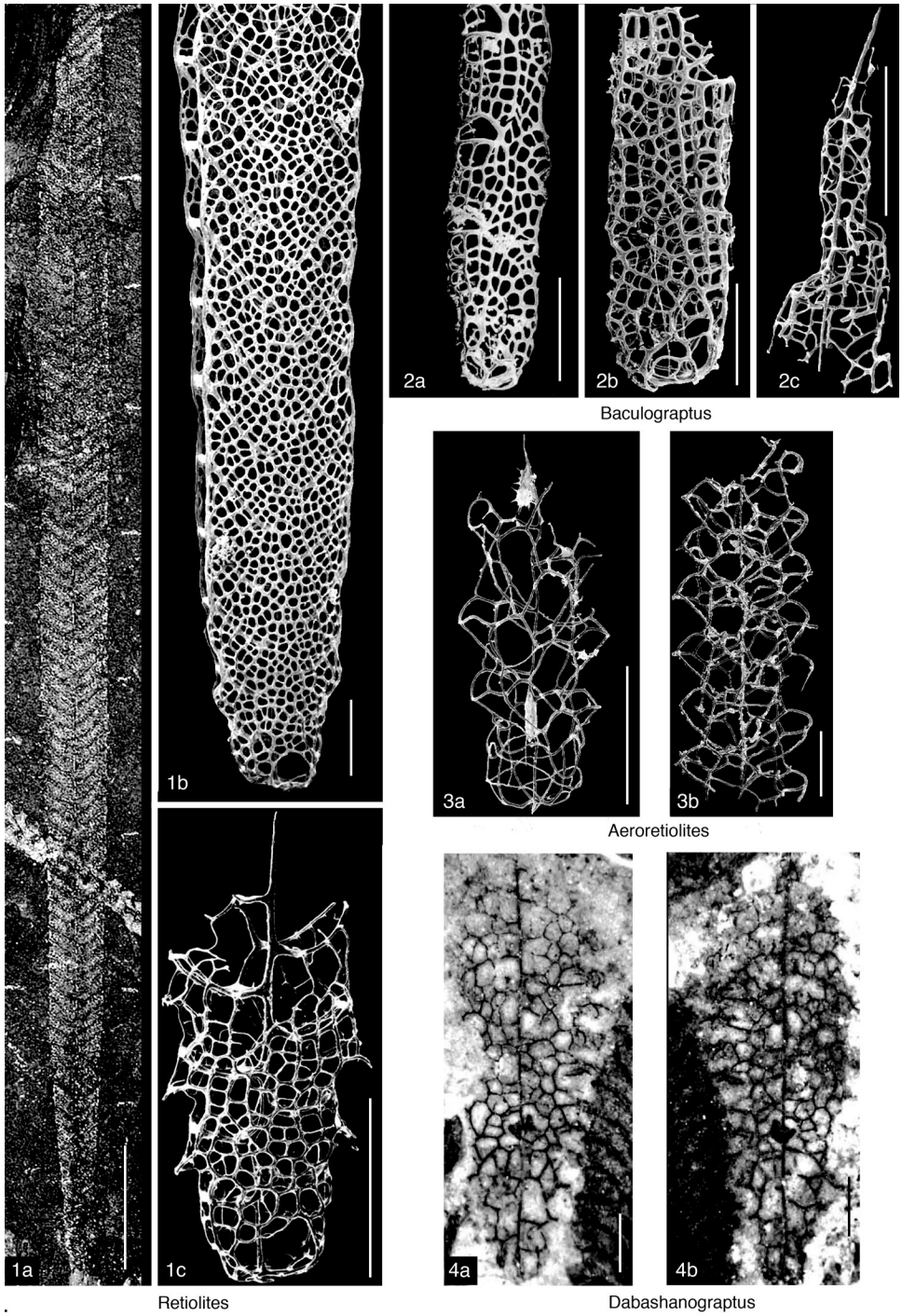


FIG. 274. Retiolitidae (Retiolitinae) (p. 402–404).

transverse lists connect obverse and reverse sides of tubarium; no reticulum; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*upper Aeronian, Lituigraptus convolutus* Biozone–*lower Telychian, Spirograptus minor/Rastrites linnaei* [=*Spirograptus guerichi*] Biozone): Siberia; Canada (Arctic).——Fig. 276,*1a.* **E. singularis* (Sennikov), holotype, image inverted to show better contrast, Llandovery, lower Telychian, *minor/linnaei* Biozone (=*guerichi* Biozone), Altai, Siberia, scale bar, 1 mm (Sennikov, 1976, pl. 8).——Fig. 276,*1b–c, E. spirifer* Melchin, Lenz, & Kozłowska, 2017; *1b,* paratype, GSC 137646, distal part showing horizontal thecal loops, parallel pleural lists, and prosicula; *1c,* GSC 137650, proximal end showing prosicula and spiraled ancora umbrella, Landovery, Aeronian, *Lituigraptus convolutus* Biozone, Arctic Canada; scale bars, 1 mm (Melchin, Lenz, & Kozłowska, 2017, fig. 13.8–13.9).

Giganteograptus Lenz & Kozłowska, 2007, p. 497 [**Plegmatograptus giganteus* Bouček & Münch, 1944, p.17 (p. 543, German text); OD]. Large tubarium with coarse meshwork of relatively thin lists; ancora umbrella unknown; nema with connecting lists joined to middle of transverse lists; thecae outlined by transverse lists, lateral apertural lists, and thecal lips with paired proximolaterally projecting spines; parietal lists on obverse side with zigzag structure, oblique lists on reverse side; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Llandovery* (*Telychian, Monoclimacis griestoniensis* Biozone–*Cyrtograptus sakmaricus* Biozone): China (Ziyang), UK, Czech Republic, Germany, Canada (Arctic).——Fig. 276,*3a–b*. **G. giganteus* (Bouček & Münch); *3a,* paratype, PŠ84a, ancora umbrella missing, Llandovery, Telychian, *Monoclimacis griestoniensis* Biozone, Czech Republic (Lenz & Kozłowska, 2007, fig. 2); *3b,* GSC 38906, isolated fragment, Llandovery, Telychian, *Cyrtograptus lapworthi* Biozone, Arctic Canada (Lenz & Kozłowska, 2007, fig. 6). Scale bars, 1 mm.

Gothograptus Frech, 1897, p. 670 [**Retiolites nassa* Holm, 1890, p. 25; OD]. Finite tubarium with appendix; ancora umbrella with strongly undulating rim and paired ventral lobes; outer ancora in some species; nema with connecting lists, incorporated into obverse ancora sleeve wall above first or second theca; reverse side of ancora sleeve with oblique parietal lists; ventral side with thecal lips, genicular lists, mid-ventral lists, long lateral apertural lists, and short pleural lists; ancora sleeve and ventral thecal walls densely reticulated; genicular hoods variably formed from microfuselli or a meshwork of lists; extensive veils cover the apertures in some taxa; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone–*Colonograptus praedeubeli/deubeli* Biozone): worldwide.——Fig. 276,*4a–b*. **G. nassa* (Holm); *4a,* holotype, NRM-PZ Cn0025546, Wenlock, upper Homerian, *Gothograptus nassa* Biozone, Gotland, Sweden (Holm, 1890, pl. 2,*12*); *4b,* mature form, Bartoszyce IG-1 drill core, Poland (Kozlowska, 2016, fig. 1A). Scale bars, 1 mm.——Fig. 276,*4c, G. diminutus* Kozłowska, Bates, Zalasiewicz, & Radzevičius, 2019, holotype *4c,* ZPAL G.29/21, Wenlock, upper Homerian, *Gothograptus nassa* Biozone, northeastern Poland (Kozłowska-Dawidziuk, 2004, fig. 5D). Scale bar, 1 mm.

Hoffmanigraptus Kozłowska, 2021, p. 933 [*H. varsoviensis;* OD]. Finite tubarium of variable length, widening from proximal end; ancora umbrella shallow with six meshes; nema free, may bear a nematularium; kidney-shaped lateral proximal orifices; ventral wall formed by thecal lips, genicular lists, lateral thecal lists and pleural lists; mid-ventral lists absent to well developed; reticulofusellar genicular processes may be present; zigzag parietal lists on obverse and reverse sides; reticulum well developed to absent; ancora sleeve lists with seams facing inward; bandages with pustules.——Fig. 276,*2. *H. varsoviensis,* holotype, obverse view; scale bar, 1 mm (Kozłowska, 2021, fig. 1A2).

Holoretiolites Eisenack, 1951, p. 153 [**Retiolites mancki* Münch, 1931, p. 35; OD] [=*Balticograptus* Bouček & Münch, 1952, p. 117 (type, *Retiolites erraticus* Eisenack, 1951, p. 136, OD), syn. by Maletz, 2008, p. 304]. Finite tubarium; shallow, asymmetrical ancora umbrella with six meshes; outer ancora in some species; nema free; proximal ventral orifices of hexagonal shape; ventral side with thecal lips, genicular lists, pleural lists(?), and long mid-ventral lists; zigzag lateral apertural lists on main parts of obverse and reverse sides; reticulum poorly developed to absent; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Lobograptus scanicus* Biozone): Kyrgyzstan, Germany, Poland, Canada (Arctic).——Fig. 277,*2a–c*. **H. mancki* (Münch); *2a,* ZPAL G.28/1, Baltic glacial boulder specimen with long appendix, Ludlow, *Lobograptus scanicus* Biozone, Jarosławiec, northeastern Poland (Kozłowska-Dawidziuk & Lenz, 2001, fig. 3,*4*); *2b,* idealized reconstruction, ventral view of specimen (Münch, 1931, fig. 4); *2c,* holotype, whereabouts unknown, Baltic glacial erratic, Ludlow, Gorstian, Uckermark, northern Germany (Münch, 1931, fig. 5). Scale bars, 1 mm.

Kirkigraptus Kozłowska & Bates, 2008, p. 108 [**K. inexpectans;* M]. Parallel sided tubarium; ancora umbrella and nema unknown; lateral (parietal?) lists connect the genicular lists of the first thecal pair; ventral side formed by thecal lips, geniculum, pleural lists, lateral apertural lists, and mid-ventral lists; horizontal parietal lists start at fourth thecal pair level; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone): Poland.——Fig. 277,*3a–b*. **K. inexpectans; 3a,* ZPAL G. 40/02, distal end of tubarium; *3b,*

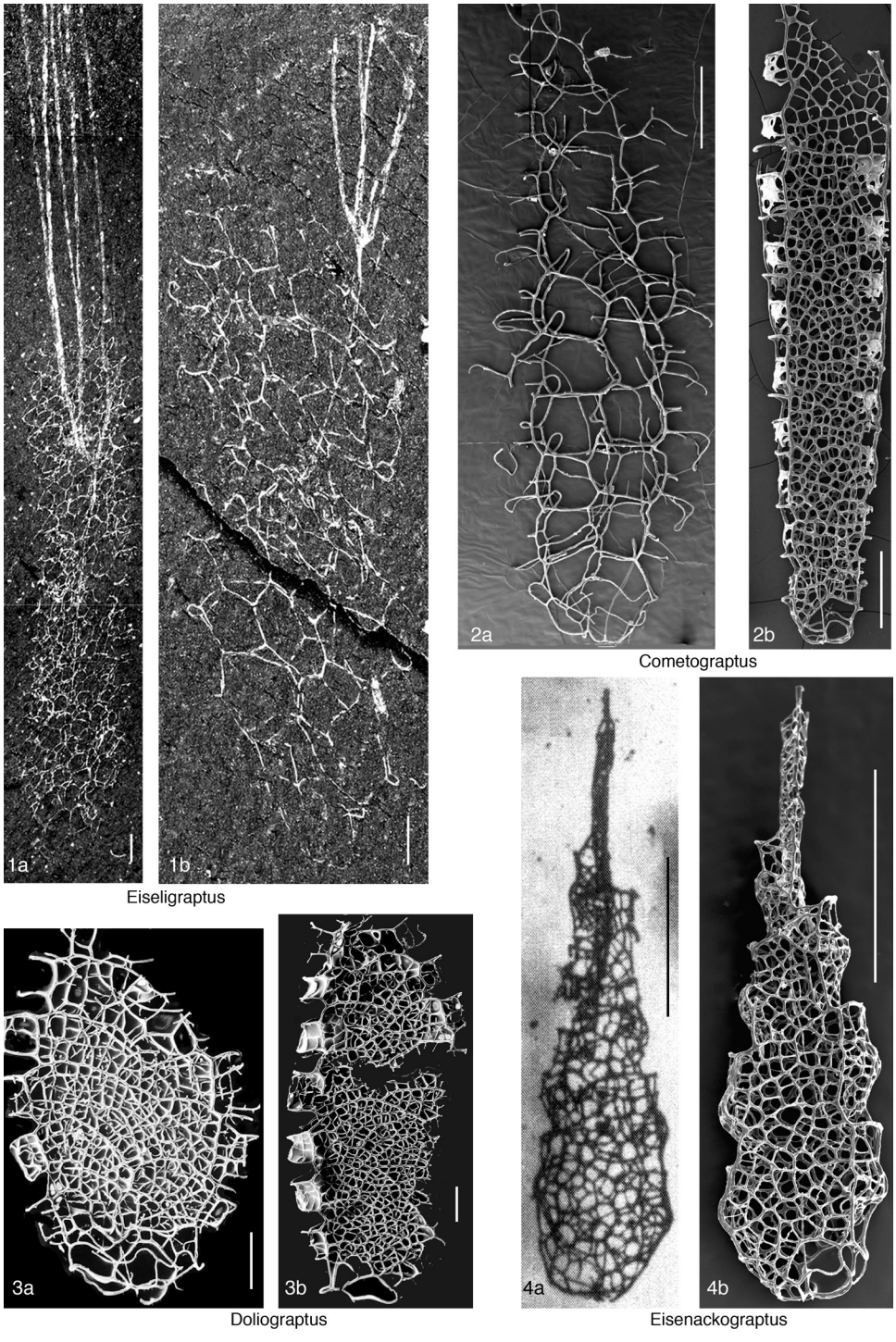


FIG. 275. Retiolitidae (Retiolitinae) (p. 404).

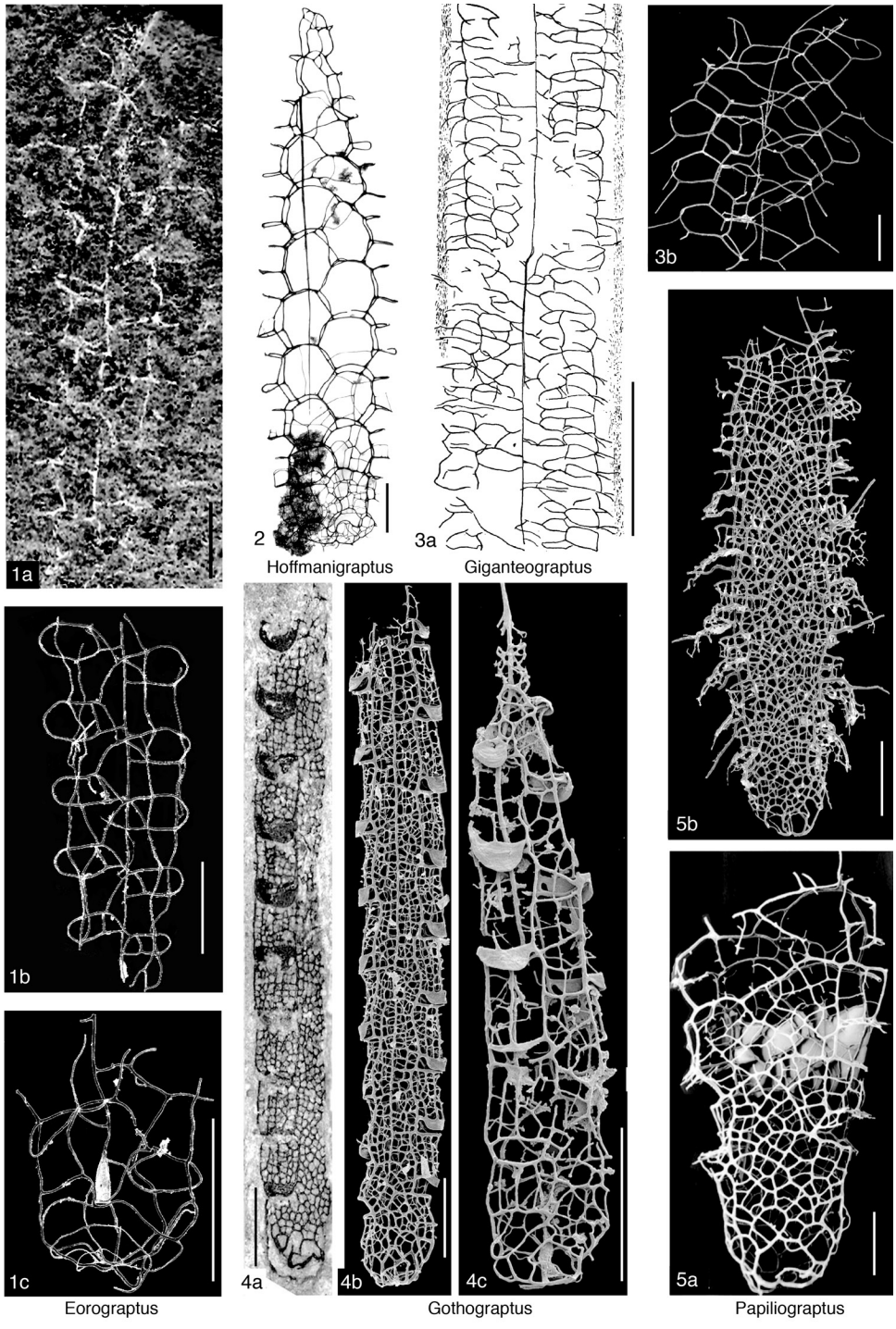


FIG. 276. Retiolitidae (Retiolitinae) (p. 404–409).

holotype, ZPAL G. 40/1, proximal part of tubarium; northeastern Poland; scale bars, 1 mm (Kozłowska & Bates 2008, fig. 3).

Neogothograptus Kozłowska-Dawidziuk, 1995, p. 303 [**N. purus;* OD]. Finite tubarium with appendix; shallow, asymmetrical ancora umbrella with seven meshes and strongly undulating rim; outer ancora may be present; nema free; ventral side with thecal lips, genicular lists, short pleural lists, long lateral apertural lists, and mid-ventral lists; genicular hoods or processes in some, rarely also on proximal ventral orifices; parietal lists on ancora sleeve walls almost horizontal; reticulum dense to absent; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli* Biozone)–*Ludlow* (*Gorstian, Lobograptus scanicus* Biozone): Kyrgyzstan, Poland, Germany, Canada (Arctic), ?Australia.——Fig. 277,*1a–b*. **N. purus; 1a,* ZPAL G.XVI/1353, small finite specimen; *1b,* holotype, ZPAL G.XVI/1341, Ludlow, Gorstian, *Lobograptus scanicus* Biozone, Baltic erratic boulder, Jarosławiec, northern Poland, scale bars, 1 mm (Kozłowska-Dawidziuk, 1995, fig. 27F–27G).——Fig. 277,*1c*. *N. thorsteinssoni* Lenz & Kozłowska-Dawidziuk, 2004, MB.G. 1083.2, Ludlow, Baltic glacial boulder, scale bar, 1 mm (Maletz, 2008, fig. 1o).

Papiliograptus Lenz & Kozłowska-Dawidziuk, 2002a, p. 331 [**P. papilio;* OD]. Finite tubarium, but appendix unknown; ancora umbrella with extensive paired ventral lobes and strongly undulating rim; ventral sides formed by thecal lips, genicular lists, pleural lists, lateral apertural lists, and mid-ventral lists; dense reticulum with indistinct zigzag or almost horizontal parietal lists; reticulate genicular hoods in some species; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli* Biozone): Lithuania, Poland, Germany, Canada (Arctic).——Fig. 276,*5a*. **P. papilio,* holotype, GSC 104681, white infilling is glue, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 12.1).——Fig. 276,*5b*. *P. retimarginatus* Kozłowska & Bates, 2021, VU RET-1, complete tubarium, Šiupyliai-69 borehole, Lithuania, scale bar, 1 mm (Kozłowska & Radzevičius, 2013, fig. 3a).

Paraplectograptus Bouček & Münch, 1952, p. 37 (also cited as *Paraplectograptus* Bouček & Münch in Příbyl, 1948a, p. 21, *nom. nud.*) [**Retiolites eiseli* Manck, 1918, p. 338; M] [=*Pseudoplectograptus* Obut & Zaslavskaya, 1983, p. 110 (type, *Plectograptus praemacilentus* Bouček & Münch, 1952, Czech text, p. 26; English text, p. 124, OD), syn. herein)]. Slender, parallel-sided to distally widening or finite tubarium; ancora umbrella with seven meshes and often incomplete rim; nema with connecting lists; ventral sides formed by thecal lips, short lateral apertural lists, and long pleural lists; transverse lists present; ancora sleeve lists well developed to lacking; ancora sleeve lists with seams facing outward; bandages with pustules. *Silurian, Wenlock* (*Sheinwoodian, Monograptus riccartonensis* Biozone–*lower Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 277,*6a*. *P. praemacilentus,* holotype, NM L2727, Wenlock, lower Homerian, *Cyrtograptus lundgreni* Biozone, Bítov, Czech Republic, scale bar, 1 mm (new).——Fig. 277,*6b*. *P. simplex* Kozłowska-Dawidziuk, 1995, GSC 119772, Wenlock, *Cyrtograptus perneri* Biozone, Arctic Canada, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2001, pl. 7).——Fig. 277,*6c*. **P. eiseli* (Manck) lectotype, BAF 8/159, ancora umbrella portion missing, Llandovery, middle Telychian, *Monoclimacis griestoniensis* Biozone, Wetterahammer, Thuringia, Germany, scale bar, 1 mm (new).——Fig. 277,*6d*. *P. senarius* Lenz & others, 2012, GSC134631, Wenlock, *Cyrtograptus perneri* Biozone, Arctic Canada, scale bar, 1 mm (Lenz & others, 2012, pl. 1).

Pileograptus Lenz & Kozłowska, 2007, p. 494 [**P. pileatus;* M]. Robust, initially widening tubarium; deep, bowl-shaped ancora umbrella with uniform polygonal meshes; prosicula preserved; nema with connecting lists; ventral side outlined by thecal lips, lateral apertural lists, and pleural lists; transverse lists present; thecal orifices with reticulated hoods; ancora sleeve with fairly dense, polygonal meshwork; chimney-like stomata with meshwork walls; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*upper Telychian, Oktavites spiralis* or *Cyrtograptus lapworthi-C. insectus* Biozone): Arctic Canada.——Fig. 278,*2a–b*. **P. pileatus; 2a,* holotype, GSC 38910, whole specimen; *2b,* enlargement of holotype, showing thecal hood; Arctic Canada; scale bars, 1 mm (Lenz & Kozłowska, 2007, fig. 3).

Plectodinemagraptus Kozłowska-Dawidziuk, 1995, p. 322 [**P. gracilis;* M]. Parallel-sided tubarium; ancora umbrella with six meshes and partially developed rim; ventral walls formed by thecal lips, genicular lists, long mid-ventral lists, pleural lists, and reduced lateral apertural lists or parietal lists; proximal ventral orifices of hexagonal shape; bandages with pustules. *Silurian, Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): Poland.——Fig. 277,*4a–b*. **P. gracilis; 4a,* holotype, ZPAL G.XVI/1406, proximal end of specimen showing ancora umbrella, two ventral orifices and mid-ventral lists of first thecae; *4b,* ZPAL G. XVI/1408, showing proximal ventral orifices and four thecae of one side of tubarium; northeastern Poland; scale bars, 1 mm (Kozłowska-Dawidziuk, 1995, fig. 34).

Plectograptus Moberg & Törnquist, 1909, p. 18 [**Retiolites macilentus* Törnquist, 1887, p. 491; OD] [=*Agastograptus* Obut & Zaslavskaya, 1983, p. 107, English translation, Obut & Zaslavskaya, 1986, p. 210 (type, *A. robustus,* OD), syn. by Kozłowska-Dawidziuk, 2002, p. 459]. Tubarium parallel sided or narrowing distally; shallow ancora umbrella with five meshes and only partially developed rim; nema free, may bear a nematularium; large proximal lateral orifices of tubarium width;

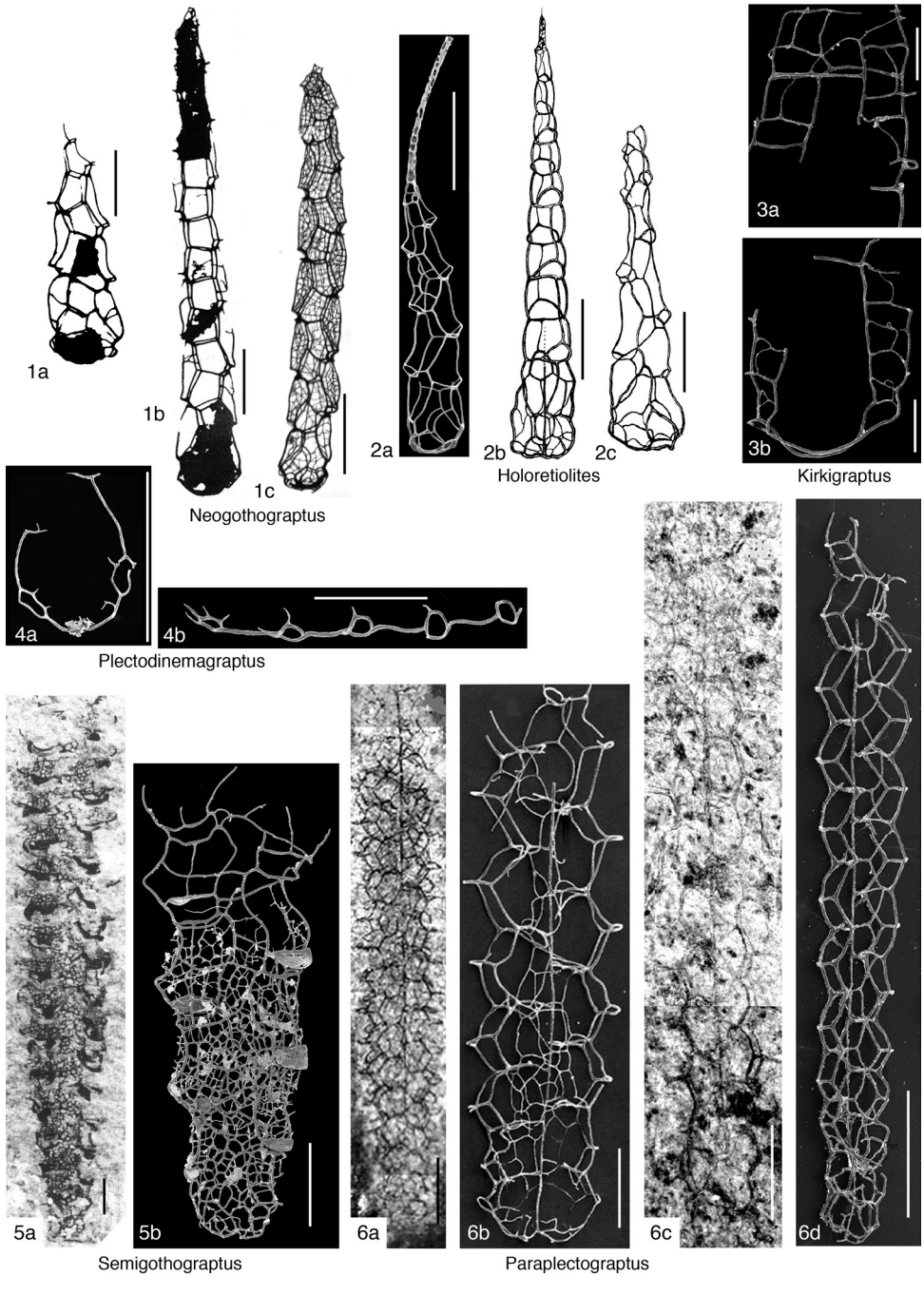


FIG. 277. Retiolitidae (Retiolitinae) (p. 406–413).

ventral sides formed by thecal lips, genicular lists, lateral apertural, lists pleural lists, and mid-ventral lists; single or paired genicular processes in some species; reticulum well developed to absent; zigzag parietal list lists; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni–Lobograptus scanicus* Biozone): worldwide.——Fig. 279,*1a–b*. **P. macilentus* (Törnquist); neotype, SMF XXIV 433, photograph and line drawing of specimen, Ludlow, Gorstian, *Neodiversograptus nilssoni* Biozone, Wetterahammer, Thuringia, Germany, scale bars, 1 mm (Bates & others, 2006, fig. 1).——Fig. 279,*1c*. *P. robustus* (Obut & Zaslavskaya, 1983), holotype, CNIGR 251/42-2, chemically isolated specimen, scale bar, 1 mm (Obut & Zaslavskaya, 1986, fig. 1).

Pseudoplegmatograptus Přibyl, 1948a, p. 22 [**Retiolites perlatus obesus* Lapworth, 1877, p. 137; OD] [=?*Sinostomatograptus* Huo, 1957 (type, *S. mui,* OD), syn. by Lenz & Kozłowska, 2007, p. 492]. Tubarium widening distally; ancora umbrella with polygonal meshes; nema with connecting lists; no virga; thecal orifices with paired apertural spines; ventral sides defined by thecal lips and pleural lists; reticular lists on ancora sleeve irregular; narrow, but deep external common canal with large stomata; inner and outer reticula of ancora sleeve present; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Aeronian, Stimulograptus sedgwickii* Biozone)–*Wenlock* (*Sheinwoodian, Monograptus riccartonensis* Biozone): worldwide.——Fig. 278,*1a–d*. **P. obesus* (Lapworth); *1a–b,* holotype, BU 1363; *1a,* whole specimen; *1b,* enlarged portion of specimen showing single curved thecal spines, some showing secondary to tertiary branching, Llandovery, lower Telychian, *Spirograptus turriculatus* Biozone, County Down, Ireland (Elles & Wood, 1908, pl. 34,*12b*); *1c,* NMW 91.52G, immature specimen with stoma (*arrow*) and shallow ancora umbrella made of few meshes, lower Telychian, *Spirograptus turriculatus* Biozone, Osmundsberget, Sweden (Bates & Kirk, 1992, fig. 180); *1d,* GSC 78423*,* mature specimen without ancora umbrella, Llandovery, lower Telychian, *Spirograptus turriculatus* Biozone, Arctic Canada (Lenz & Melchin, 1987, pl. 1,*1*). Scale bars, 1 mm.

Pseudoretiolites Bouček & Münch, 1944, p. 22, *ex Retiolites* (*Pseudoretiolites*) Bouček & Münch, 1944, p. 22, Obut, Sobolevskaya, & Nikolaev, 1967, p. 82 [**Retiolites perlatus* Nicholson, 1868a, p. 530; OD] [=?*Tscharyschograptus* Sennikov, 1984, p. 51 (type, *T. altaicus* Sennikov, 1984, p. 51, OD), syn. by Loydell, 1993, p. 61]. Robust, distally widening, parallel-sided or ovate tubarium; prosicula preserved; deep, spiraled ancora umbrella; nema with connecting lists; thecal lists on reverse side with zigzag; ventral sides defined by looping thecal lips and curved pleural lists; mid-ventral lists with distinct ventral zigzag structure distally; ancora sleeve with dense, irregular meshwork; small lateral orifices present proximally; stomata present in some species; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Telychian, Cyrtograptus insectus* Biozone): worldwide.——Fig. 278,*3a–d*. **P. perlatus* (Nicholson); *3a,* GSC 137613, complete specimen with well-developed spiral ancora umbrella and well-preserved zigzag list thecal ventral walls, Llandovery, upper Aeronian, *Lituigraptus convolutus* Biozone, Arctic Canada (Melchin, Lenz, & Kozłowska, 2017, fig. 7,*1*); *3b, 3d,* holotype, BU 1361, Llandovery, upper Aeronian, Cumbria (English Lake District), UK (new); *3c,* GSC 137617, ancora umbrella showing well-developed spiral pattern and sicula, Llandovery, upper Aeronian, *Lituigraptus convolutus* Biozone, Arctic Canada (Melchin, Lenz, & Kozłowska, 2017, fig. 7,*6*). Scale bars, 1 mm.

Reticuloplectograptus Kozłowska, Bates, & Piras, 2010, p. 1412 [**R. serpaglii;* M]. Robust tubarium; ancora umbrella shallow with incompletely developed rim; nema free; medium size proximal lateral orifices; ventral wall with thecal lips, genicular lists, pleural lists, lateral thecal lists, and mid-ventral lists; paired, reticular genicular processes; ancora sleeve with small lateral and ventral proximal orifices; dense reticulum on ancora sleeve and ventral thecal walls; zigzag parietal list on obverse and reverse sides; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Lobograptus progenitor* Biozone): Czech Republic, Poland.——Fig. 279,*3a–b*. *R. serpaglii; 3a,* holotype, ZPAL G.43/01; *3b,* paratype, ZPAL G.43/02, less mature specimen, complete ancora umbrella, Ludlow, *Neodiversograptus nilssoni* Biozone, northeastern Poland, scale bars, 1 mm (Kozłowska, Bates, & Piras, 2010, fig. 6–7).

Rotaretiolites Bates & Kirk, 1992, p. 265 [**R. exutus;* OD]. Minute tubarium with few thecae; nema with connecting lists; sicula represented by prosicular apertural ring; shallow ancora umbrella with four radial ribs and subcircular rim; ancora umbrella rim joined to mid-ventral list of theca 1^2 by unseamed list; thecae outlined by everted apertural loops, transverse lists, and mid-ventral lists; zigzag list on reverse side extends from prosicular ring; mid-ventral list of theca 1^1 attached directly to ancora umbrella rim; spines on mid-ventral lists and lateral thecal rims may be present; ancora sleeve not recognized; bandages with coarse parallel striae. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone–*Spirograptus turriculatus* Biozone): Sweden, Canada (Arctic).——Fig. 279,*2*. **R. exutus,* holotype, NMW91.52G.345, lower Telychian, *Spirograptus turriculatus* Biozone, Dalarna, Sweden, scale bar, 1 mm (Bates & Kirk, 1992, fig. 66).

Sagenograptoides Lenz & Kozłowska, 2010, p. 156, *nom. nov. pro Sagenograptus* Lenz & Kozłowska-Dawidziuk, 2001, p. 15, *non Sagenograptus* Obut & Sobolevskaya, 1962, p. 74 (Anisograptidae)

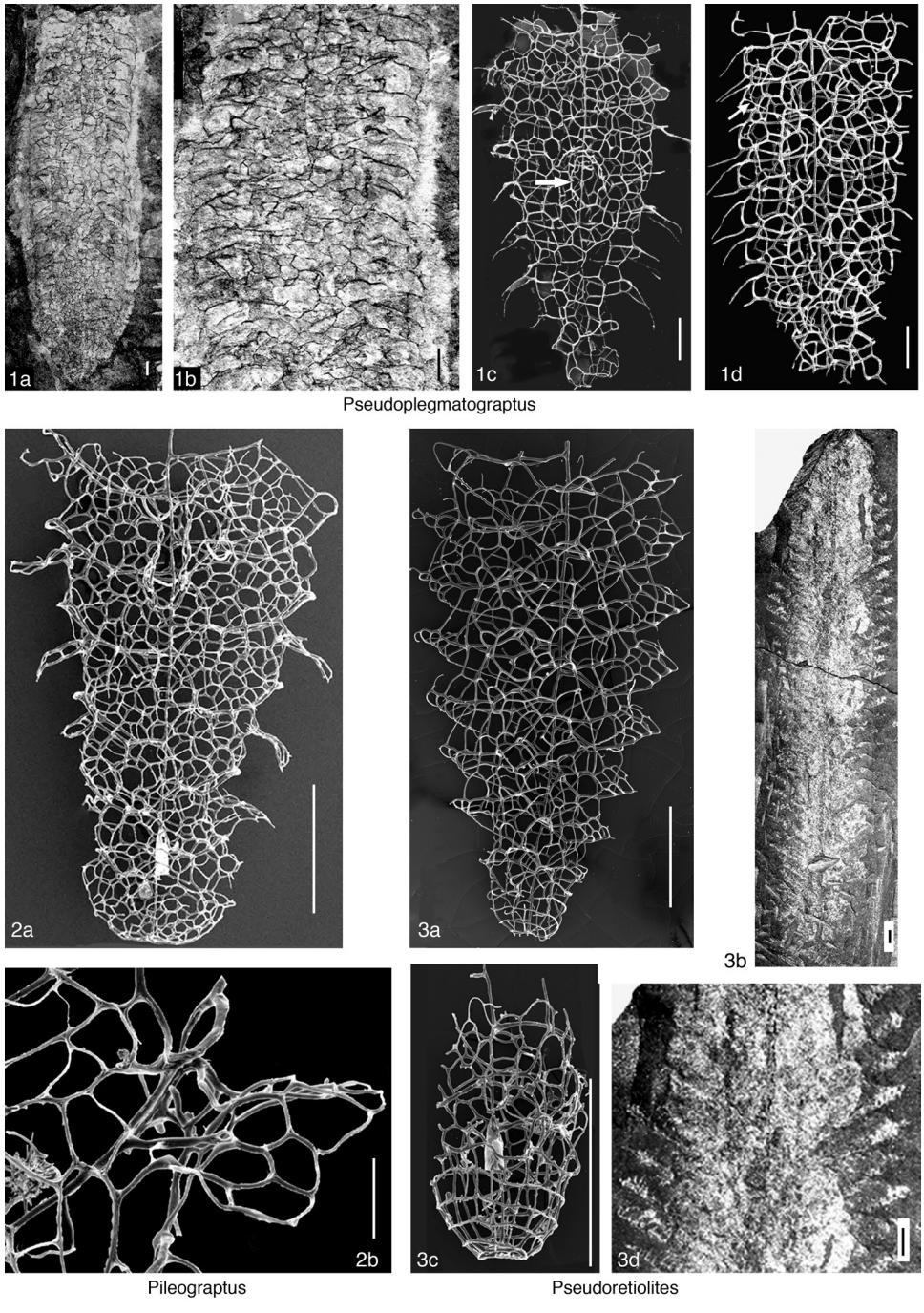


FIG. 278. Retiolitidae (Retiolitinae) (p. 409–411).

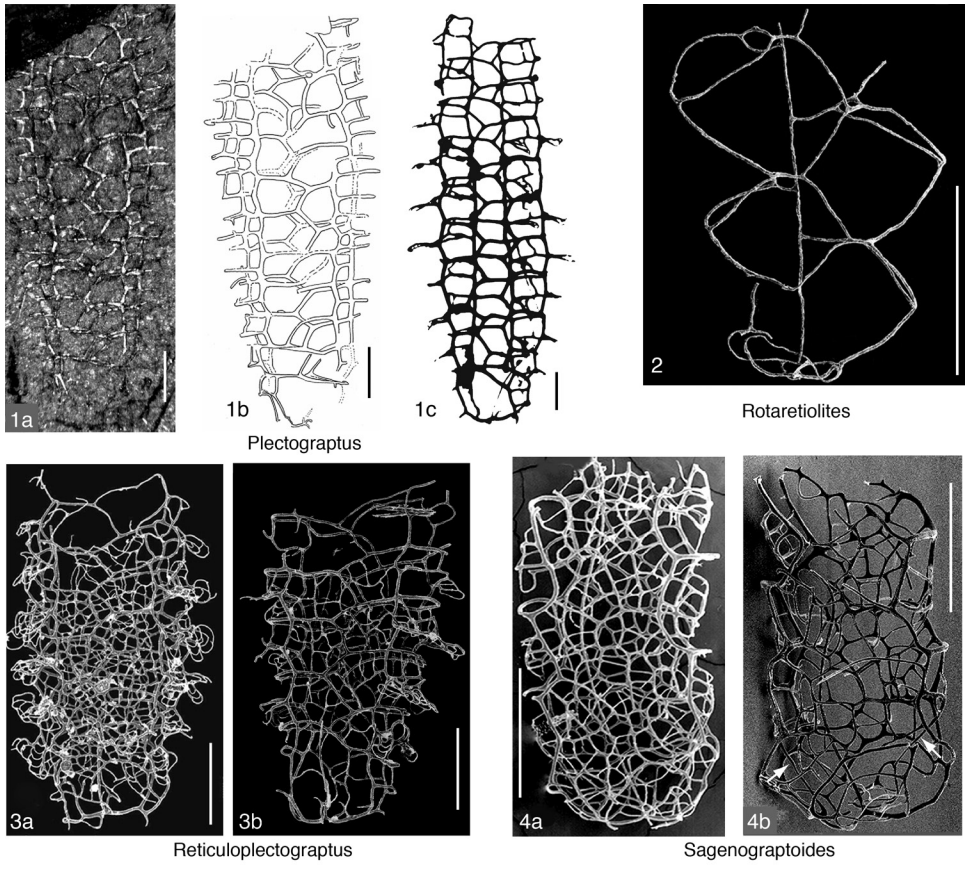


Fig. 279. Retiolitidae (Retiolitinae) (p. 409–413).

[**S. arctos* Lenz & Kozłowska-Dawidziuk, 2001, p. 15; M]. Tubarium parallel sided; ancora umbrella shallow; nema free; proximal lateral orifices kidney-shaped; ventral wall defined by thecal lips, pleural lists, and lateral apertural lists, mid-ventral lists on thecae 1^1 and 1^2 attached to ancora umbrella rim; transverse lists in first pairs of thecae; irregular reticulum on ventral thecal walls and ancora sleeve; lists of ventral walls with pustules and seams inside; ancora sleeve lists with seams facing outward; outer ancora sleeve lists with seams facing inward may be present. *Silurian, Wenlock* (*lower Homerian, Cyrtograptus lundgreni* Biozone): Canada (Arctic).——Fig. 279,*4a–b*. **S. arctos; 4a,* holotype, GSC 99179; *4b,* GSC 119775, showing complete mid-ventral lists of $th1^1$ and $th1^2$ (*arrows*); Wenlock, lower Homerian, *Cyrtograptus lundgreni* Biozone, Arctic Canada, scale bars, 1 mm (Lenz & Kozłowska-Dawidziuk, 2001, pl. 8).

Semigothograptus Kozłowska, 2016, p. 536 [**Gothograptus*? *meganassa* Rickards & Palmer, 2002, p. 228; OD]. Tubarium initially widening gradually from proximal end; ancora umbrella asymmetrical with undulating rim; nema free; proximal ventral orifices of triangular shape; lateral orifices kidney-shaped; ventral wall represented by thecal lips, genicular lists, long convex lateral apertural lists, short pleural lists, and mid-ventral lists; massive genicular hoods; parietal lists oblique; reticulum irregular; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone–*Colonograptus deubeli* Biozone): UK, Czech Republic, Germany, Poland.——Fig. 277,*5a–b*. **S. meganassa* (Rickards & Palmer); *5a,* SM X28550a, holotype, Shropshire, UK, scale bar, 1 mm (Rickards & Palmer, 2002, fig. 4A); *5b,* ZPAL G54/1, Bartoszyce drill core at 1649.2 m, Poland, scale bar, 1 mm (Kozłowska, 2016, fig. 1D).

Semiplectograptus Kozłowska-Dawidziuk, 1995, p. 320 [**S. urbaneki;* M]. Tubarium parallel sided; ancora umbrella incompletely known; nema free; ventral wall formed by thecal lips, genicular lists, and mid-ventral lists; proximal ventral orifices and thecal orifices rhomboid; large proximal lateral orifices; zigzag parietal lists start on level of first pair of thecal orifices; no reticulum; ancora sleeve lists with seams facing inward; bandages with pustules.

Silurian, Ludlow (*lower Ludfordian, Cucullograptus hemiaversus* Biozone–*Cucullograptus aversus* Biozone): Poland.——Fig. 280,*1a–b*. **S. urbaneki; 1a,* holotype, ZPAL G.XVI/1392; *1b,* paratype, ZPAL G.XVI/1394; Ludfordian, *Saetograptus leintwardinensis* Biozone; northeastern Poland; scale bars, 1 mm (Kozłowska-Dawidziuk, 1995, fig. 34a and fig. 27j, respectively).

Sokolovograptus Obut & Zaslavskaya, 1974, p. 161 (English text, Obut & Zaslavskaya, 1976, p. 127) [**Plectograptus*? *textor* Bouček & Münch, 1952, p. 29; OD]. Tubarium parallel sided or widening distally; shallow ancora umbrella with four or more meshes and sometimes incompletely developed rim; outer ancora may be present; nema free; ventral wall built of looping thecal lips and vertical pleural lists; proximal lateral orifices of variable shape and size; ancora sleeve with or without irregularly positioned parietal lists; reticulum variable, from dense to lacking, formed irregularly; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Llandovery* (*Telychian, Cyrtograptus lapworthi* Biozone)–*Wenlock* (*lower Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 280,*2a–c*. **S. textor* (Bouček & Münch); *2a–b,* holotype, NM L2740, complete specimen and enlargement, Wenlock, *Cyrtograptus rigidus* Biozone, Czech Republic (both images inverted to increase contrast), scale bars, 1 mm (new; photo by Petr Štorch); *2c,* GSC 134638, Wenlock, *Cyrtograptus perneri* Biozone, Arctic Canada, scale bar, 1 mm (Lenz & others, 2012, pl. 3).

Spinograptus Bouček & Münch, 1952, p. 130 [**Retiolites spinosus* Wood, 1900, p. 485; OD] [=*Quattuorgraptus* Dobrowolska, 2013, p. 14 (type, *Retiolites muenchi* Eisenack, 1951, p. 138, *nom. correct*. Maletz, 2010b, p. 512 *pro Retiolites münchi* Eisenack, 1951, p. 138, OD), syn. herein]. Tubarium parallel sided or finite, ending with appendix; ancora umbrella shallow with six meshes; outer ancora possible; nema free; kidney-shaped lateral proximal orifices; ventral sides formed of thecal lips, genicular lists, lateral apertural lists, pleural lists; mid-ventral lists absent to well developed; reticulofusellar genicular processes paired, simple to complex, sometime also on ventral prethecal orifices; parietal lists zigzag to irregular; reticulum well developed to absent; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli* Biozone)–*Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone): worldwide.——Fig. 280,*3a–b*. **S. spinosus* (Wood); *3a,* lectotype, BU 1366, Ludlow, *Neodiversograptus nilssoni* Biozone, Wales, UK, scale bar, 1 mm (new); *3b,* ZPAL G. XVI1/1904, Ludlow, *Neodiversograptus nilssoni* Biozone, northeastern Poland, scale bar, 1 mm (new).——Fig. 280,*3c*. *S. clathrospinosus* (Eisenack, 1951), GSC 104663, specimen with completely preserved ancora sleeve wall, Arctic Canada, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 14).——Fig. 280,*3d–e*. *S. muenchi* (Eisenack, 1951); *3d,* holoype, GPIT 180, Nr. 11; *3e,* longer specimen; Baltic erratic boulder, Germany, scale bars, 1 mm (Eisenack, 1951, pl. 22,*9* and 24,*1* (not preserved).

Stomatograptus Tullberg, 1883, p. 42 [**S. toernquisti;* M, =*Retiolites grandis* Suess, 1851, p. 99, see Törnquist, 1890, p. 8]. Tubarium gradually widening initially; ancora umbrella bowl-shaped, with hexagonal meshwork; prosicula present; nema with connecting lists; transverse lists present; ventral walls defined by thecal lips, strongly inclined lateral apertural lists and pleural lists; pleural lists attached to middle part of outward-inclined lateral apertural lists; ancora sleeve well developed, with polygonal meshes; narrow external common canal with stomata; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone)–*Wenlock* (*lower Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 281,*1a–b*. *S. grandis* (Suess); *1a,* neotype, NM L31630 (selected by Štorch, Serpagli, & Barca, 2002, p. 102), Llandovery, upper Telychian, *Cyrtograptus lapworthi* Biozone, Prague region, Czech Republic (new); *1b,* GSC 78432, thecal fusellar floors partially preserved, Llandovery, *Cyrtograptus centrifugus* or *Cyrtograptus murchisoni* Biozone, Arctic Canada (new). Scale bars, 1mm.——Fig. 281,*1c*. *S. canadensis* Lenz, 1988c, GSC, Llandovery, *Cyrtograptus sakmaricus* Biozone, Arctic Canada, scale bar, 1 mm (new).——Fig. 281,*1d–e*. **S. toernquisti; 1d,* holotype, LO 481T, Röstånga, Scania, Sweden; *1e,* LO 482t, Motala, Östergötland, Sweden (specimen missing); scale bars, 1 mm (Tullberg, 1883, pl. 1).

Valentinagraptus Piras, 2006, 584. [**V. simplex;* M]. Tubarium parallel sided; ancora umbrella with four branches, without developed rim; nema free, with nematularium; large proximal lateral orifices; ventral walls composed of vertical pleural and lateral apertural lists, genicular lists and thecal lips; parietal lists more or less horizontal; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Lobograptus progenitor* Biozone): Albania, Czech Republic.——Fig. 281,*2*. **V. simplex,* holotype, CGS SP 183a, Bykoš, Czech Republic, scale bar, 1 mm (Piras, 2006, fig. 7a).

Virgellograptus Kozłowska, 2015, p. 454. [**V. perrarus;* M]. Parallel-sided tubarium; connecting lists link virgella with lateral wall on obverse side; nema free; shallow ancora umbrella with four meshes; ventral wall formed by thecal lips, genicular lists, long lateral apertural lists, and short pleural lists; ancora sleeve with oblique parietal lists on reverse side; reticulum irregularly developed; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Sheinwoodian, Cyrtograptus ellesae* Biozone): Poland.——Fig. 281,*3*. **V. perrarus,* holotype, ZPAL G.52/1, Wenlock, Bartoszyce IG-1 drill core, Poland, scale bar, 1 mm (Kozłowska, 2015, fig. 2).

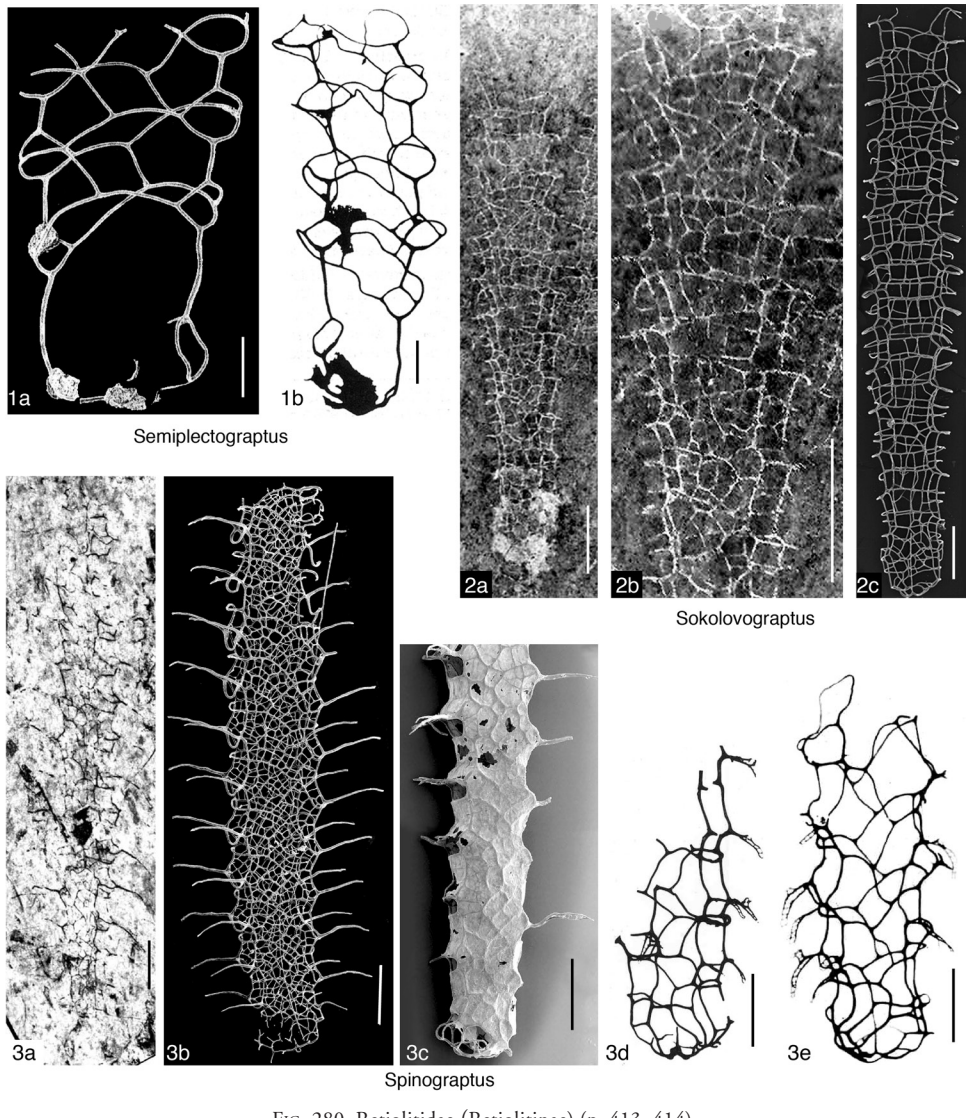


FIG. 280. Retiolitidae (Retiolitinae) (p. 413–414).

Family UNCERTAIN

A number of genera must be regarded as Retiolitidae *incertae sedis* due to incomplete or fragmentary preservation of the material. The genera *Demicystograptus, Parademicystograptus,* and *Thecocystograptus* were introduced by HUNDT (1950) based on the construction of their nematularia. The illustrated material originated from the Aeronian to Telychian of Germany and may be related to *Parapetalolithus,* but due to the poor preservation and illustration, the material cannot be identified with certainty.

Demicystograptus HUNDT, 1950, p. 293 (also cited as *Demicystograptus* HUNDT, 1944 in HUNDT, 1953a, p. 40) [**D. nindeli;* herein] [=*Demicystifer* HUNDT, 1959, pl. 6,*1, nom. nud.* (misspelling of *Demicystograptus* HUNDT, 1950)]. [The genus was not recognized by BULMAN (1970) and was rejected by JONES and RICKARDS (1967). Some species included in the genus *Demicystograptus* may be referred to *Parapetalolithus.*] *Silurian, Llandovery* (*Aeronian,*

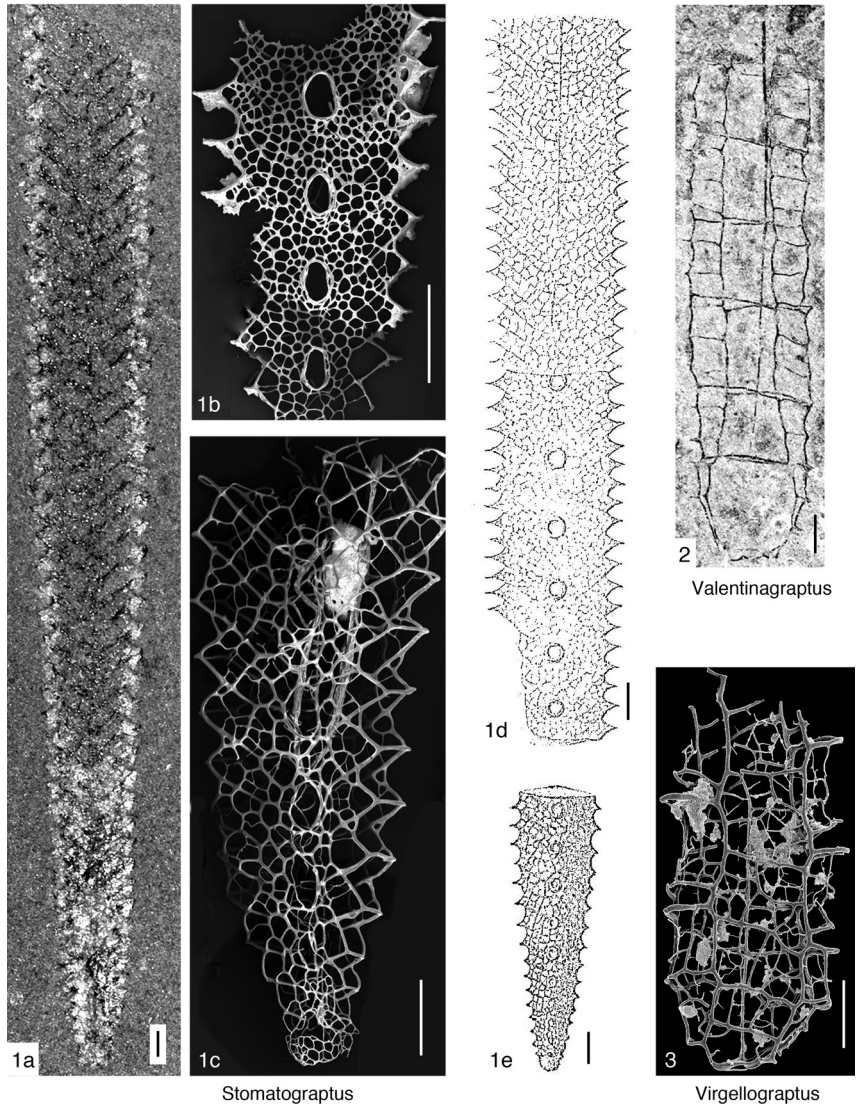


FIG. 281. Retiolitidae (Retiolitinae) (p. 414).

Lituigraptus convolutus Biozone): Germany.——FIG. 282,*3*. **D. nindeli*, BAF H4/68/2295, Igelsberg bei Ronneburg, Thuringia, Germany, scale bar, 5 mm (Hundt, 1950, fig. 11).

Mirorgraptus LENZ & KOZŁOWSKA, 2007, p. 499 [**M. arcticus;* OD]. Straight nema with some lists similar to connecting lists arising from more or less same row along one side of nema and, alternately curving to left or right, diverging 180° to each other, between which loops arise from near base of each connecting list, oriented 90°, distally connecting lists bifurcate and trifurcate; connecting rods and vertically oriented loops probably fully covered by fusellar banding originally. [The type material of *Mirorgraptus* consists of poorly preserved fragments of a long and robust nema with some lists and attached remains of membranes. It may represent a fragment of a retiolitid, but could alternatively be identified as a poorly preserved biserial indet., not necessarily related to the retiolitids.] *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone): Canada (Arctic).——FIG. 282,*1*. **M. arcticus,* holotype, GSC 38919, oblique view, Silurian, Llandovery, Canada, scale bar, 1 mm (Lenz & Kozłowska, 2007, fig. 7).

Neoglyptograptus RICKARDS & others, 1995, p. 26 [**N. sussmilchi;* OD]. Small, biserial, with strongly alternating thecae having flowing sigmoidal curva-

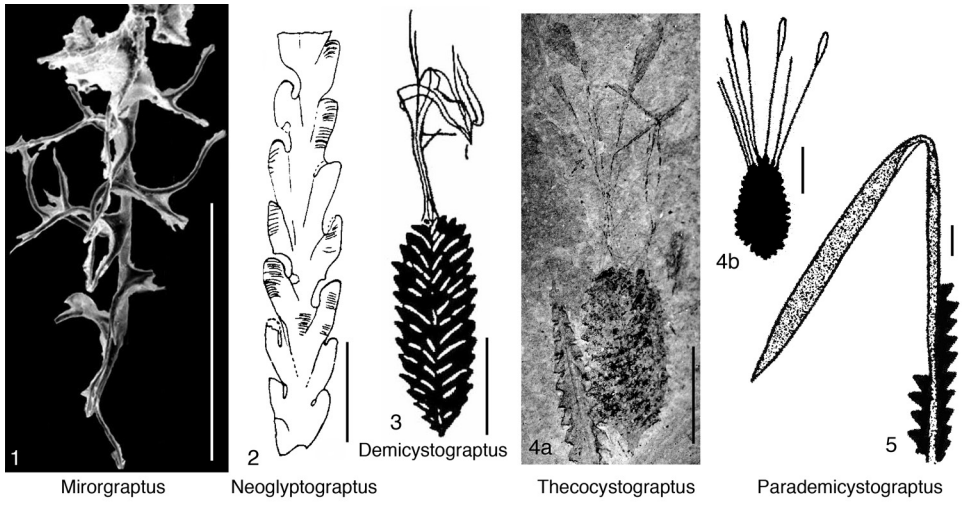


FIG. 282. Retiolitidae *incertae sedis* (p. 415–417).

ture, but with strongly introverted thecal apertures, pronounced lateral excavations, and thickened rims; possibly aseptate distally; fusellum possibly reduced proximally. [The taxon is based on a single incomplete specimen lacking the proximal end. It may be interpreted as a fragment close to the genus *Gothograptus.*] *Silurian, Wenlock* (*Homerian, Colonograptus ludensis* Biozone): Australia.——FIG. 282,*2. *N. sussmilchi;* holotype, AMF 81743 (G4/3440), Locality G4, New South Wales, Australia, scale bar, 1 mm (Rickards & others, 1995, fig. 18c).

Parademicystograptus HUNDT, 1950, p. 293 (no type species named). [Genus uncertain based on distal fragment of tubarium with long nematularium, most probably a fragment of a *Parapetalolithus* species]. *Silurian, Llandovery* (*Aeronian, Rastrites peregrinus* Biozone): Germany.——FIG. 282,*5.* No specimen number (the specimen, part of the Hundt collection at Bergakademie Freiberg, has not been identified), Kanigsberg bei Lichtenberg bei Ronneburg, Thuringia, Germany, scale bar, 1 mm (Hundt, 1950, fig. 3).

Thecocystograptus HUNDT, 1950, p. 293 [**T. polycystus;* M]. Biserial tubarium with eight possible floats. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone): Germany.——FIG. 282,*4a–b. *T. polycystus; 4a,* NIGP 170803, Dingjiapo, Hubei Province, China; *4b,* holotype, BAF 186/4707, Wachtelberg/Frankenberg, Thuringia, Germany, scale bars, 5 mm (Hundt, 1950, fig. 14).

SUPERFAMILY MONOGRAPTOIDEA

Jörg Maletz

Superfamily MONOGRAPTOIDEA Lapworth, 1873

[Monograptoidea Lapworth, 1873b, table 1, facing p. 555, *nom. correct.* Melchin & others, 2011, p. 294, *pro* Monograptidae Lapworth, 1873b] [incl. suborder Monograptina Lapworth, 1880**f**, p. 191, *nom. correct.* Obut, 1957, p. 18, *pro* Monograpta (Monoprionida) Lapworth, 1880f, p. 191]

Biserial to uni-biserial and uniserial graptoloids with pattern J or derived pattern astogenies (patterns J, M, N); colony shape and thecal style highly variable; cladial branching and secondarily multiramous colonies common in taxa with pattern M astogeny. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Lower Devonian* (*Pragian, Uncinatograptus yukonensis* Biozone): worldwide.

Melchin (1998, Table 1) referred the families Dimorphograptidae and Monograptidae to the Diplograptoidea and did not differentiate the Monograptoidea, following Mitchell (1987), who regarded the Monograptinae as a subfamily of the Monograptidae (see Neograptina in Melchin & others, 2011).

Fortey, Zhang, and Mellish (2005, p. 1255) introduced the name Monograptoidea but did not discuss the concept. Melchin and others (2011, p. 294) defined the Monograptoidea as "the most recent common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendants" and referred to node 1 in their figures 2 and 3 (2011, p. 284, 286), thus defining the taxon by reference to a cladistic diagram (see Fig. 283). The analysis of Melchin and others (2011, fig. 7) showed the Monograptoidea as a monophyletic clade with possible ancestral relationships to the genera *Normalograptus* Legrand, 1987 and *Avitograptus* Melchin & others, 2011, as an intermediate step to the akidograptids (*Akidograptus* and *Parakidograptus*). The authors recognized the families Dimorphograptidae and Monograptidae as members of the Monograptoidea.

Family DIMORPHOGRAPTIDAE Elles & Wood, 1908

[Dimorphograptidae Elles & Wood, 1908, p. 347] [=Heteroprionidae Tullberg, 1883, p. 14] [incl. Akidograptinae Li & Ge, 1981, p. 227]

Biserial and uni-biserial axonophoran graptoloids with a pattern J astogeny or a derived one; $th1^2$ absent in derived taxa with proximally uniserial tubarium; length of uniserial portion variable; colonies commonly septate with straight median septum, but median septum may be delayed; sicula may bear an ancora. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian* (*Llandovery, Rhuddanian, Coronograptus cyphus* Biozone): China, Russia, Australia (Victoria), Belgium, UK, Denmark, Sweden, Norway, Spain, Canada, USA, Argentina.

Elles and Wood (1908) originally defined the Dimorphograptidae as uni-biserial graptolites with a uniserial proximal portion and a biserial distal colony portion, following the original concept of Tullberg's (1883) Heteroprionidae. Elles and Wood (1908, p. 348) suggested the name change with the only argument being "to bring it into harmony with the names of the other families of the Graptoloidea." The change has been universally accepted, and the term Heteroprionidae is no longer used. Li (1987) discussed a possible independent origin of several lineages of dimorphograptids but did not include details of the proximal development. The idea was supported by the cladistic analysis of Melchin and others (2011), which included the presence of uni-biserial genera in more than one place in their cladistic interpretation. A uni-biserial development exists independently

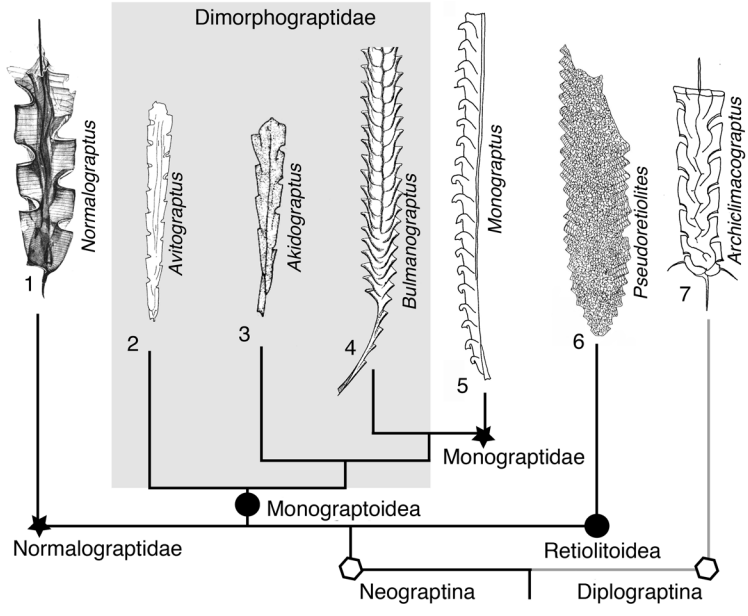


FIG. 283. Diagram showing the concept of the Dimorphograptidae (in gray box), following MELCHIN and others (2011). Specimen examples include: *1, Normalograptus brevis* (ELLES & WOOD, 1906); *2, Avitograptus avitus* (DAVIES, 1929); *3, Akidograptus ascensus* (DAVIES, 1929); *4, Bulmanograptus swanstoni* (LAPWORTH, 1876d); *5, Monograptus priodon* (BRONN, 1835); *6, Pseudoretiolites perlatus* (NICHOLSON, 1868a); *7, Archiclimacograptus* sp. (new, diagram adapted from data in Melchin & others 2011, fig. 2; graptolite specimens from various sources, not to scale).

in *Agetograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968; *Dimorphograptoides* KOREN' & RICKARDS, 1996; and *Rhaphidograptus* BULMAN, 1936b.

ŠTORCH and SERPAGLI (1993) emended the Akidograptinae, originally referred to the Orthograptidae (see LI & GE, 1981), and included the subfamilies Dimorphograptinae and Akidograptinae in the Dimorphograptidae. They changed the original concept of the Dimorphograptidae of TULLBERG (1883) considerably by including normal biserial taxa. KOREN' and RICKARDS (1996) elevated the Akidograptinae to family rank and kept the Dimorphograptidae and Akidograptidae as separate families. MELCHIN (1998, p. 301) provided a detailed diagnosis of the Dimorphograptidae. He indicated a pattern J astogeny with uni-biserial or fully biserial tubarium, a long, fully exposed sicula, variable thecal form, and a fully or partly septate tubarium. MELCHIN and others (2011, p. 295) defined the Dimorphograptidae as the "partial clade that includes the common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendents, including *Dimorphograptus elongatus* but excluding those taxa included in the family Monograptidae (i.e., excluding the uniserial monograptids)." The taxon is a paraphyletic clade at the base of the traditional monograptids, the Monograptidae *s. str.* (see Fig. 283).

MORPHOLOGY

The Dimorphograptidae, as defined by MELCHIN and others (2011), include fully biserial to uni-biserial taxa with a variety of thecal shapes, thus differing considerably from the original concept of TULLBERG (1883), who included only taxa with a uniserial proximal end and a biserial distal end but did not consider the importance of details of the thecal construction. The phylogenetic relationships of many taxa are difficult to establish, and the morphological variation of these is extreme.

The colonies of most Dimorphograptidae are slightly dorsally curved at the proximal

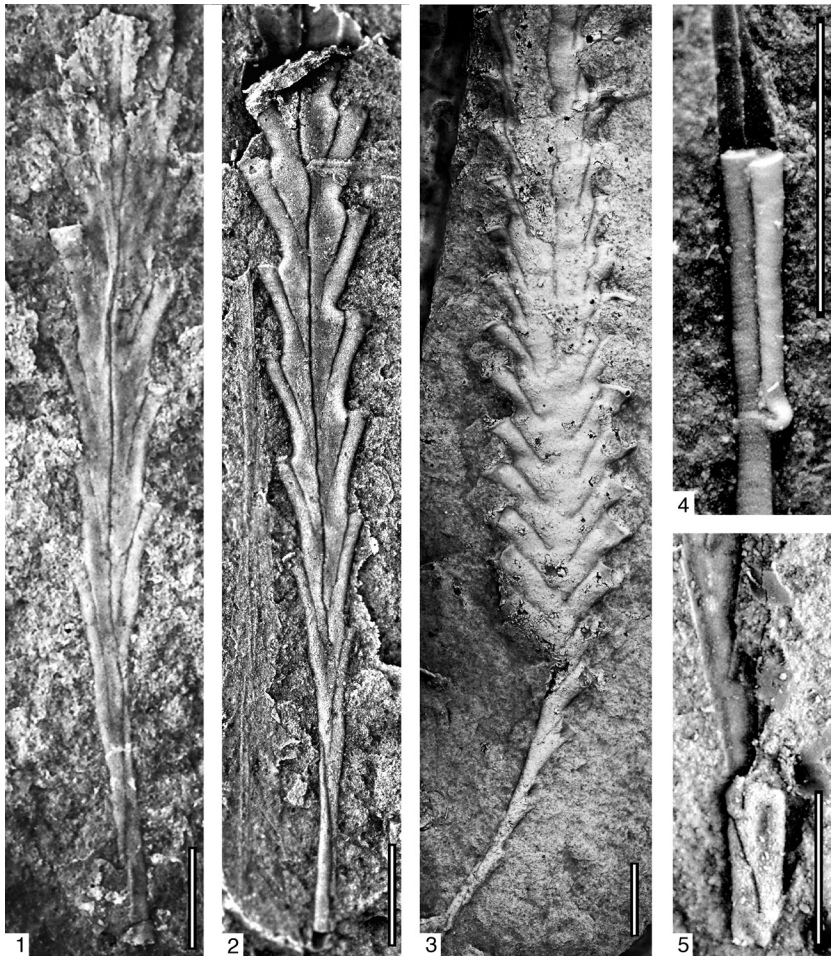


Fig. 284. *1–2, Parakidograptus acuminatus* (Nicholson, 1867a); *1,* LO 1283t, obverse view, low relief, latex cast, Tomarp, Scania (new); *2*, LO 1284t, reverse view, low relief, latex cast, Tomarp, Scania (new); *3, Bulmanograptus swanstoni* (Lapworth, 1876d), LO 476t, reverse view, latex cast, showing delay of median septum on reverse side, Bollerup, Scania (new); *4, Huttagraptus acinaces* (Törnquist, 1899), LO 11856t, specimen showing origin and initial growth of th1, Röstånga drill core, Scania (Maletz, Ahlberg, & others, 2014, fig. 1F); *5, Dimorphograptus* sp., reverse view, Röstånga drill core, 33.55–33.62 m (new). Scale bars, 1 mm in all photos.

end, at least in the uniserial part of derived taxa, but this tendency is also present in *Akidograptus* and *Parakidograptus*. The two genera have colonies with strongly protracted proximal ends and long, slender thecae, either with a distinct geniculum and slightly outward-inclined, supragenicular thecal walls or with outward-inclined, ventral thecal walls and without a geniculum (Fig. 284.1–284.2). The thecal overlap is relatively high and the interthecal septa start slightly below the aperture of the previous theca. The straight median septum is complete on the obverse side but slightly delayed on the reverse side, indicating that th2[1] is the dicalycal theca.

Proximal Development

A pattern J or derived pattern J (J′) astogeny is generally assumed for the Dimorphograptidae (Melchin & Mitchell, 1991; Melchin, 1998; Melchin & others, 2011), but these patterns are unknown from isolated

material. Pattern J astogeny (Fig. 285.1) is supposed to have a very short downward-growing part of th1[1] and a normal biserial development with a distal origin of th1[2] on the upward-growing part of th1[1] (see pattern H′ astogeny, MELCHIN, 1998, fig. 4B). A pattern H and H′ have two foramina at the base of the downward-growing part of th1[1], but in pattern J, th1[1] grows directly upward onto itself, and the foramina are lacking (MELCHIN, 1998, fig. 2). In pattern J′ astogeny (Fig. 285.2), the proximal end is uniserial with a variable number of thecae in the uniserial part of the tubarium, and the growth direction of th1[2] is supposedly redirected above the first theca (see MELCHIN & others, 2011, p. 289).

The cladistic implications indicate that *Avitograptus* may be positioned at the base of the Dimorphograptidae and Monograptidae (MELCHIN & others, 2011, fig. 2). Thus, the interpretation of the proximal development of the genus *Avitograptus* is vital for the understanding of the origin of the group. This development is uncertain (MELCHIN & others, 2011, p. 295) because there are no isolated specimens available that indicate the presence of foramina at the termination of the downward growth of th1[1]. A pattern H or I would therefore be an alternative interpretation for *Avitograptus*, not the pattern J astogeny as indicated by MELCHIN and others (2011).

Pattern J astogeny is observed in *Parakidograptus acuminatus* (NICHOLSON, 1867a) (Fig. 284.1–284.2) in partial relief and appears to be very similar to the development of early Monograptidae (see LUKASIK & MELCHIN, 1994, 1997; DAWSON & MELCHIN, 2007), in which the first theca does not grow downward but immediately outward and upward from its origin (Fig. 284.4). BULMAN (1932b) interpreted the development of the closely related *Akidograptus acuminatus* quite differently. He indicated the presence of an initial downward growth of th1[1] and the presence of a reduced th1[2] in the proximal end. This construction has not been verified from further specimens.

A pattern J′ astogeny of *Dimorphograptus* (Fig. 285.2) with a distinct initial downward growth of the first theca and delay of the dicalycal theca (Fig. 285.3) was suggested in an illustration in KOREN' and RICKARDS, 1996 (fig. 22*j*) but is not known from relief specimens.

Delay and Development of th1[2]

The earliest members of the Dimorphograptidae can be described as simple biserial axonophoran graptolites with an indeterminate proximal end. However, the name *Dimorphograptus* is generally related to taxa with a uniserial proximal end and a biserial distal end in which the uniserial proximal end is formed through the redirection of th1[2] (pattern J′ astogeny). The length of the uniserial proximal end can range from one to numerous thecae and appears to be constant in length within each species. The delay of th1[2] development, the "dimorphograptid condition" of MELCHIN (1998, p. 278) may have developed at least four times in the evolution of Silurian axonophorans according to RICKARDS, HUTT, and BERRY (1977) and LI (1987), whereas MITCHELL (1987) thought this pattern arose only once. However, in the absence of isolated material for most taxa, this suggestion has not been verified.

MELCHIN and others (2011) recognized the origin of the aseptate genus *Agetograptus* with a delayed th1[2] as being independent from *Rivagraptus* KOREN' & RICKARDS, 1996 and suggested these genera were derived from a *Glyptograptus*-type ancestor (MELCHIN & others, 2011, fig. 7). These authors did not include the genus *Dimorphograptoides* in the analysis but thought that it might be closely related to *Pseudorthograptus obuti* (RICKARDS & KOREN', 1974), which has similar development, thereby suggesting another independent origin of an uni-biserial colony development. The proximal end illustrated by BULMAN (1970, fig. 61), thought to show the development of *Dimorphograptus,* was re-identified as representing

a specimen of *Agetograptus* (Melchin, 1998, p. 274).

Median Septum

The genera *Akidograptus* and *Parakidograptus* appear to have a complete median septum on the obverse side and a slight delay on the reverse side, indicating a dicalycal theca th2[1] (Fig. 285.1). The median septum is straight or nearly straight, as is visible from its trace on the lateral tubarium wall. A relief specimen of *Bulmanograptus confertus* (Nicholson, 1868a) from the Röstånga drill core has a complete median septum on the obverse side (Fig. 286.4). A single relief specimen of *Bulmanograptus swanstoni* (Lapworth, 1876d) (Fig. 284.3) has four thecae in the uniserial proximal end, followed by eight pairs of alternating thecae before the median septum starts on the reverse side. However, for most taxa referred to the Dimorphograptidae, the development of the median septum has not been described and considerable variation may be expected.

Thecal Style

The thecal style of the Dimorphograptidae varies between distinctly geniculate thecae with outwardly inclined, suprageniculare, ventral thecal walls, to thecae with straight, outwardly inclined, ventral thecal walls. Details of the thecal development are not documented for most taxa. Geniculare flanges appear to be absent or at least not visible in flattened specimens. The thecal apertures are straight and range from outwardly inclined to perpendicular to the length of the colony. In *Bulmanograptus confertus* and related taxa, the thecal apertures appear slightly convex and bear a distinct apertural thickening. Fragments in ventral preservation show a distinct lateral widening of the thecal apertures associated with the thickened rims and the possible presence of paired apertural spines that are not visible in laterally preserved specimens (Fig. 286.2).

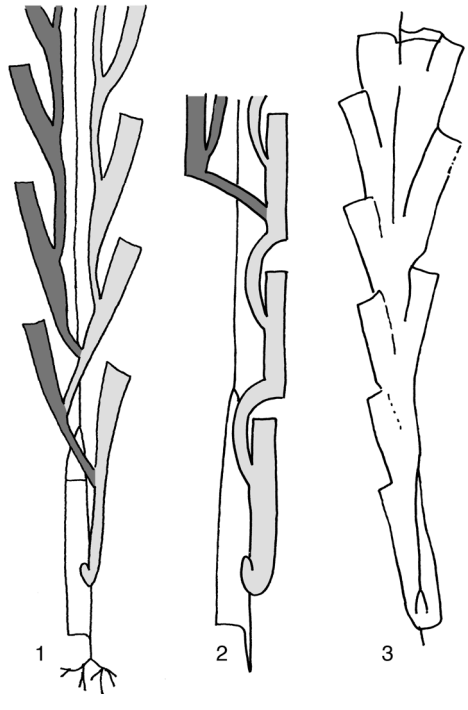


Fig. 285. Proximal development. *1*, *Parakidograptus*, pattern J astogeny (adapted from Štorch & Serpagli, 1993, fig. 4); *2*, *Dimorphograptus,* pattern J′ astogeny, (adapted from Melchin, 1998, fig. 8); *3*, *Dimorphograptus erectus*, showing initial downward growth of th1 in obverse view (adapted from Koren' & Rickards, 1996, fig. 22*j*).

The Ancora

Specimens of *Akidograptus ascensus* Davies, 1929 and *Parakidograptus acuminatus* typically have a distal branching of the virgella (Stein, 1965; Koren' & Rickards, 1996; Štorch & Feist, 2008) reminiscent of the ancora umbrella of the Retiolitidae. This construction is best seen in juvenile specimens and is not preserved in most mature material. The construction, similar to that of the ancora of the Retiolitidae, is formed from a short virgellar spine that branches into two bars. At least two further dichotomous branching points may occur in the ancora of *Akidograptus ascensus* (Fig. 285.1; Fig. 286.1). A branched virgellar spine is also documented for a single specimen of *Avitograptus*

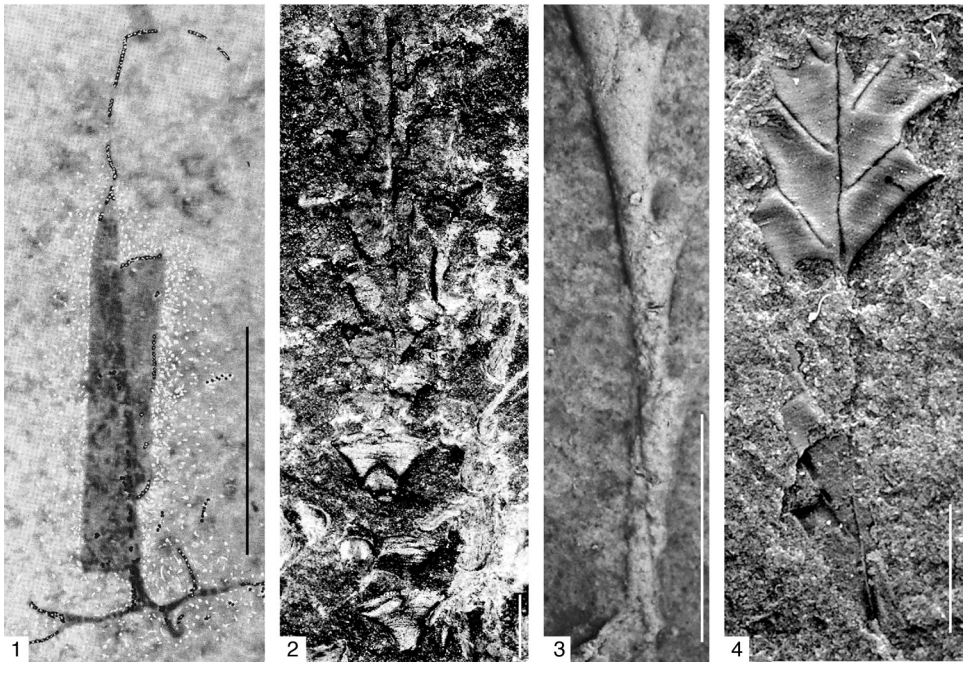


FIG. 286. *1*, *Akidograptus ascensus* (DAVIES, 1929), juvenile specimen showing ancora, Göttingen, 506-48 (Stein, 1965, pl. 15*B*); *2*, *Bulmanograptus* sp., fragment, ventral view, Röstånga drillcore, Scania, 36.40–36.30 m (new); *3*, *Bulmanograptus swanstoni* (LAPWORTH, 1876d), LO 476t, counterpart, latex cast showing origin of th1 (new); *4*, *Bulmanograptus confertus* (NICHOLSON, 1868a), Röstånga drillcore, Scania, 38.80–38.70 m, obverse view of distal end with complete median septum, proximal end preserved as a mold (new). Scale bars, 1 mm.

sp. cf. *Avitograptus avitus* (MELCHIN & others, 2011, fig. 6c) and was shown by STEIN (1965) in *Avitograptus avitus*.

Dimorphograptus LAPWORTH, 1876, p. 545 [**D. elongatus* LAPWORTH, 1876, p. 547; SD BASSLER, 1915a, p. 441] [=*Metadimorphograptus* PŘÍBYL, 1948b, p. 39 (Czech text), p. 47 (English text) (type, *D. extenuatus* ELLES & WOOD, 1908, p. 358, OD, herein)]. Straight to proximally curved dimorphograptid with long uniserial part; thecae with distinct geniculum and small, slit-like apertures; proximal development pattern probably of pattern J′ astogeny; biserial portion probably fully septate. *Silurian*, *Llandovery* (*Rhuddanian, upper Cystograptus vesiculosus* Biozone): Morocco, China, ?New Zealand, UK, France, Germany, Denmark, Sweden, Serbia, Canada (Arctic).——FIG. 288,*1a–b. D. extenuatus* ELLES & WOOD, 1908; *1a,* lectotype (selected by HUTT, 1974c, p. 55), UM K736 (Elles & Wood, 1908, pl. 35,*10a*); *1b,* SM A20814, proximal end showing sicula (Příbyl, 1948, fig. 4). Scale bars, 1 mm.——FIG. 288,*1c–e*. **D. elongatus; 1c,* BU 1423, curved specimen (Bulman, 1970, fig. 97,*2B*); *1d,* lectotype, BU 1423, straight specimen (Elles & Wood, 1908, pl. 35,*11a*); *1e,* curved specimen, Bornholm, Denmark, (Koren' & Bjerreskov, 1997, fig. 17*B*). Scale bars, 1 mm.

Akidograptus DAVIES, 1929, p. 9 [**A. ascensus;* OD] [=*Acidograptus* DAVIES, 1929 (misspelling in BULMAN, 1929, p. 172)]. Biserial monograptoid with protracted proximal end and early upward growth of first two thecae; proximal end probably with pattern J astogeny; thecae slender and elongated, strongly geniculate, with straight apertures lacking genicular flanges. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus* Biozone–*Atavograptus atavus* Biozone): China, UK, Germany, Denmark, Norway, Sweden, Canada (Arctic), USA.——FIG. 287,*2a–b. *A. ascensus; 2a,* holotype, SM A10021 (adapted from Melchin & others, 2011, fig. 6*G*); *2b,* holotype (adapted from Rigby, 2000). Scale bars, 1 mm.

Avitograptus MELCHIN & others, 2011, p. 295 [**Glyptograptus* (?) *avitus* DAVIES, 1929, p. 8, fig. 21; OD]. Biserial monograptoid with slender proximal end and possibly pattern J astogeny; $th1^1$ upturned at level of sicular aperture; $th1^2$ arises from point low within upward-grown portion of $th1^1$; thecae geniculate, slightly to moderately inclined; first

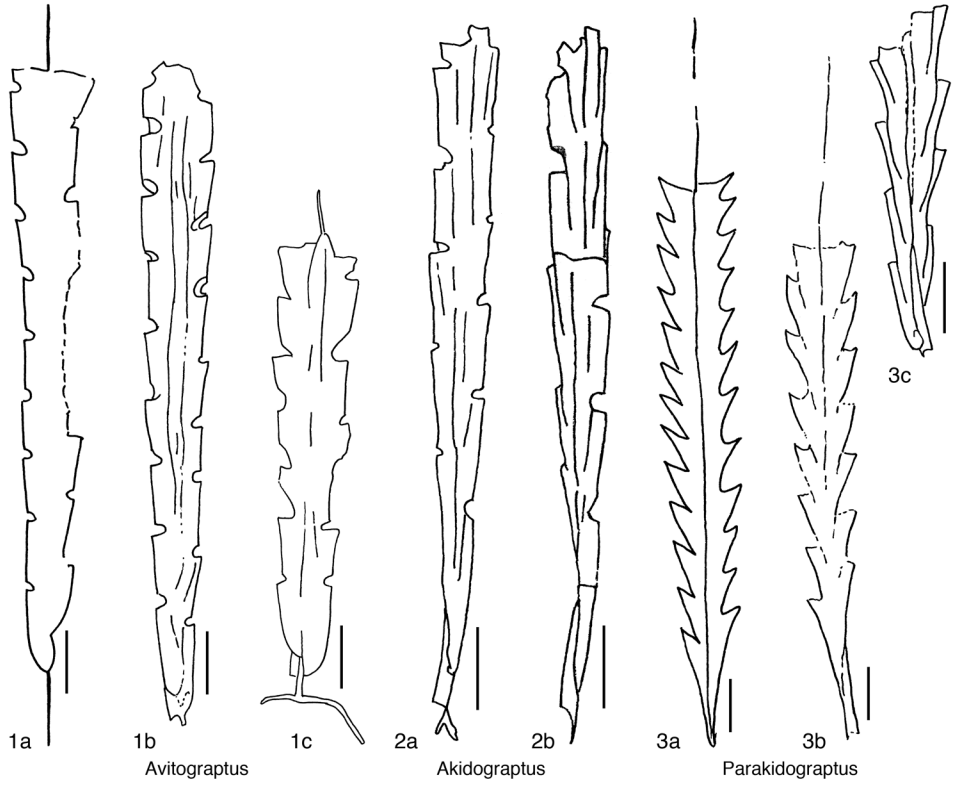


Fig. 287. Dimorphograptidae (p. 424–426).

thecal pair slightly elongated relative to subsequent thecae; complete median septum. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus* Biozone): UK, Germany, Canada (Arctic).——Fig. 287,*1a–b. *A. avitus* (Davies); *1a,* holotype, SM A10019 (adapted from Davies, 1929, fig. 21); *1b,* topotype, GLAHM 131711 (adapted from Melchin & others, 2011, fig. 6*B*). Scale bars, 1 mm.——Fig. 287,*1c. Avitograptus* sp. aff. *A. avitus,* GLAHM 131712, showing branched virgella, scale bar, 1 mm (adapted from Melchin & others, 2011, fig. 6C).

Bulmanograptus Příbyl, 1948b, p. 39 (Czech text), p. 47 (English text)[**Diplograpsus confertus* Nicholson, 1868a, p. 526; OD] [=*Cardograptus* Hundt, 1965, p. 117 (type, *C. primus,* M, =*Cardograptus elongatus* Hundt, 1959, p. 19, *nom. nud.,* herein), syn. herein]. Robust dimorphograptid with slender, often curved, uniserial proximal end of variable length; thecae proximally slender, with high inclination and straight ventral sides in biserial part; biserial part with or without median septum; thecae typically with considerably thickened apertural rim. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus* Biozone–*Atavograptus atavus* Biozone): Morocco, China, Russia, UK, Czech Republic, Germany, Poland, Denmark, Sweden, Serbia, USA (Alaska), Canada (Arctic).——Fig. 288,*2a–b. *B. confertus* (Nicholson); *2a,* SM A20699, typical specimen (Elles & Wood, 1908, pl. 35,*3a*); *2b,* BU 1368, proximal end (Elles & Wood, 1908, fig. 227a), Scale bars, 1 mm.——Fig. 288,*2c. B. primus* (Hundt, 1965), holotype, BAF 186/1715, scale bar, 1 mm (new).

Parakidograptus Li & Ge, 1981, p. 229 [**Diplograpsus acuminatus* Nicholson, 1867a, p. 109; OD]. Biserial monograptoid with protracted proximal end and early upward growth of first two thecae; proximal end probably with pattern J astogeny; thecae slender and elongated, tubular, with straight, outward-inclined apertures; median septum complete. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian, Llandovery* (*Rhuddanian, Atavograptus atavus* Biozone): China, Australia (Victoria), UK, Czech Republic, Germany, Poland, Denmark, Sweden, Spain, Canada, USA.——Fig. 287,*3a–b. *P. acuminatus* (Nicholson); *3a,*

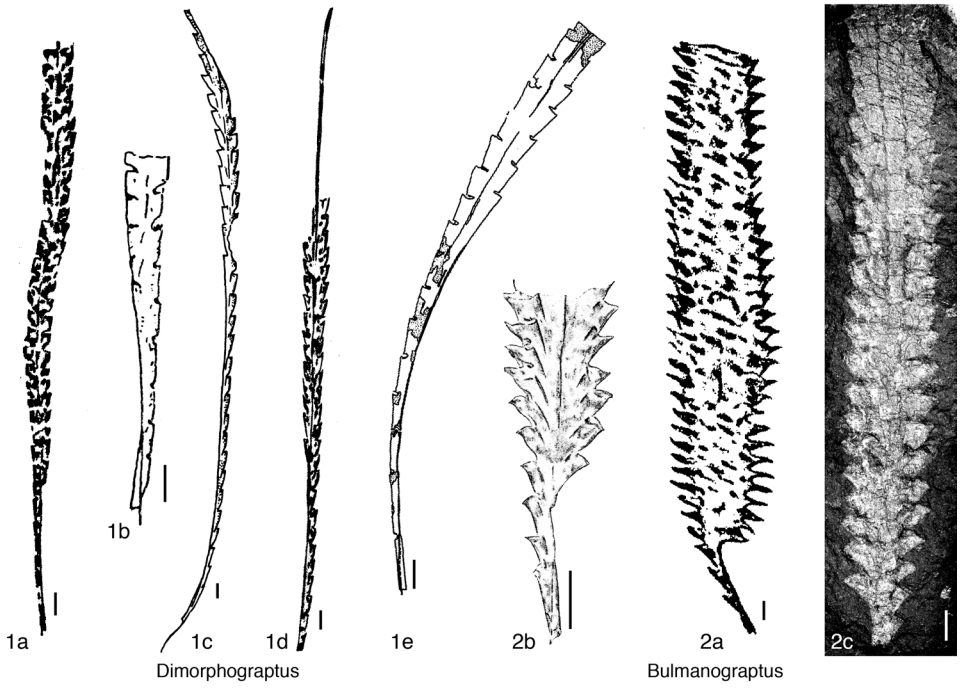


FIG. 288. Dimorphograptidae (p. 424–425).

?NHMUK PM 1310 (adapted from Nicholson, 1867a, fig. 16a); *3b,* SM A20672, small specimen (adapted from Elles & Wood, 1908, fig. 199). Scale bars, 1 mm.——Fig. 287,*3c. P. acuminatus praematurus* (DAVIES, 1929), holotype, SM A10023, specimen showing obverse view and possible downward initial growth of th1, scale bar, 1 mm (adapted from Zalasiewicz, 2008c, Atlas, Folio 2.71).

FAMILY MONOGRAPTIDAE

Jörg Maletz and David K. Loydell

AUTHOR CONTRIBUTIONS

David K. Loydell wrote the majority of the generic descriptions and provided almost all of the information regarding type species and their stratigraphical and geographic ranges. Jörg Maletz is responsible for the remainder, including illustrations, suprageneric classification, discussions and descriptions of terminology, family, and subfamily level subdivisions.

TERMINOLOGY AND TAXONOMIC NOTE

Mitchell and others (2013) suggested use of the term tubarium (Lankester, 1884), initially used exclusively for extant Pterobranchia, for the housing construction of all Pterobranchia including fossil and extant taxa and suggested replacing the term rhabdosome previously used for the graptolites. Not all researchers have accepted this replacement and several (e.g. Štorch, Roqué Bernal, & Gutiérrez-Marco, 2019; Loydell, 2020), including one of the authors of this chapter, much prefer to use the term rhabdosome. The term tubarium is used herein for consistency with other chapters in the *Treatise*.

One remaining problem for the taxonomy and understanding of the Monograptidae is the old and much used genus *Monograptus sensu lato*. Geinitz (1852) used the genus *Monograptus* to include all single-stiped Silurian to Early Devonian graptoloids. Lapworth (1873b) separated the genus *Rastrites* Barrande, 1850, based on its isolated thecae, and the genus *Cyrtograptus* Carruthers in Murchison, 1867a with its compound tubarium. Numerous monograptid species have been included in *Monograptus* over the years due to a lack of understanding of their constructional details and evolutionary relationships. Even though more than 100 genera are now described to subdivide the original genus *Monograptus,* many species are still included in the form genus *Monograptus sensu lato* or '*Monograptus*' (e.g., Bulman, 1970; Koren', 1983; Štorch & others, 2018) as their differentiation is uncertain. Lenz (2013, p. 1101) still employed the genus *Monograptus* as a "form genus for those whose thecae are not fully understood" and included within it a number of Early Devonian taxa. Thus, numerous not necessarily closely related monograptid species have been and continue to be included under this umbrella name. These taxa are not included in the overview or classification herein.

Family MONOGRAPTIDAE Lapworth, 1873

[Monograptidae Lapworth, 1873b, table 1, facing p. 555] [=Pristiograptidae Gürich, 1908, p. 32; =Rastritidae Gürich, 1908, p. 35; =Cyrtograptidae Averianow, 1929, p. 103; =Demirastritidae Hundt, 1943, p. 263; =Diversograptidae Hundt, 1943, p. 263; =Dibranchiograptidae Hundt, 1949a, p. 20; =Gangliograptidae Hundt, 1949a, p. 21; =Linograptidae Obut, 1957, p. 18; =Wolynograptidae Tsegelnjuk, 1976, p. 110; =Tirassograptidae Tsegelnjuk, 1976, p. 118]

Uniserial Neograptina with and without cladia; thecal apertures on main or primary stipe oriented in opposite direction to sicular aperture. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus/Parakidograptus acuminatus* Biozone)–*Lower Devonian* (*Emsian, Uncinatograptus yukonensis* Biozone): worldwide.

Monograptidae is regarded as a monophyletic clade (Melchin & others, 2011) forming the Monograptoidea with the paraphyletic stem group, the Dimorphograptidae. Melchin and others (2011) indicated that the loss of the dicalycal theca and the loss of any downward growth of the first theca are the defining synapomorphies of the clade. However, they indicated that a number of biserial Neograptina lack a dicalycal theca; thus, this character may be

a plesiomorphic character or was derived independently more than once.

Přibyl (1946) introduced a number of subfamilies, most of them including a single genus, but this was before many monograptid genera were established. Urbanek (1958, p. 6) discussed Přibyl's (1946) approach as a "purely pragmatic rather than a theoretically evidenced taxonomy" and regarded it as a starting point for further discussion. A number of additional family and subfamily groups were introduced subsequently to the monograptid classification and are discussed herein as appropriate in the text. Some of these taxonomic units are used herein as a guide to differentiate particular groups within the Monograptidae. These may or may not represent monophyletic taxa and details are provided where available. Bulman (1955, 1970) did not acknowledge these suprageneric taxa in the previous versions of the *Treatise* and ignored any subdivisions of the Monograptidae, except for the acceptance of the Cyrtograptidae for taxa with cladial branching. Bulman and Rickards (1970), in an addendum to Bulman (1970), discussed some of the available monograptid genera but regarded most of them to be of dubious value. They did not mention or discuss any of the previously introduced subfamilies and families. Rickards, Hutt, and Berry (1977) took the same approach and again none of the monograptid subfamilies was mentioned in their discussions.

There is no cladistic analysis available to differentiate phylogenetically meaningful units within the Monograptidae. However, in the light of the high number of genus-level taxa (more than 100 described genera), it seems reasonable to use previously established taxonomic units or clades herein. These names were introduced to separate morphologically distinctive groups based on characters considered to be phylogenetically meaningful by the original authors.

A differentiation into cladia-bearing and non cladia-bearing taxa was introduced by Yin (1937) and Mu (1950b), who referred all cladia-bearing monograptids to the Cyrtograptinae and all other monograptids to the Monograptinae. This division has been maintained in the last two editions of the Graptolite *Treatise* (Bulman, 1955, 1970) and is included in most classification systems (see overview in Rigby, 1986). The few attempts at a cladistic interpretation of monograptids (Muir, 1999; Melchin & Koren', 2001; Lenz & Melchin, 2008) cover only a very limited number of taxa. Muir (1999, abstract) stated that "at present, many genera are polyphyletic," a statement that still may be true and indicates the need for a thorough investigation of monograptid phylogeny.

MORPHOLOGY

Sicular Development

All Monograptidae initially grew a single stipe from a sicula of variable (conical) shape and dimensions, and the definition of the family Monograptidae is essentially that of Lapworth (1873b). Little is known about the development of a conus and cauda in the prosicula, even though numerous chemically isolated monograptids have been described. Kraft (1926) discussed the nema prosiculae (cauda) in a species of *Monograptus* (Fig. 289.1) and described the spiral line and the longitudinal rods of the conus (prosicula proper). A cauda has not been mentioned in later descriptions of chemically isolated monograptids. The shape of the sicula ranges from very slender and long (e.g., in *Coronograptus*), short and straight (e.g., in *Streptograptus*), or variably curved (e.g., in *Spirograptus*). Siculae with a broad triangular outline and a considerably widened aperture appear in several groups independently (Fig. 289.5–289.7). These features were initially described from the Wenlock species *Colonograptus deubeli* (Jaeger, 1959) but appear independently in the early Wenlock species *Monograptus riccartonensis* Lapworth, 1876b (see Loydell & Large, 2019); in the Ludlow species *Saetograptus leintwardinensis* (Lapworth, 1880a) (see Maletz, 1997d; Štorch, Manda, & Loydell, 2014); in the Devonian *Uncinatograptus hercynicus*

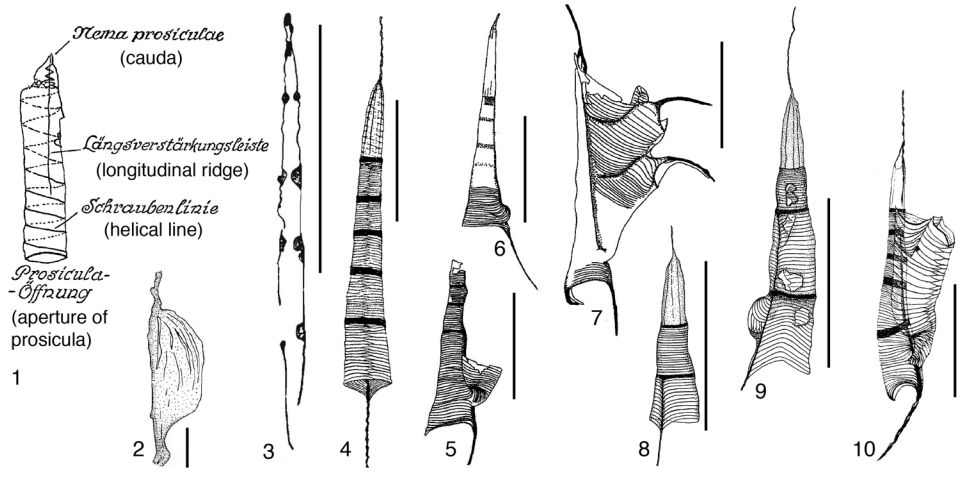


FIG. 289. The sicular development of the uniserial Axonophora (Monograptidae). *1,* monograptid prosicula, schematic (Kraft, 1926, fig. 2); *2–3,* cross section of sicula (*3*) and enlargement of sicular annulus (*2*) (Urbanek, 1958, fig. 5A, 6C); *4, Pristiograptus frequens* JAEKEL, 1889, sicular development (Kraft, 1926, fig. 3); *5–7, Saetograptus leintwardinensis* (LAPWORTH, 1880a), showing sicular shape and annuli (Maletz, 1997d, fig. 1); *8–9, Skalograptus ultimus* (PERNER, 1899), siculae with longitudinal rods, showing origin of virgella at first metasicular annulus (Kříž & others, 1986, fig. 35); *10, Pristiograptus frequens*?, showing sicular annuli (Kraft, 1926, fig. 4). Scale bars, 0.01 mm in *2,* all others, 1 mm.

(PERNER, 1899); and may be present in other genera as well.

Longitudinal ridges (see KRAFT, 1926) are present on the prosicula of many graptoloids, but their origin and further evolution has not been investigated. It is unclear whether these ridges were formed in constant numbers in the graptoloids or were formed randomly. They first appeared as paired ridges in Floian taxa (WILLIAMS & CLARKE, 1999) and are present in latest Silurian monograptids (Fig. 289.8–289.9). KOREN', KIM, and WALLISER (2007) described longitudinal rods in the Early Devonian *Uncinatograptus falcarius* (KOREN', 1969).

Sicular annuli occur in many monograptids (Fig. 289.2–289.6, Fig. 289.8–289.10). The origin and constructional purpose of the sicular annuli are unknown. Sectioned material clearly shows the secretion of the annuli to be cortical additions on the inside of the sicula (WALKER, 1953; URBANEK, 1958) (Fig. 289.2–289.3). They are typically present in many Homerian (late Wenlock, Silurian) and later monograptids (LENZ & KOZŁOWSKA-DAWIDZIUK, 1998). Very little is known about sicular annuli in older taxa because these have rarely been investigated in detail. Sicular annuli appear to have formed in fixed positions in most monograptids (URBANEK, 1997a). MALETZ (1997d) recognized a variable number of sicular annuli in *Saetograptus leintwardinensis* (Fig. 289.5–289.7), ranging from two to six, with most specimens possessing four to six annuli. The first of the sicular annuli appeared at the boundary between the prosicula and metasicula. The later ones were more indistinct and indicate their successive construction as the metasicula grew (MALETZ, 1997d). PORĘBSKA (1984) recognized sicular annuli in many latest Silurian to Early Devonian monograptids but was unable to confirm their presence in all specimens of the taxa because she had only shale material at hand.

The development of the foramen for the origin of th1 changed considerably throughout the evolution of the Monograptidae (MALETZ & others, 2019). Initially, a resorption foramen (Fig. 290.1) was present in species of the genera *Atavograptus*, *Coronograptus*, *Lagarograptus*, *Pernerograptus*, and

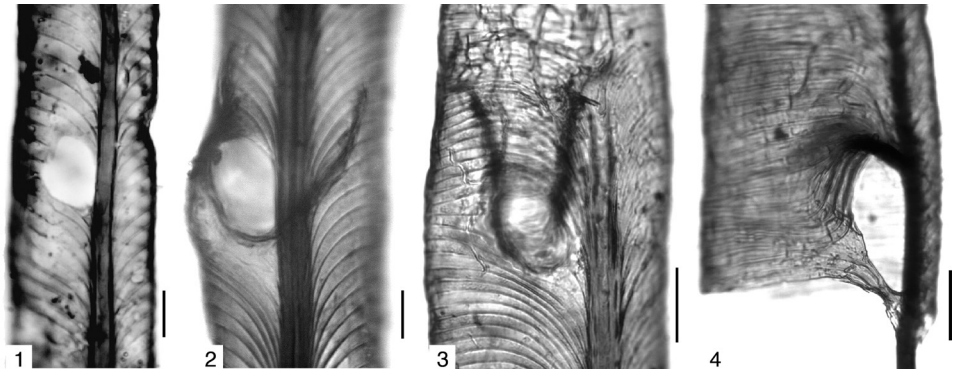


Fig. 290. The porus type in the Monograptidae. *1*, *Coronograptus gregarius* (Lapworth, 1876c), resorption foramen in metasicula, GSC 116236; *2*, *Monoclimacis*? *galeritus* Melchin & Koren', 2001, modified resorption foramen, GSC 118589; *3*, *Monograptus* cf. *Monograptus arciformis* Chen & Lin, 1978, lenticular porus, GSC 130563; *4*, *Monograptus priodon* (Bronn, 1835), primary porus with sinus and lacuna stages, GSC 130558. Scale bars, 0.1 mm (Maletz & others, 2019, fig. 5).

probably in early *Monoclimacis* (Lukasik & Melchin, 1994, 1997; Melchin & Koren', 2001). Most details are unknown for the contemporary *Pribylograptus* because very few siculae have been attributed to this genus, and they are not known in enough detail (see Koren' & Bjerreskov, 1997, fig. 22L regarding ?*Pribylograptus* sp.; and Russel-Houston, 2001, pl. 5e regarding *Pribylograptus leptotheca* Lapworth, 1876b). Melchin and Koren' (2001) discussed a modified resorption foramen in specimens of *Monoclimacis* (Fig. 290.2), in which the fuselli involved in the formation of the foramen are slightly deflected with the sicula bulging outward at this point. A lenticular porus (Fig. 290.3) is present as a third type in early monograptids (Dawson & Melchin, 2007). In this type, a number of pre-porus fuselli are deflected proximally and a few truncated fuselli are present. The post-porus fuselli are deflected in the opposite direction, forming the lenticular porus in *Paramonoclimacis* and *Streptograptus*. Derived monograptids may have a primary porus (Fig. 290.4) formed through the typical sinus and lacuna stage of development described by Eisenack (1942) for *Pristiograptus frequens* Jaekel, 1889. This porus type was considered to be typical of all monograptids (e.g., Bulman, 1970). Dawson and Melchin (2007) illustrated this primary porus for *Monograptus priodon* (Bronn, 1835) from the middle Sheinwoodian, representing the stratigraphically earliest known record of this character.

Tubarium Shape

The tubarium shape is highly variable in monograptids and/or ranges from straight to dorsally and ventrally curved uniserial stipes to multiramous taxa with numerous cladial branches. The shape appears to be characteristic for certain groups and also for certain stratigraphical intervals. However, particular shapes appear to have also evolved independently in separate groups. Spirally coiled tubaria are common in a number of taxa and may be planispiral or trochospiral. However, in many taxa, the precise mode of coiling is difficult to recognize. Large specimens of *Oktavites spiralis* (Geinitz, 1842) may appear to be planispiral (Fig. 291.5), but the astogeny derived from early growth stages indicates a trochospiral development if viewed in lateral preservation (Schauer, 1971). High trochospiral development is typical of *Spirograptus turriculatus* (Barrande, 1850) (Fig. 291.7), a species usually preserved in lateral view. Also, many specimens of *Cyrtograptus* (Fig. 291.2) are coiled in a trochospiral fashion, even though larger specimens appear to have

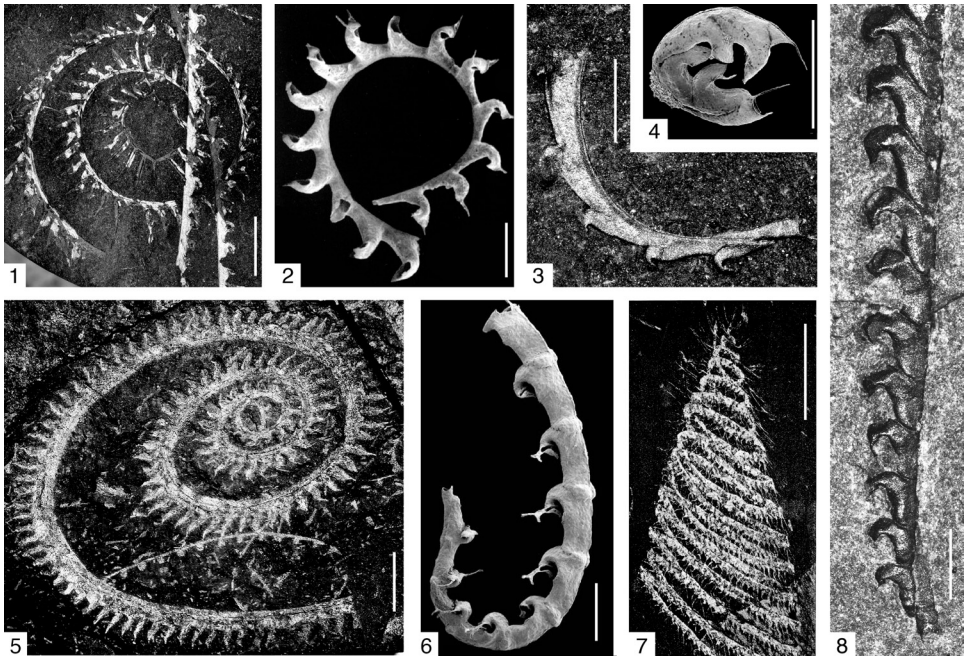


Fig. 291. The tubarium shape. *1*, *Lituigraptus convolutus* (Hisinger, 1837), dorsally coiled tubarium, NIGP 168325, Yangtze platform, China (Maletz, Wang, & Wang, 2021, fig. 11E); *2*, *Cyrtograptus* sp. cf. *C. laqueus* Jackson & Etherington, 1969, dorsally curved proximal end lacking the sicula, Cape Phillips Formation, Arctic Canada (Lenz & Melchin, 1989, fig. 3c); *3*, *Pernerograptus variabilis* (Ni, 1978), dorsally curved proximal end, NIGP 168346, Yangtze Platform, China (Maletz, Wang, & Wang, 2021, fig. 17A); *4*, *Cochlograptus veles* (Richter, 1871), GSC 34909, Devon Island, Arctic Canada (Lenz & Melchin, 2008, fig. 1D); *5*, *Oktavites spiralis* (Geinitz, 1842), seemingly planispiral colony, dorsally coiled, SMF XXIV 188, Johannesberg, Thuringia, collected by Hemmann, 1942 (new); *6, Pseudostreptograptus williamsi* Loydell, 1991a, ventrally curved fish-hook-shape, NMW UCWG935B, Osmundsberget, Dalarna, Sweden (Loydell & Maletz, 2004, fig. 23); *7*, *Spirograptus turriculatus* (Barrande, 1850), high spiral, dorsally coiled, BAF 111/H/4135, Hohenleuben, Thuringia (Hundt, 1949b, fig. on p. 330); *8, Monograptus priodon* (Bronn, 1835), nearly straight tubarium, SMF 75780, glacial boulder (new). Scale bars 5 mm in 1, 5, and 7. All others 1 mm.

a planispiral shape when preserved on shale surfaces (Bouček, 1933; Lenz & others, 2012). The shape of colonies of *Cyrtograptus* has been modeled as a logarithmic spiral forming planispiral colonies and this has been suggested as a character useful for the discrimination of taxa (e.g., Huo, Fu, & Shu, 1986; Deng, 1986).

It is important to differentiate dorsally (Fig. 291.1–291.3) and ventrally (Fig. 291.4) curved taxa. Dorsally coiled tubaria were particularly common during the Telychian (e.g., Pernerograptinae, Monograptinae), whereas ventrally curved taxa proliferated during Gorstian and early Ludfordian times (e.g., Linograptinae), but details need to be investigated. A high degree of variation of dorsally, dorso-ventrally, and ventrally curved tubaria occur especially in streptograptines, in which both types appear. Many of the slender taxa are quite variable in shape, but a distinct dorsal curvature may be present along the first few thecae in *Streptograptus*. Distally, the curvature changes to ventral or the stipe is straight (as is shown in an overview of the biostratigraphical ranges of streptograptine genera by Maletz & others, 2019, fig. 4). This is also present in the straight to slightly dorsally curved proximal end and strong ventral curvature of the distal part in *Pseudostreptograptus* (Fig. 291.6) and the *Streptograptus exiguus* group, with

their fish-hook-shaped tubaria (Loydell & Maletz, 2004).

CLADIA

Cladia are a way of secondary branching (Maletz, Lenz, & Bates, 2016), first developed by the Dichograptina (e.g., *Pterograptus,* see Skwarko, 1974) and the Diplograptina (e.g., *Nemagraptus,* see Finney, 1985a) during the Ordovician. For a number of monograptid taxa, cladial branching was used as an option to form multiramous colonies. Cladia were the only way in which monograptids added new stipes to their tubaria. In this way, they differed from the earlier Dichograptina, in which dichotomous branching was the main mode of producing additional stipes (see Maletz, Lenz, & Bates, 2016). The cladia in monograptids invariably included the formation of a secondary nema along which the cladial stipe grew (Thorsteinsson, 1955). Urbanek (1963) differentiated the procladium (the main stipe) and the metacladia (sicular and thecal cladia) and recognized that cladia of several orders may be developed in some taxa. The term procladium for the main stipe should no longer be used as it might be misleading (see Glossary, p. 176). An analysis of the appearance of cladial branching has never been attempted, but it appears certain that cladia originated independently in several clades of monograptids. Thus, the family Cyrtograptidae of earlier workers, represents a highly polyphyletic taxonomic unit and should not be used. The genus *Cyrtograptus* is the most prominent taxon in which cladial branching has been investigated from chemically isolated material (Thorsteinsson, 1955; Teller, 1976), but cladial development has also been described in great detail for the linograptines (Urbanek, 1963, 1997b).

Early taxa with cladial branching appeared during the upper Aeronian and lower Telychian with the genera *Paradiversograptus* and *Sinodiversograptus* (Manck, 1923; Loydell, 1990a). Little is known about the development of the cladia in these taxa because chemically isolated material does not exist. The genus *Sinodiversograptus* from the *Spirograptus guerichi* Biozone (Loydell, 1990a) is the stratigraphically earliest record of regular and frequent thecal cladial branching in a Silurian monograptid. The process began with the formation of a strongly curved bipolar tubarium. It appears that thecal cladia were produced from each theca on the main stipe, but it is uncertain at what stage in the astogeny of the colony the cladial growth was initiated.

An independent origin of cladial branching occurred in Linograptinae. Urbanek (1963) discussed in great detail the development of cladial branching in this clade, indicating that the stratigraphically early taxon *Neodiversograptus* had a bipolar tubarium with a single cladium originating from the sicular aperture. The derived taxa *Linograptus* and *Abiesgraptus* produced numerous cladia, either from the sicula (*Linograptus*) or paired cladia from the sicula and from later thecae (*Abiesgraptus*) (Urbanek, 1997b). In *Abiesgraptus,* a single sicular cladium initially formed a bipolar tubarium from which additional paired thecal cladia were formed at certain distances, producing a multiramous tubarium.

Subfamily PERNEROGRAPTINAE Hundt, 1943

[Pernerograptinae Hundt, 1943, p. 263, *ex* Pernerograptidae Hundt, 1943, p. 263; Přibyl, 1946, p. 277]

Uniserial Neograptina without cladia; single stipe straight to strongly dorsally curved, commonly variable; resorption foramen for emergence of th1 or a derived pattern, but development unknown in most species; sicula may be elongated; thecal style highly variable with or without geniculum; various apertural modifications may be present, mainly based on apertural hood or hook. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus/Parakidograptus acuminatus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.

Přibyl (1946) discussed the Pernerograptinae as a subfamily, but it was initially listed by Hundt (1943) as a family. However,

this taxonomic unit has not been discussed in detail subsequently and needs considerable attention. PŘIBYL (1946) differentiated the subfamily from the Monograptinae due to the biform nature of the thecal development in *Pernerograptus*. A differentiation into taxa with short and with long siculae may be useful and has been made herein. Further investigation is necessary to understand the evolutionary relationships of early monograptids. All taxa have a slightly to considerably dorsally curved tubarium, at least proximally. The sicular length is quite variable. The thecae are slender with low overlap or lacking overlap proximally, but overlap may increase considerably distally. A geniculum is commonly present and the thecal apertures are simple, hooded, or provided with lateral lobes. According to MELCHIN and others (2011, fig. 7), *Atavograptus* and the derived monograptids originated in the early Rhuddanian *Akidograptus ascensus*/*Parakidograptus acuminatus* Biozone as a sister group to the genus *Dimorphograptus*.

The proximal end and thecal style of early monograptids appear to be quite variable but can be reduced to a few fundamental features. MELCHIN and others (2011) considered the species *Atavograptus ceryx* (RICKARDS & HUTT, 1970) from the *Akidograptus ascensus*/*Parakidograptus acuminatus* Biozone to be the earliest monograptid. The sicula is approximately 1.5–1.8 mm long, gradually widening toward the aperture (Fig. 292.1). The origin of th1 is in the lower third of the metasicula. The thecae widen from the origin, forming a rounded geniculum, after which they are parallel-sided, nearly parallel to the dorsal line of the stipe. They have low thecal overlap and apparently no or only a slight increase of this feature distally. *Atavograptus ceryx* has considerable dorsal curvature (Fig. 292.2), reminiscent of the tubarium shape in the genus *Coronograptus*. An early thecal differentiation in *Atavograptus atavus* (ZALASIEWICZ, 2000f) has very slender proximal thecae and a conspicuous but gradual distal widening of the stipes.

Distinct elongation of the slender metasicula is present in *Coronograptus* (Fig. 292.4) and also in a few other genera (RICKARDS, HUTT, & BERRY, 1977) as well as an enhancement of the geniculum with the formation of genicular flanges (Fig. 292.6, 292.8). A differentiation of the thecal apertures with the formation of lateral apertural flanges and lobes also occurs (Fig.292.5–292.8). The precise evolutionary relationship of these features has not been studied.

GENERA WITH SHORT SICULAE

The sicula is approximately 1–2 mm long in these taxa, but details of the development are rarely available. The dimensions of the prosicula are unknown in most taxa.

Atavograptus RICKARDS, 1974, p. 141 [**Monograptus atavus* JONES, 1909, p. 531; OD]. Straight to somewhat dorsally curved tubarium that becomes straight distally; sicula 1.2–1.8 mm long; first theca arises from middle part of metasicula via a resorption porus; thecae simple overlapping tubes, commonly with rounded genicula; thecal apertures simple, straight. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus/Parakidograptus acuminatus* Biozone–*Aeronian, Neodiplograptus magnus* Biozone): worldwide.——FIG. 293,*1a–c.* **A. atavus* (JONES); *1a,* lectotype, GSM 23710, stipe fragment (Zalasiewicz, 2000d, Atlas, Folio 1.6); *1b,* latex cast of topotype, proximal end with sicula, GSM 95254 (Zalasiewicz, 2000d, Atlas, Folio 1.6); *1c,* proximal end, PŠ 3521, Czech Republic (Štorch, 2015, fig. 10M). Scale bars, 1 mm.

Euroclimacis ŠTORCH, 1998c, p. 120 [**Monograptus aduncus* BOUČEK, 1931, p. 295; OD]. Tubarium dorsally curved proximally and ventrally curved or almost straight distally; sicula short; thecae with sharp geniculum, narrow aperture, and pronounced apertural hoods formed by elongated dorsal thecal wall, particularly in proximal thecae. [ŠTORCH (1994) discussed the strong intraspecific variation in the development of the genicular hoods of *E. adunca*.] *Silurian, Llandovery* (*Telychian, Monoclimacis crenulata* Biozone)–*Wenlock,* (*Homerian, Cyrtograptus lundgreni* Biozone): Spain, Czech Republic, UK, Estonia, Latvia, Morocco, Arctic Canada.——FIG. 293,*2a–c.* **E. adunca* (BOUČEK); *2a,* ?lectotype (selected by PŘIBYL, 1940b, p. 8), NMP L30665, showing the shape of the colony, Vyskočilka, Czech Republic (Zalasiewicz & Williams, 2000, Atlas, Folio 1.43); *2b,* proximal end from type slab NMP L30665 (Zalasiewicz & Williams, 2000, Atlas, Folio 1.43); *2c,* PŠ 475, *Cyrtograptus murchisoni* Biozone, Velká Ohrada, Czech Republic (ŠTORCH, 1994, fig. 5,*20c*). Scale bars, 1 mm.

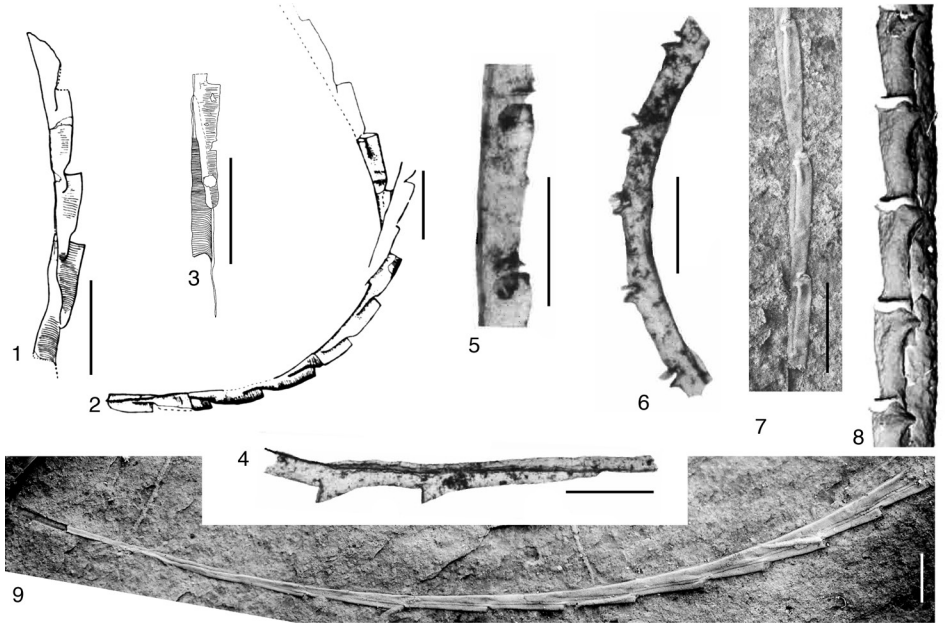


FIG. 292. The proximal end and thecal development of early monograptids. *1–2, Atavograptus ceryx* (RICKARDS & HUTT, 1970); *1,* SM A67088, complete proximal end of longer specimen (Rickards & Hutt, 1970, fig. 1D), *2,* holotype, SM A67087, pyritic internal mold (Rickards & Hutt, 1970, fig. 2A); *3*, *Atavograptus primitivus* (LI in YANG & others, 1983) proximal end (Lukasik & Melchin, 1994, fig. 1,*1*); *4*, *Coronograptus gregarius* (LAPWORTH, 1876b), proximal end, GSC 116247 (Lukasik & Melchin, 1997, fig. 7I); *5, Pribylograptus pleganopsis* LUKASIK & MELCHIN, 1997, stipe fragment showing genicular hoods and lateral apertural lobes, GSC 116240 (Lukasik & Melchin, 1997, fig. 7B); *6*, *Huttagraptus tholians* LUKASIK & MELCHIN, 1997, stipe fragment showing genicular hoods and flared apertures, note fragment of prosicula, GSC 116254 (Lukasik & Melchin, 1997, fig. 7P); *7*, *Pribylograptus incommodus* (TÖRNQUIST, 1899), fragment, latex cast of part of specimen, LO 1456T (new); *8*, *Pribylograptus argutus* (Lapworth, 1876b), thecal style, NMW 2002/19G.29D (adapted from Loydell & Maletz, 2009, pl. 6,*7*); *9*, *Huttagraptus acinaces* (TÖRNQUIST, 1899), holotype, LO 1436T, latex cast, showing long sicula and increasing thecal overlap (new). Scale bars, 1 mm.

Monoclimacis FRECH, 1897, p. 621 [**Graptolites vomerinus* NICHOLSON, 1872a, p. 52; OD] [=*Hemimonograptus* ZHAO, 1984, p. 101 (type, *Monoclimacis opercula* MU & others, 1974, p. 218, OD), syn. by MALETZ, herein] [?=*Hubeigraptus* LI, 1995, p. 268 (type, *H. semilunatus,* OD), syn. by MALETZ, herein]. Tubarium straight or dorsally curved proximally; sicula short; first theca originated via modified resorption porus or derived type; thecae geniculate, with supragenicular wall parallel to or less commonly inclined to axis of tubarium; apertural excavations semi-circular or semi-elliptical, commonly with overhanging hood, outgrowth of the dorsal wall; in some species, small number of proximal thecae hooked. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 293,*3a–c*. **M. vomerina* (NICHOLSON); *3a,* neotype (STRACHAN, 1971, p. 91), proximal end only, Riccarton Beds, Elliotsfield, Scotland (Zalasiewicz, 2000f, Atlas, Folio 1.48); *3b–c,* proximal end and distal fragment, BGS RCV2012, BGS RCV236, Buttington quarry, Wales (Loydell & Cave, 1993, fig. 7E–F). Scale bars, 5 mm.

Pernerograptus PŘIBYL, 1941, p. 9 [**Graptolites argenteus* NICHOLSON, 1869, p. 239; OD] [=*Pernerograptus* (*Quasipernerograptus*) ZHAO, 1984, p. 105 (type, *P.* (*Q.*) *leptotheca,* OD), syn. by LOYDELL, herein; =*Pseudopernerograptus* WANG in WANG & others, 1987, p. 380 (type *Monograptus revolutus* KURCK, 1882, p. 299, OD), syn. by LOYDELL, herein]. Straight to dorsally curved proximal part of tubarium with straight distal part; dorsal curvature accentuated in mesial part of colony; biform thecae; sicula small, apex not reaching to first metatheca; proximal thecae slender, axially elongated without overlap, terminated by apertural hoods that are either simple or transversely expanded; apertural hoods retreat in mesial thecae leaving only lateral lappets and dorsal apertural hoods that also subsequently retreat, resulting in simple, cylindrical, greatly overlapping distal thecae. *Silurian, Llandovery* (*Rhuddanian, Pernerograptus revolutus/Coro-*

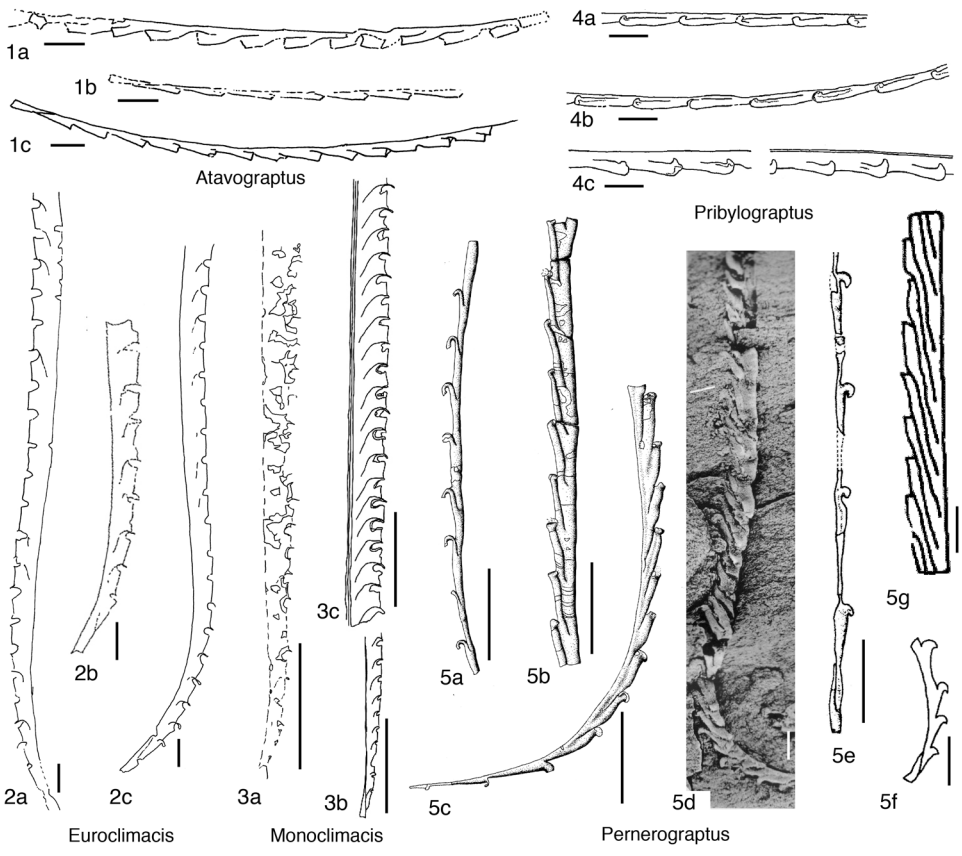


FIG. 293. Pernerograptinae (short siculae) (p. 433–435).

nograptus cyphus Biozone–*Aeronian*, *Lituigraptus convolutus* Biozone): worldwide.——FIG. 293,*5a–b*. *P. revolutus* (KURCK), syntype, LO 475t, Bollerup, Scania, Sweden, scale bars, 1 mm (Hutt, 1974b, fig. 1a–b).——FIG. 293,*5c*. *P. sudburiae* (HUTT, 1974b), holotype, LO 4454T, Tommarp, Sweden, scale bar, 1 mm (Hutt, 1974b, fig. 1d).——FIG. 293,*5d–e*. **P. argenteus* (NICHOLSON); *5d,* lectotype, NHMUK Q3148, Skelgill, Lake District, England (Hutt, 1975, pl. 17,*3*); *5e*, proximal end with sicula, SM A85016, Yewdale Beck, England (Hutt, 1975, fig. 17,*2*). Scale bars, 1 mm.——FIG. 293,*5f–g*. *P. leptotheca* (ZHAO, 1984), proximal and distal fragments (Zhao, 1984, fig. 4A,C). Scale bars, 1 mm.

Pribylograptus OBUT & SOBOLEVSKAYA, 1966, p. 33 [**Monograptus incommodus* TÖRNQUIST, 1899, p. 11; OD]. Tubarium long, variably and gently curved proximally, straight distally; sicula rarely recorded but usually 1.8–2.0 mm long; thecae simple, gradually widening tubes proximally, commonly with increasing overlap distally; transitions between thecal morphologies gradual; thecal apertures flanked by lateral lappets throughout colony; geniculate thecae with flanges or hoods overhanging thecal apertures; unpaired genicular or supragenicular spines may be present. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Stimulograptus sedgwickii* Biozone): worldwide.——FIG. 293,*4a–c*. **P. incommodus* (TÖRNQUIST), Röstånga, Scania, Sweden; *4a–b,* holotype, LO 1456T, thecal style (Koren' & Bjerreskov, 1997, fig. 21A); *4c,* paratype, LO 1457t, fragment (Koren' & Bjerreskov, 1997, fig. 21B). Scale bars, 0.1 mm.

GENERA WITH LONG SICULAE

The sicula is more than 2 mm long in all taxa included in this group, and siculae of as much as 16 mm in length have been documented for *Coronograptus maxiculus* ŠTORCH, 1988 (see ŠTORCH, 1988).

Coronograptus OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 92 [**Monograptus gregarius* LAPWORTH, 1876c, p. 317; OD]. Strongly dorsally curved tubarium that may become straight

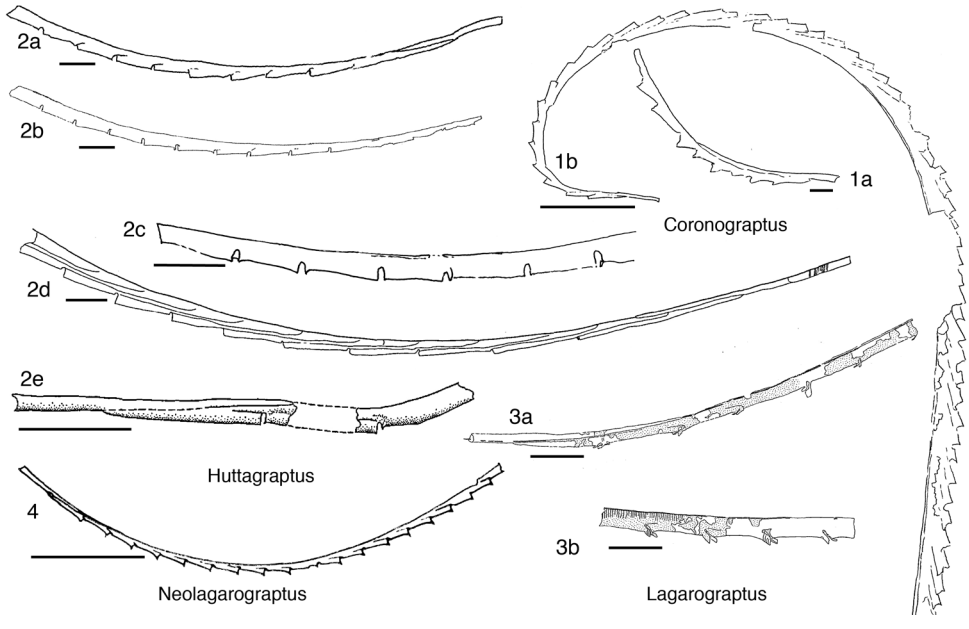


FIG. 294. Pernerograptinae (long siculae) (p. 435–437).

distally; sicula long (2.5–16 mm), with majority of length contributed by metasicula, which possesses a resorption porus; first theca emerges high on metasicula; thecae long overlapping tubes; geniculate immediately above or below thecal apertures, with concave free ventral thecal walls subaperturally at least in proximal thecae; flared, unornamented thecal apertures; genicular hoods may be developed proximally or throughout tubarium but are absent in most species. *Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): worldwide.——FIG. 294,*1a*. **C. gregarius* (LAPWORTH), syntype, BU 1435, Dob's Linn, Scotland, scale bar, 1 mm (Zalasiewicz, 2000e, Atlas Folio 1.13).——FIG. 294,*1b*. *C. cyphus* (LAPWORTH, 1876b), typical specimen BU 1430, Dob's Linn, Scotland, scale bar, 5 mm (Zalasiewicz, Williams, & Akhurst, 2003, fig. 2A).

Huttagraptus KOREN' & BJERRESKOV, 1997, p. 13 [**Atavograptus praestrachani* HUTT & RICKARDS in RICKARDS, HUTT, & BERRY, 1977, p. 102; OD]. Long, slender, slightly to strongly dorsally curved tubarium; sicula long (2–7 mm); first theca originated high on metasicula via resorption foramen; typically long overlapping thecae with free ventral walls at very low angle or parallel to tubarium axis and with pronounced angular geniculum proximally, creating marked thecal excavation, and in some species these features retained mesially or throughout entire tubarium; genicular flanges may overhang thecal apertures forming distinct hoods; geniculum retreats gradually and thecae become simple tubes with increased inclination of free ventral wall to the tubarium axis in species with thecae lacking genicula mesially or distally. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Demirastrites triangulatus* Biozone): worldwide.——FIG. 294,*2a–c,e*. **H. praestrachani* (HUTT & RICKARDS in RICKARDS, HUTT, & BERRY), holotype, SM A60415a–b, Keisley, northern England, scale bars, 1 mm (Hutt & Rickards, 1970, fig. 3C; Zalasiewicz, 2008d, Atlas, Folio 2.73); *2e,* MGUH 24205, proximal end, Kos-Istek region, southern Urals, Russia, scale bars, 1 mm (Koren' & Bjerreskov, 1997, fig. 10B).——FIG. 294,*2d*. *H. acinaces* (TÖRNQUIST, 1899), holotype, LO 1436T, scale bar, 1 mm (Koren'& Bjerreskov, 1997, fig. 12H).

Lagarograptus OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVESKAYA, & MERKUREVA, 1968, p. 90 [**L. inexpeditus;* OD]. Narrow, dorsally curved tubarium; long sicula (1.9–4.35 mm); first theca originated via a resorption porus; overlapping, sharply geniculate thecae with free ventral walls subparallel to tubarium axis; shallow and narrow apertural excavations; tonguelike ventral apertural process and dorsal apertural hood present on all thecae. *Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Campograptus curtus* Biozone): Siberia, Kazakhstan, northern and Arctic Canada, China.——FIG. 294,*3a–b*. **L. inexpeditus* OBUT & SOBOLEVSKAYA; *3a,* proximal end, MGUH 24347, Kos-Istek region, southern Urals, Russia (Koren' & Bjerreskov, 1997, fig. 23H); *3b,* distal fragment, MGUH 24343, Kos-Istek region, southern Urals, Russia (Koren' & Bjerreskov, 1997, fig. 23B). Scale bars, 1 mm.

Neolagarograptus Štorch, 1998a, p. 228 [**Lagarograptus helenae* Štorch, 1988, p. 24; OD]. Tubarium arcuately dorsally curved, gradually expanding in dorso-ventral width, with tendency to be parallel sided; sicula long (3.5–5.1 mm); long, overlapping, geniculate thecae with simple, slightly widened apertures, shallow apertural excavations and, in some species, a single ventral apertural process. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone–*Stimulograptus sedgwickii* Biozone): Czech Republic, Great Britain, Latvia, Myanmar, Iran, Saudi Arabia.——Fig. 294,*4*. **N. helenae* (Štorch), holotype, PŠ 274, Tmaň, Czech Republic, scale bar, 5 mm (Štorch, 1988, fig. 4D).

'STREPTOGRAPTINES'

Dorsally or ventrally curved to proximally vaguely S-shaped and distally straight to fish-hook-shaped tubaria; proximal thecae without overlap in earlier taxa bearing thecae with distally increasing overlap; younger taxa lacking thecal overlap; sicula small with comparably large prosicula; origin of th1 from lenticular porus development low in sicula if known (sinus and lacuna stages not described or illustrated for any taxon of the group); isolated metathecae with coiled apertural part, bearing proximo-ventrally directed nozzle; thecae originating through paired cupulae in derived taxa; thecae typically bear genicular platform with longitudinal convexity; uncoiled initial part of thecae widening distally or with bulge, widest part at base in some. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.

Bouček and Přibyl (1943, 1951) and Bouček and Přibyl in Přibyl, 1948a) discussed *Streptograptus* and *Mediograptus* as characterized by their special thecal apertures but identified them as subgenera of *Monograptus*. The authors differentiated several distinct groups in the two taxa. Maletz and others (2019) used the term streptograptid to describe the characteristic thecal construction of the genus *Streptograptus* and of related genera, herein included in an informal group referred herein to as the 'streptograptines.' The streptograptines may be identified as a subfamily if the constructional details prove to be phylogenetically meaningful. They can be viewed as related through their complex thecal apertures bearing conspicuous distal (lateral) lobes and the proximally directed nozzle (Fig. 295.3, Fig. 296.4). The tubarium shape is highly variable, ranging from dorsally curved in *Paramonoclimacis* (Fig. 295.1) to fish-hook-shaped, with initial dorsal curvature and distal ventral curvature. Many slender forms are more variable in shape but are only slightly sinuously curved. The isolated hooked distal metathecae may be of a variable length but are often conspicuous. The apertures are strongly introverted and open into the ventral metathecal sides, typically into a platform with thickened rim (Fig. 296.10) (Loydell & Maletz, 2004). Earlier taxa without cupulae usually possess metathecae with a relatively long, isolated hook (Fig. 296.1) before the development of the thecal aperture.

Specimens of the genus *Paramonoclimacis* may easily be misidentified as *Pernerograptus* species with simple apertural hoods when flattened. A thecal gradient comparable to that of *Pernerograptus* is also visible in *Paramonoclimacis* (see Fig. 295.1, displacement of cupulae) but not in other genera of the group and may indicate the phylogenetic relationship of the streptograptines to the earlier pernerograptines.

Important characters such as the characteristic cupulae (Fig. 296) of derived streptograptines or the increasing thecal overlap of earlier forms (Fig. 295.1) are typically not recognizable in flattened material. Therefore, the generic assignment of many species is difficult. Chemically isolated material clearly has remains of cupulae in *Mediograptus* species and also the characteristic thecal apertural nozzle. The cupulae may be reduced in size. Teller (1986) described isolated specimens of *Mediograptus antennularius* (Meneghini, 1857) and *Mediograptus flexuosus* (Tullberg, 1883) from the *Monograptus flexilis* Biozone (Sheinwoodian, Wenlock) of Poland. *Mediograptus flexuosus* appears to have cupulae (Teller, 1986, pl. 6.11). The illustrations are partly simplified (Fig. 296.9)

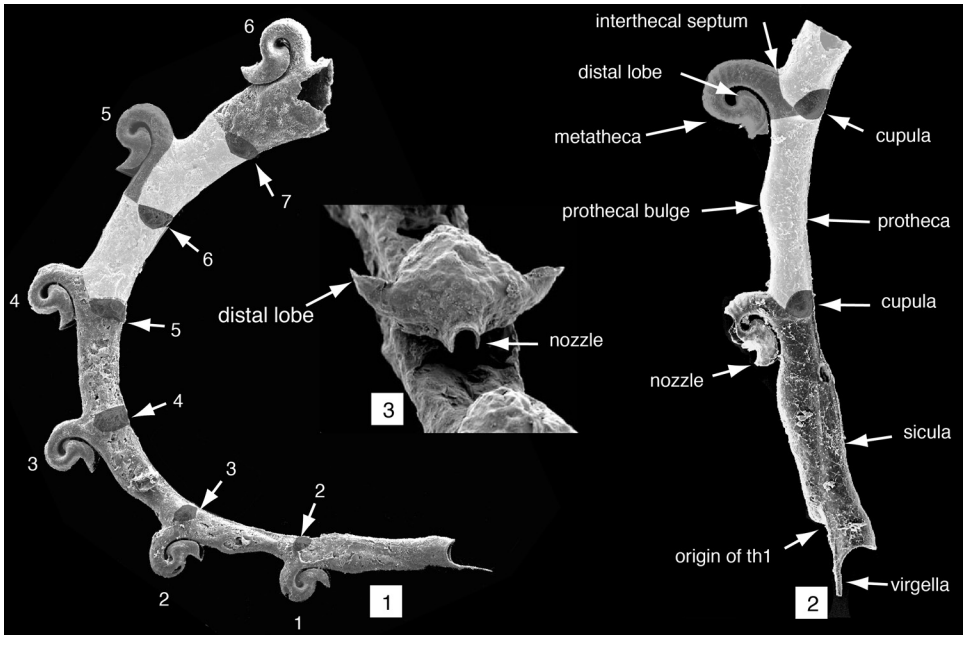


FIG. 295. Streptograptine proximal ends and colony construction. *1–2, Paramonoclimacis sidjachenkoi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & BONDAREV, 1965); *1*, thecal apertures and associated cupulae are labeled; *2*, proximal end illustrating important tubarium features (based on Maletz & others, 2019, fig. 1); *3, Streptograptus dalecarlicus* LOYDELL & MALETZ, 2004, thecal aperture showing distinct nozzle and outward-directed distal lobes on thecal aperture.

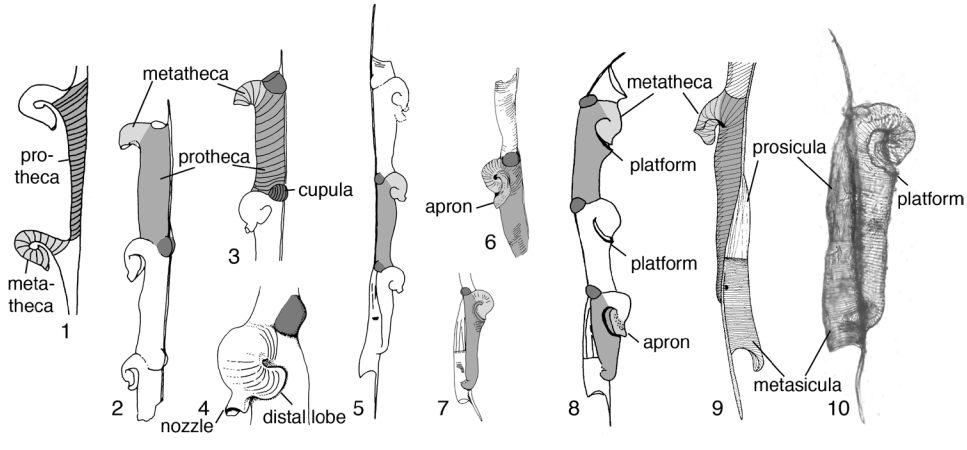


FIG. 296. Tubarium character of streptograptines. *1*, *Streptograptus ansulosus* (TÖRNQUIST, 1892), thecal style with long isolated part, lacking cupulae and platform; *2–5*, *Streptograptus dalecarlicus* LOYDELL & MALETZ, 2004, showing cupulae and laterally extended distal lobes; *6–7, Streptograptus sartorius* (TÖRNQUIST, 1881) with apron covering the platform in mature thecae; *8*, *Streptograptus johnsonae* (LOYDELL, 1991a), proximal end with complete th1 showing apron, th2 and th3 without apron (*1–8,* new); *9, Mediograptus antennularius* (MENEGHINI, 1857), reconstruction of proximal end showing simplified metatheca and origin of th2 (adapted from Teller, 1986, fig. 8); *10, Streptograptus sartorius* specimen, Solberga, Dalarna, Sweden (Maletz & others, 2019, fig. 3L). Illustrations not to scale.

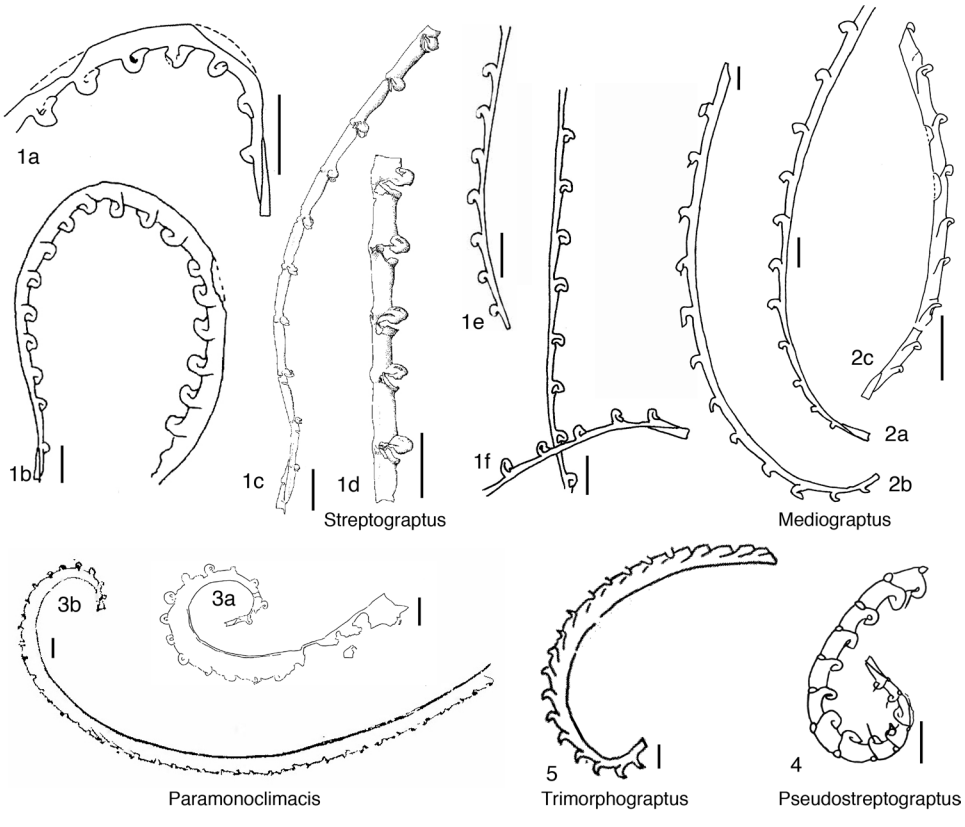


FIG. 297. Streptograptines (p. 439–440).

but show the main characters of the tubaria. JAEGER (1991) described *Streptograptus serexiguus* (JAEGER, 1991) from the Homerian *Testograptus testis* Biozone (equivalent to the *Cyrtograptus lundgreni* Biozone) of Nevada as the youngest form within the *Streptograptus exiguus* group.

Streptograptus YIN, 1937, p. 297 [**Graptolithus plumosus* BAILY, 1871, p. 22; SD ICZN, Opinion 1714, 1993, p. 90 (replacement of *Monograptus nodifer* TÖRNQUIST, 1881, *sensu* ELLES & WOOD, 1913, pl. 46,2a–d; YIN, 1937, p. 297; proposed to ICZN by LOYDELL & CHEN, 1991)] [=*Globosograptus* BOUČEK & PŘIBYL in PŘIBYL, 1948a, p. 37 (type, *Monograptus wimani* BOUČEK 1932, p. 153, OD), syn. by LOYDELL, 1996, p. 891; =*Awarograptus* ZALASIEWICZ & HOWE, 2003, p. 45 (type, *Monograptus nodifer* TÖRNQUIST, 1881, OD), syn. by LOYDELL & NESTOR, 2006, p. 590]. Tubarium straight, dorsally, ventrally or dorso-ventrally curved; sicula small; first theca originated via a lenticular porus; metathecae coiled; thecal apertures with central, proximo-ventrally directed nozzle, in some taxa developed only in the apron. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 297,*1a–b.* **S. plumosus* (BAILY); *1a,* neotype, BELUM K12274d, Tieveshilly, County Down, Northern Ireland, scale bar, 1 mm (Loydell, 1990b, fig. 1); *1b,* larger specimen showing tubarium shape, MGM6646-0, El Pintado reservoir, Seville Province, Spain, scale bar, 1 mm (Loydell, Frýda, & Gutiérrez-Marco, 2015, fig. 21AQ).——FIG. 297,*1c–d. S. nodifer* (TÖRNQUIST), neotype (ZALASIEWICZ & HOWE, 2003, p. 46), proximal end and distal thecal style, LO 6465t, Nitsjö, Dalarna, Sweden (Zalasiewicz & Howe, 2003, fig. 1). Scale bars, 1 mm.——FIG. 297,*1e–f. S. wimani* (BOUČEK, 1932); *1e,* lectotype (BOUČEK & PŘIBYL in PŘIBYL, 1948a, p. 38), Vyskočilka, Czech Republic (Bouček, 1932, fig. 1i); *1f,* proximal end showing sicula, MGM 142-S, Jabalón River section, central Spain (Loydell & others, 2009, fig. 4F). Scale bars, 1 mm.

Mediograptus BOUČEK & PŘIBYL in PŘIBYL, 1948a, p. 39 [**Monograptus kolihai* BOUČEK, 1931; OD]. Slender, dorsally or dorso-ventrally curved tubarium; sicula short, apex reaching no higher than top of first theca; long, narrow prothecae in some

species with cupulae at base; metathecae complex, the aperture comprising central, more or less well defined, proximal-facing portion, and two laterally curved parts, which may face laterally, dorsally, ventrally, proximally, distally, or a combination of the above depending on degree of twisting of horn-like lateral regions of metatheca; thecae exhibit overlap throughout tubarium. *Silurian, Llandovery* (*Telychian, Cyrtograptus insectus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 297,*2a–b*. **M. kolihai* (Bouček); *2a,* lectotype (Přibyl, 1948a, p. 39), NMP L30671 Motol Formation, Vyskočilka near Malá Chuchle, Prague, Czech Republic (Bouček, 1931, fig. 8A); *2b,* proximal end, PŠ 481.11 (Štorch, 1994, fig. 5.*6*) Scale bars, 1 mm.——Fig. 297,*2c. M. flittoni* Loydell & Cave, 1996*,* holotype, BGS RCV3587, Banwy River section, Powys, Wales, scale bar, 1 mm (Loydell & Cave, 1996, fig. 13B).

Paramonoclimacis Wang & Ma in Wang & others, 1977, p. 360 [**P. typicalis;* OD; =*Pernerograptus sidjachenkoi;* Obut & Sobolevskaya in Obut, Sobolevskaya, & Bondarev, 1965; syn. by Mu & others, 2002, p. 896]. Initially dorsally planispirally coiled, distally straight distinctly widening tubarium; small sicula; cupulae at base of prothecae; proximal thecae lack overlap and have coiled metathecae with lateral apertural lobes and nozzle; thecal overlap increases distally; distally coiling of metathecae becomes steadily less pronounced and distalmost thecae have a thecal apertural excavation and overhanging hood. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone): China, Russia, Canada, USA (Alaska).——Fig. 297,*3a–b*. **P. sidjachenkoi* (Obut & Sobolevskaya); *3a,* holotype, proximal end, CNIGR 8783/89, Taimyr (Maletz & others, 2019, fig. 2A); *3b,* **P. typicalis,* holotype, large specimen (Wang & others, 1977, fig. 47). Scale bars, 1 mm.

Pseudostreptograptus Loydell, 1991a, p. 236 [**P. williamsi;* OD]. Tubarium strongly ventrally curved; sicula small; prominent cupulae at base of prothecae; retroverted metathecae terminate in upturned lip as in *Streptograptus* but are also laterally expanded and furnished with lateral spines or more distally branching spatulate processes; platform concave. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone): Wales, Spain, Sweden, Australia.——Fig. 297,*4*. **P. williamsi,* topotype, BGS DKL 1372, south of Craig-y-Delyn, Aberystwyth, Wales, scale bar, 1 mm (Loydell, 1991a, fig. 9H).

Trimorphograptus Zhao, 1984, p. 102 [**Pernerograptus qijiangensis* Ye, 1978, p. 478; OD]. Tubarium dorsally curved considerably near proximal end, straight distally; proximal end unknown; proximal thecae hooked; mesial thecae with geniculum, apertural excavation and thecal hoods; distal thecae with rounded geniculum or straight ventral walls; thecal details unknown. *Silurian* (*Aeronian*): China.——Fig. 297,*5*. *T. minor* Zhao, 1984, nearly complete specimen, scale bar, 1 mm (Zhao, 1984, fig. 3).

Subfamily MONOGRAPTINAE Lapworth, 1873

[Monograptinae Lapworth, 1873b, table 1, facing p. 555, *ex* Monograptidae Lapworth, 1873b, table 1, facing p. 555] [=Rastritinae Gürich, 1908, p. 35, *ex* Rastritidae Gürich, 1908, p. 35, Přibyl, 1946, p. 276; =Demirastritinae Hundt, 1943, p. 263, *ex* Demirastritidae Hundt, 1943, p. 263, Přibyl, 1946, p. 276; =Diversograptinae Hundt, 1943, p. 263, *ex* Diversograptidae Hundt, 1943, p. 263, Přibyl, 1946, p. 276; =Spirograptinae Obut, 1950, p. 265; =Cyrtograptinae Averianow, 1929, p. 103, *ex* Cyrtograptidae Averianow, 1929, p. 103, Yin, 1937, p. 296]

Straight to dorsally coiled, planispiral to trochospiral, S-shaped, or ventrally coiled tubarium with hooked, triangular to rastritid thecae with or without thecal overlap; hooks may be lost and thecal overlap may increase distally; sicula with lenticular porus or derived one; apertures hooked, generally bearing paired apertural spines or lappets. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.

The subfamilies introduced by Hundt (1943) and Přibyl (1946) for taxa here included in the Monograptinae are not considered necessary. Obut (1950) used the subfamily Spirograptinae in his text, but the taxon was never defined or discussed further. Přibyl (1946) included the genus *Spirograptus* in his subfamily Monograptinae, however, Obut (1957, 1964) did not mention the Spirograptinae.

MORPHOLOGY

Most taxa of the Monograptinae have a variably developed dorsal curvature, either planispiral or trochospiral. Distally, the stipes may be straight. The relationships to the ventrally curved genera *Cochlograptus* and *Testograptus* with similar thecal style have been uncertain in the past. Lenz and Melchin (2008) analysed the two genera and concluded that both originated independently from monograptid ancestors as a result of convergent evolution. *Cochlograptus* may be related to *Stimulograptus* or *Monograptus* and *Testograptus* could have its origin in a *Monograptus flemingii* type ancestor.

The thecae in the Monograptinae (Fig. 298) are quite variable at first sight, but they have certain commonalities. They are

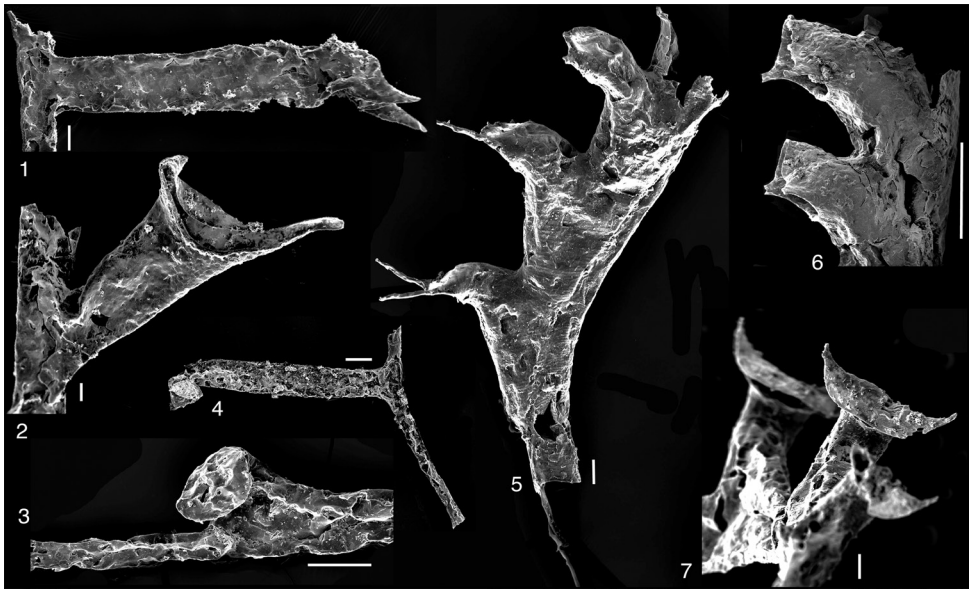


FIG. 298. Thecal style in the Monograptinae. *1–2, Lituigraptus convolutus* (HISINGER, 1837), isolated thecae in lateral (*1*) and ventral (*2*) views; *3*, *Torquigraptus* sp., isolated theca with torsion and laterally widened aperture; *4*, *Rastrites* sp., single theca; *5*, *Spirograptus turriculatus* (BARRANDE, 1850), juvenile; *6*, *Stimulograptus sedgwickii* (PORTLOCK, 1843), two thecae with paired spines; *7*, *Oktavites contortus* (PERNER, 1897), thecal apertures with pointed lateral extensions and wide hood (new). All specimens Kalholn Shale, Dalarna. Scale bars, 1 mm in 6; all others 0.1 mm.

variably elongated with an apertural hood or hook, thus an opening that is proximally or ventrally directed. The shape may change gradually along the stipes in a typical biform fashion. In general, it is triangular with an isolated apertural part, however, parallel-sided isolated prothecae are also common. Metathecae may be completely isolated and parallel sided as in *Rastrites* or in the proximal thecae of *Lituigraptus* (Fig. 298.1–298.2, 298.4) and early *Torquigraptus,* such as *Torquigraptus decipiens* (TÖRNQUIST, 1899). In *Lituigraptus,* the thecae bear paired laterally directed hornlike extensions in distal thecae. The thecal aperture is directed proximally or ventrally and bears a wide dorsal hood (Fig. 298.2). Distally, the thecae are more robust and the prothecae widen considerably (LOYDELL & MALETZ, 2009). The apertural hood may be strongly laterally extended as in *Oktavites contortus* (Fig. 298.7). Thecal overlap may be close to none, as in *Spirograptus* and *Oktavites,* but is absolutely none in *Rastrites,* with its very slender parallel-sided prothecae (Fig. 298.4). Considerable thecal overlap is present in many species of *Monograptus*. *Campograptus harpago* (TÖRNQUIST, 1899) and *Campograptus lobiferus* (M'COY, 1850) have proximal thecae with hooked apertures and distinct paired spines as do species of the genus *Monograptus,* for example, as in *Monograptus priodon.* The spines diminish distally and the thecal apertures curve and grow back on themselves as they also do in *Lapworthograptus grayae* (CHOPEY-JONES, WILLIAMS, & ZALASIEWICZ, 2003). In *Stimulograptus sedgwickii*, the thecal apertures bear paired lateral spines, but a dorsal hood is lacking. The central part of the thecal aperture is directed ventrally with the paired spines in a proximal position (Fig. 298.6), producing a wide and much more open aperture in distal thecae. Proximal thecae clearly possess the apertural hood and paired lateral spines, indicating a considerable transformation of thecal shapes along the stipes in the Monograptinae, leading to the development of biform thecal styles.

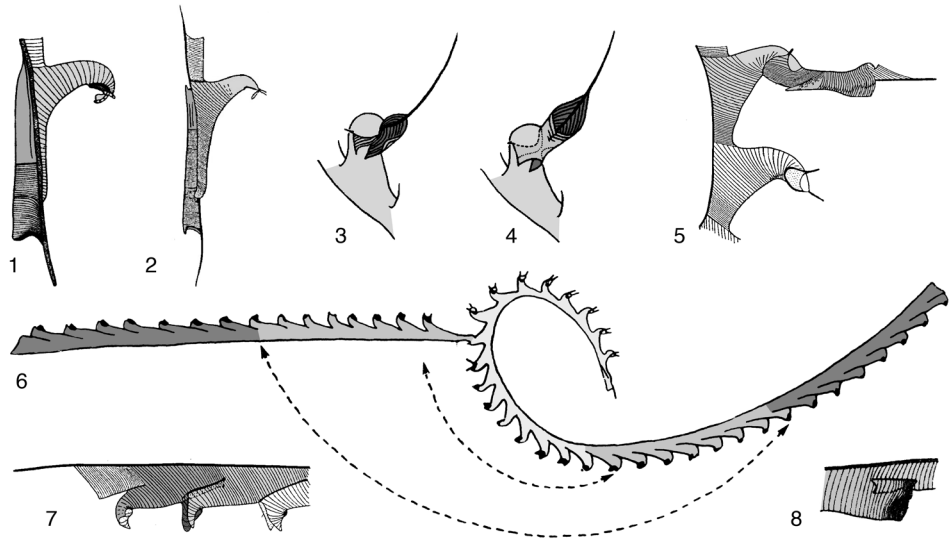


FIG. 299. Tubarium development in *Cyrtograptus*. *1* and *8*, *Cyrtograptus hamatus* (BAILY, 1862) (adapted from Teller, 1976, fig. 11–12); *2–7, Cyrtograptus perneri* BOUČEK, 1933 (*2,5,7;* adapted from Thorsteinsson, 1955, fig. 1–4 as *Cyrtograptus rigidus* n. ssp.; LENZ & others, 2012, p. 32); 3–*4*, adapted from Bulman (1955, fig. 47); *6*, adapted from Bulman (1970, fig. 65; correction after Bulman, 1955, fig. 47). Illustrations not to scale.

Torsion of the metathecae occurs in *Torquigraptus,* in which the thecal apertures are twisted to the reverse side of the tubarium, and the thecal hood may be somewhat laterally expanded (Fig. 298.3). Asymmetry without torsion is visible in the thecae of *Spirograptus turriculatus* (Fig. 298.5), in which the second apertural spine is missing in most thecae and the aperture becomes tear-shaped (MELCHIN & LENZ, 1986).

Triangulate thecae with a distinct hood or hook and a proximally oriented aperture bearing paired spines, along with a strong dorsal hood or lobe (Fig. 299.1–299.2), are also present in many *Cyrtograptus* species (see TELLER, 1976). However, their cladial stipes often bear more simple thecae with some thecal overlap and distally directed, paired apertural lobes (Fig. 299.7). These hooked apertures and apertural spines are either symmetrical or asymmetrical in species of *Cyrtograptus* (LENZ & MELCHIN 1989). A distinct thecal gradient from triangulate thecae proximally to those with low inclination may also occur. Increased thecal overlap also signals changes in the apertural development (Fig. 299.6). Simple apertural development, without any hooks, hoods, or lobes, is present in *Cyrtograptus hamatus* (Fig. 299.8) and some other species of the genus *Cyrtograptus*. The genus has been suggested to be polyphyletic (e.g., RICKARDS, HUTT, & BERRY, 1977; FU, 1994; WILLIAMS & ZALASIEWICZ, 2004; URBANEK & TELLER, 1997), and LENZ and others (2012) decided not to use the family Cyrtograptidae but include the genus *Cyrtograptus* in Monograptidae instead.

Taxa with and without cladia are differentiated herein for purely practical reasons. The differentiation does not have any taxonomic implications, and the cladia-bearing taxa may have evolved independently from other taxa of the Monograptinae. The presence or absence of cladia cannot be regarded as a useful taxonomic character but has been used as an important and even defining character for the genus *Cyrtograptus* in the past.

TAXA WITHOUT CLADIA

RICKARDS, HUTT, and BERRY (1977; fig. 1) provided the only available interpretation of early monograptids, suggesting the origination of several independent lineages from the

genus *Atavograptus* and of the *Monograptus priodon* group from *Monoclimacis*. The taxa of the Monograptinae without cladia form a paraphyletic taxon and gave rise to cladia-bearing taxa multiple times.

Campograptus Obut, 1949, p. 24 [**Monograptus convolutus* var. *communis* Lapworth, 1876b, p. 358; SD Obut, 1964, p. 328]. Tubarium gently to strongly dorsally curved proximally, becoming almost straight distally; thecae triangular with no overlap; prothecal bases broad; simply hooked metathecae, thecal hook proximally involving primarily dorsal and, to much lesser extent, ventral thecal wall, and mesially and distally probably dorsal wall only; thecal apertures of proximal, mesial and, in some species, even distal thecae possess paired ventro-laterally or proximo-laterally directed spines; proximal thecae may be axially elongated. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Stimulograptus sedgwickii* Biozone): worldwide.——Fig. 300,*1a–b*. **C. communis* (Lapworth); *1a,* lectotype (Přibyl, 1948a, p. 48), BU 1684a, proximal end not shown (Lapworth, 1876b, fig. 4a); *1b,* proximal end in relief, internal mould, SM A24487, C horizon (*Demirastrites triangulatus* Biozone), Rheidol Gorge (Sudbury, 1958, fig. 20). Scale bars, 1 mm.

Cochlograptus Obut, 1987, p. 142 [**Nautilus veles* Richter, 1871, p. 243, fig. 1; OD]. Disk-shaped, ventrally and continuously planispirally coiled tubarium with sharp ventral deflection near apex of sicula; tubarium development by means of pseudovirgula; sicula moderately to strongly ventrally curved; prominent triangular dorsal tongue on sicular aperture; thecae hooked, with well-developed, paired lateral spines. *Silurian, Llandovery* (*Telychian, Streptograptus crispus* Biozone–*Oktavites spiralis* Biozone): worldwide.——Fig. 300,*2a–b*. **C. veles* (Richter); *2a,* lectotype, BGR X11901a, Thuringia, Germany (precise locality unknown) (Maletz, 2001a, fig. 3a); *2b,* holotype of *Monograptus discus* Törnquist, 1883, LO 1071T, Kallholn, Dalarna, Sweden (Maletz, 2017c, fig. 6D). Scale bars, 1 mm.

Cultellograptus Loydell & Nestor, 2006, p. 602 [**Monograptus cultellus* Törnquist, 1881, p. 434; OD]. Tubarium straight, except for initial ventral curvature that involves the sicula; thecae with extremely wide metathecae, hooked, nonspinose, lacking overlap; common canal narrow. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone)–*Wenlock* (*Sheinwoodian, Cyrtograptus murchisoni* Biozone): UK, Czech Republic, Germany, Romania, Baltic States, Sweden, Morocco.——Fig. 300,*9a–b*. **C. cultellus; 9a,* MGUH 31.681, Sommerodde-1 core, Bornholm, Denmark, (Loydell & others, 2017, fig. 16I); *9b,* isolated proximal end, Ventspils D-3 drill core, Latvia (adapted from Loydell & Nestor, 2006, fig. 9E). Scale bars, 1 mm.

Demirastrites Eisel, 1912, p. 27 [**Rastrites triangulatus* Harkness, 1851, p. 59; SD Bulman, 1929, p. 175]. Tubarium with proximally accentuated dorsal curvature; sicula small, apex reaching to about level of first metatheca at maximum; metathecae isolated, inclined at high angle to the tubarium axis; thecal apertural hoods or hooks may be extended transversely into a pair of lateral horns; mesial and distal thecae are more or less high-triangular in profile; first theca rastritid or triangular, axially elongated; up to several succeeding proximal thecae may have very slender elongated prothecae, slightly widening toward the base of widely separated, parallel-sided rastritiform metathecae. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Demirastrites pectinatus* Biozone): worldwide.——Fig. 300,*3a–c*. **D. triangulatus* (Harkness); *3a,* lectotype (Přibyl & Münch, 1941, p. 5), strongly distorted specimen, BGS 6941, Birkhill Shales, Frenchland Burn, Scotland (Zalasiewicz, 2008e, Atlas, Folio 2.92); *3b,* specimen missing proximal end, PŠ 3517, Všeradice, Czech Republic (Štorch, 2015, fig. 17f); *3c,* proximal end, PŠ 3643, Všeradice, Czech Republic (Štorch, 2015, fig. 17m). Scale bars, 1 mm.

Lapworthograptus Bouček & Přibyl, 1952b, p. 13, *ex Monograptus* (*Lapworthograptus*) Bouček & Přibyl, 1952b, p. 13; Zalasiewicz, 1995, p. 30. [**Cyrtograptus Grayi* Lapworth, 1876d, p. 545; OD] [=*Prochnygraptus* Přibyl & Štorch, 1985, p. 159 (type, *Monograptus singularis* Törnquist, 1892, p. 22, OD), syn. by Zalasiewicz, 1995, p. 34]. Tubarium irregularly curved or coiled in loose spiral; prothecae narrow, expanding gradually distally; metathecae initially growing ventrally to dorso-ventrally, then bending sharply through 180 degrees to grow dorsally; thecal apertures face dorsally or proximally. [Possible cladium only known from holotype (Zalasiewicz & Loydell, 2008); needs to be verified.] *Silurian, Llandovery*, *Telychian* (*Monoclimacis crenulata* Biozone–*Oktavites spiralis* Biozone): UK, Germany, Sweden, Baltic States.——Fig. 301,*3a–c*. **L. grayae* (Lapworth); *3a–b,* holotype, NHMUK Q847, specimen and thecal detail, Penwhapple Glen, Girvan, Scotland, scale bars, 5 mm (Zalasiewicz & Loydell, 2008, Atlas, Folio 2.33); *3c,* isolated thecae, NRM PZ Holm 1352, Stygforsen, Dalarna, Sweden, scale bar, 1 mm (Bulman, 1932c, pl. 6,*13*–6,*14*).——Fig. 301,*3d. L. singularis* (Törnquist, 1892), PŠ 218/1, fragment, Prague-Řepy, Czech Republic, scale bar, 1 mm (Přibyl & Štorch, 1985, fig. 3C).

Lituigraptus Ni, 1978, p. 412, *ex Rastrites* (*Lituigraptus*) Ni, 1978, p. 412, Štorch, 1998a, p. 248 [**Rastrites* (*Lituigraptus*) *glomeratus;* OD; =*Prionotus convolutus* Hisinger, 1837, syn. by Štorch, 1998a, p. 248] [=*Corymbites* Obut & Sobolevskaya in Obut, Soboleveskaya, & Nikolaev, 1967, p. 132 (type, *C. sigmoidalis,* OD) syn. by Loydell, herein; *non Corymbites* Linnaeus, 1758 (Coleoptera, Elateridae, modern beetle)]. Dorsally enrolled spiral tubarium; distally tubarium axis may gradually twist and thecae may be situated ventrally or perpendicular to spiral plane; proximal thecae rastritiform, with thread-like prothecae and straight, tubular metathecae

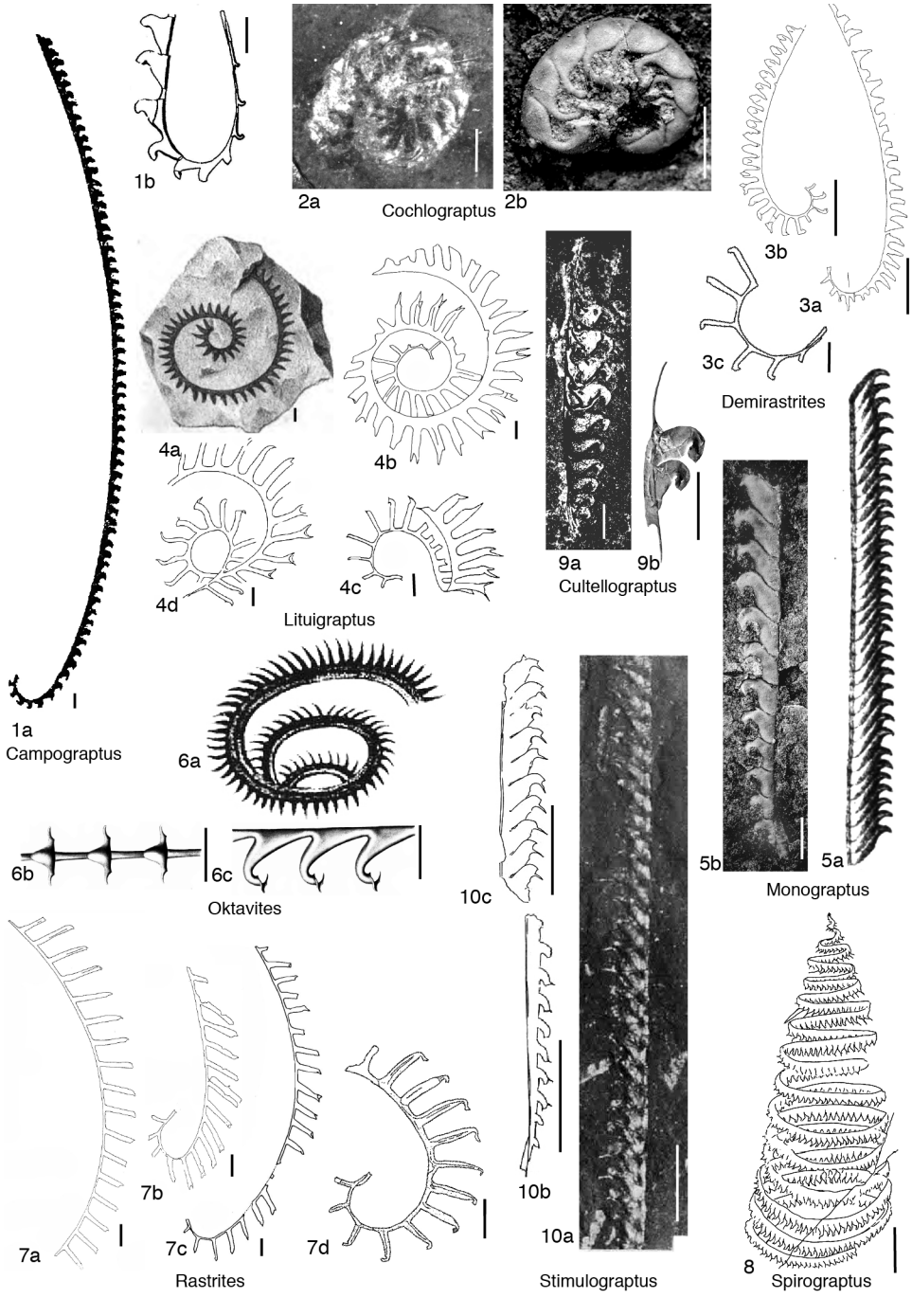


FIG. 300. Monograptinae (p. 443–446).

with hooded apertures; mesially thecae gradually become high triangular; apertural hoods gradually retreat being substituted by prominent paired, ventrally to ventro-proximally directed, lateral processes. *Silurian, Llandovery* (*Aeronian, Demirastrites simulans* Biozone–*Telychian*, *Spirograptus guerichi* Biozone): worldwide.——Fig. 300,*4a–d*. *P. convolutus* (Hisinger); *4a,* holotype, NRM Cn 68951, Furudal, Dalarna, Sweden (Hisinger, 1837, pl. 35.*7*); *4b,* medium-sized specimen with thecal apertures, BB 697, Tmaň, Czech Republic (Štorch, 1998a, fig. 11.*7B*); *4c,* proximal end with sicula, PŠ 724, Tmaň, Czech Republic (Štorch, 1998a, fig. 11,*7D*); *4d*, holotype of **L. glomeratus* Ni, 1978, NIGP 45401 (Ni, 1978, fig. 7.*7*). Scale bars, 1 mm.

Monograptus Geinitz, 1852, p. 32, *nom. correct. pro Monograpsus* Geinitz, 1852, p. 32; ICZN, Opinion 198, 1954b; *pro Lomatoceras* Bronn, 1835, p. 56; *pro Monoprion* Barrande, 1850, p. 36, ICZN, Opinion 198, 1954b [**Lomatoceras priodon* Bronn, 1835; SD Bassler, 1915b, p. 822] [=*Pomatograptus* Jaekel, 1889, p. 677 (type, *Lomatoceras priodon* Bronn, 1835, SD Bulman, 1929, p. 180), obj.; =*Priodon* Nilsson cited in Bronn, 1835, p. 56; =*Ancylograptus* Obut & Morozova in Obut & others, 1988, p. 62; *ex Monograptus* (*Ancylograptus*) Obut & Morozova in Obut & others, 1988, p. 62 (type, *Monograptus flexilis* Elles, 1900, p. 407; OD; =*Graptolithus* (*Monograpsus*) *belophorus* Meneghini, 1857, p. 165, type syn. by Štorch & Manda, 2019, p. 53), syn. herein]. Tubarium straight or dorsally curved proximally and then straight; thecae hooked with or without paired apertural spines or processes; thecal apertures face proximally or proximo-dorsally; thecae overlap, typically for half their length or more distally. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone–*Wenlock, Homerian, Colonograptus praedeubeli-deubeli* Biozone): worldwide.——Fig. 300,*5a–b*. **M. priodon* (Bronn); *5a,* holotype, fragment (Bronn, 1835, pl. 1.*13;* not found in the Bronn collection at the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (personal communication, Jessica D. Cundiff, 2014), scale unknown; *5b,* proximal end in relief, SMF 75780, glacial boulder, scale bar, 1 mm (Maletz, 2017a, pl. 15B).

Oktavites Levina, 1928, p. 10 [**Graptolithus spiralis* Geinitz, 1842, p. 700; SD Obut, 1964, p. 328] [=*Obutograptus* Mu, 1955, p. 10 (type, *Graptolithus spiralis* Geinitz, 1842, p. 700, OD, obj.)]. Dorsally curved or spirally coiled tubarium; metathecae triangular, sometimes almost rastritiform proximally, with little or no overlap; thecal apertures laterally expanded, sometimes asymmetrically; torsion, affecting the entirety of metatheca, developed distally; extension of metathecal dorsal wall over central portion of aperture causes this to face dorsally. *Silurian, Llandovery* (*Aeronian, Stimulograptus sedgwickii* Biozone–*Telychian, Cyrtograptus lapworthi* Biozone): worldwide.——Fig. 300,*6a–c*. **O. spiralis* (Geinitz); *6a,* syntype (not preserved, see Maletz, 2001a, p. 171) (Geinitz, 1842, pl. 10.*26*); *6b–c,* stipe fragments showing thecal style, Dalarna, Sweden (Bulman, 1932c, pl. 6,*15–16*). Scale unknown.

Rastrites Barrande, 1850, p. 64 [**R. peregrinus;* SD Hopkinson, 1869, p. 158] [=*Rastrograptus* Hopkinson & Lapworth, 1875, p. 633 *pro Rastrites* Barrande, 1850; =*Stavrites* Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968, p. 111 (type, *S. rossicus,* OD), syn. by Loydell, herein]. Tubarium straight or dorsally curved proximally to various degrees, straight distally; threadlike prothecae; straight, isolated metathecae, inclined at high angle to tubarium axis throughout length of colony; thecal apertures slightly hooked or hooded, sometimes with small paired apertural spines or lateral extensions. [Rickards, Hutt, and Berry (1977) and Štorch and Loydell (1992) discussed a possibly polyphyletic concept of the genus]. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Telychian, Monoclimacis griestoniensis* Biozone): worldwide.——Fig. 300,*7a–c*. **R. peregrinus; 7a,* lectotype, fragment, NMP L27954, Libomyšl, Czech Republic (Štorch, 2000b, Atlas, Folio 1.87); *7b,* complete specimen, NMP L30073, Bykoš, Czech Republic (Štorch, 2000b); *7c,* long specimen with complete sicula, PŠ 724, Tmaň, Czech Republic (Štorch, 1998a, fig. 11,*3B*).—— Fig. 300,*7d*. *R. rossicus* (Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968) holotype, CNIGR 270/9765 (Sun & others, 2022, fig. 12Q). Scale bars, 1 mm.

Spirograptus Gürich, 1908, p. 34 [**Graptolithus turriculatus* Barrande, 1850, p. 56; SD Bulman, 1929, p. 182] [=*Tyrsograptus* Obut, 1949, p. 24 (type, *Graptolithus turriculatus* Barrande, 1850, p. 56, SD Obut, 1964, p. 328), obj.]. Tubarium trochospirally coiled; sicula small (<1.5 mm) and dorsally curved, and in one species at least also exhibits dextral torsion; thecae hooked in manner of those of *Stimulograptus,* and bearing one or two apertural spines; thecal apertures may be symmetrical or asymmetrical resulting from differential development of the apertural margin, but without significant torsion; thecal overlap is negligible; common canal wide. *Silurian, Llandovery* (*Aeronian, Stimulograptus halli* Biozone–*Telychian, Streptograptus sartorius* Biozone): worldwide.—— Fig. 300,*8*. **S. turriculatus* (Barrande), lectotype, NMP L27597, Litohlavy, Czech Republic, scale bar, 5 mm (Štorch, 2000c, Atlas, Folio 1.92).

Stimulograptus Přibyl & Štorch, 1983, p. 221, *ex Monograptus* (*Stimulograptus*) Přibyl & Štorch, 1983, p. 221[**Graptolithus halli* Barrande, 1850, p. 48; OD]. Tubarium straight, dorso-ventrally curved, or dorsally curved proximally then straight distally; sicula less than 2 mm long; hooked, triangular thecae bear paired latero-ventrally directed spines; thecal overlap insignificant; distal thecae may be ventrally directed and without hook. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone–*Telychian, Oktavites spiralis* Biozone): worldwide.——Fig. 300,*10a–c*. **S. halli* (Barrande); *10a,* lectotype, NMP L20322, *Rastrites*

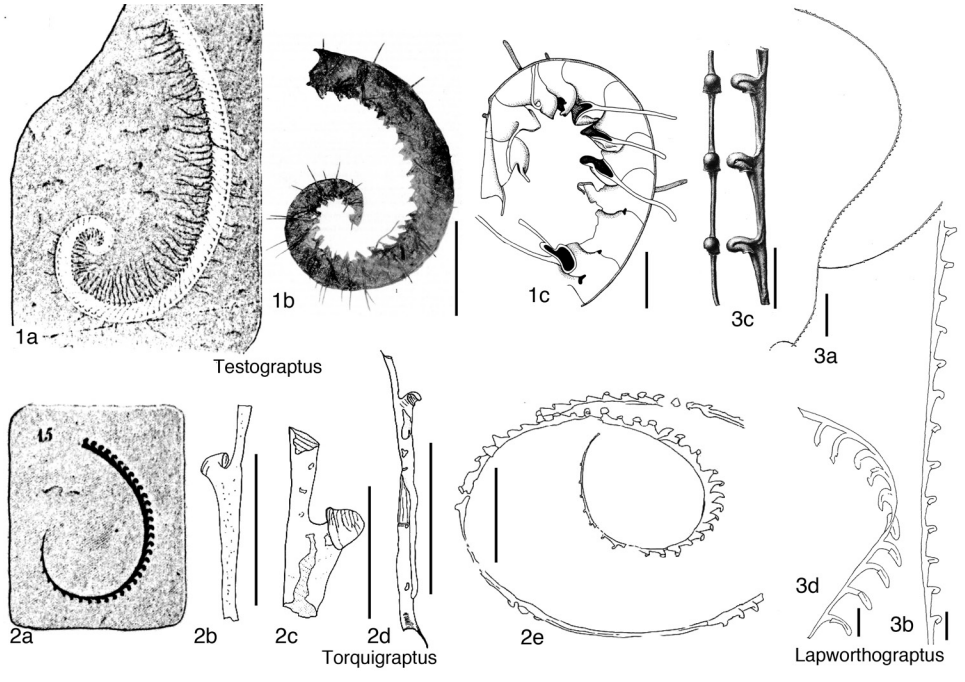


FIG. 301. Monograptinae (p. 443–446).

linnaei Biozone, Želkovice, Czech Republic (Přibyl & Štorch, 1983, pl. 2.*1*); *10b,* proximal end, PŠ 106b, Hlásná Třebaň, Czech Republic (Přibyl & Štorch, 1983, fig. 2A); *10c,* distal fragment, PŠ 108/3, Hlásná Třebaň, Czech Republic (Přibyl & Štorch, 1983, fig. 2B). Scale bars, 5 mm.

Testograptus PŘIBYL, 1967a, p. 49, *ex Monograptus* (*Testograptus*) PŘIBYL, 1967a, p. 49; LOYDELL & CAVE, 1994, p. 612 [**Graptolithus testis* BARRANDE, 1850; OD]. Tubarium planispirally and ventrally coiled through up to 450°, curvature strongest proximally with abrupt ventral flexure immediately distal of sicular apex; sicula weakly ventrally curved; tubarium development occasionally by means of pseudovirgula; thecae biform, with long, paired, laterally directed spines; proximalmost thecae with strongly hooked metatheca, distal thecae with lesser hook; thecal overlap ~50–75%. *Silurian, Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 301,*1a–c*. **T. testis* (BARRANDE); *1a,* ?lectotype, scale unknown (Barrande, 1850, pl. 3.*19*); *1b,* isolated specimen, scale bar, 5 mm (Urbanek & Teller, 1974, pl. 24); *1c,* small isolated specimen showing tubarium details, scale bar, 1 mm (Urbanek & Teller, 1974, fig. 1).

Torquigraptus LOYDELL, 1993, p. 112 [**Graptolithus proteus* var. *plana* BARRANDE, 1850, p. 58; OD]. Tubarium curved, or coiled, bearing thecae that exhibit torsion only of apertural part of the metatheca, toward reverse side of tubarium, in most cases throughout length of the colony, in some species only mesially and distally; thecal apertures simple, with no marked asymmetry or lateral expansion; early thecae may be axially elongate or rastritiform; distal thecae triangulate. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone–*Telychian, Oktavites spiralis* Biozone): worldwide.——FIG. 301,*2a–e*. **T. planus* (BARRANDE); *2a,* ?holotype, Czech Republic (Barrande, 1850, pl. 4.*15*); *2b–d,* isolated specimens, Dalarna, Sweden, scale bars 1 mm (Hutt, Rickards, & Skevington, 1970, pl. 3,*51–52,54,* as *Monograptus proteus*); *2e,* large specimen, Wales, UK, scale bar, 5 mm (Loydell, 1993, fig. 21,*19*).

TAXA WITH CLADIA

The cladia-bearing Monograptinae have previously been included in the family Cyrtograptidae (see AVERIANOW, 1929; BOUČEK, 1933). YIN (1937) defined the subfamily Cyrtograptinae as branched, suggesting the presence of cladia as the sole character to separate the taxon from the rest of the Monograptidae. BULMAN (1955, 1970) separated the Cyrtograptidae, with its two subfamilies Cyrtograptinae and Linograptinae, from the Monograptidae. It is now clear that the Cyrtograptidae is

not as useful taxonomically as was originally intended and needs to be abandoned. Cladia appear independently in a number of monograptid lineages. The compilation of the cladia-bearing taxa here is for purely practical reasons and does not imply any phylogenetic relationship.

Cyrtograptus Carruthers in Murchison, 1867a, p. 540, *nom. correct.* Lapworth, 1873b original spelling as *Cyrtograpsus* changed in ICZN Opinion, 650, 1963; *non Cyrtograpsus* Dana, 1851, p. 288 (Decapoda) [**C. murchisoni;* OD] [=*Pleurograptoides* Averianow, 1931, p. 21 (type, *P. erectus,* OD), syn. by Loydell, herein; =*Averianowograptus* Obut, 1949, p. 29 (type, *Cyrtograptus magnificus* Averianow, 1931, p. 9, OD), syn. by Loydell, herein; =*Damosiograptus* Obut, 1950, p. 270 (type, *Cyrtograptus spiralis* Averianow, 1931, OD), syn. by Rickards, Hutt, & Berry, 1977, p. 76; =*Uralograptus* Koren', 1962, p. 724 (type, *U. insuetus* Koren', 1962, p. 724, OD), syn. by Bulman, 1970, p. 135; =*Kurganakograptus* Golikov, 1969, p. 515 (type, *K. primus*, OD), syn. by Loydell, herein]. Dorsally curved, low helically spiralled or dorsally curved then straight tubarium bearing at least one thecal cladium; thecae of main stipe hooked throughout, often laterally expanded and spinose, or hooked proximally then with hooks retreating distally, becoming hooded initially and then simple tubes with lateral lappets flanking aperture; thecae of thecal cladia hooked, hooded, simple adnate or isolated tubes in some cases with lateral lappets flanking aperture; secondary and tertiary cladia may develop from cladial thecae. [The genus has been considered polyphyletic, e.g., Rickards, Hutt, and Berry (1977) and needs re-investigation]. *Silurian, Llandovery* (*Telychian, Cyrtograptus lapworthi* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 302,*1a–c*. **C. murchisoni,* Builth District, Wales; *1a,* counterpart of holotype, GSM 10718; *1b,* topotype, proximal end, GSM 10716; *1c,* topotype, proximal end with sicula, GSM 10716, scale bars, 5 mm, 1 mm in *1b* (*a–c,* Zalasiewicz & Williams, 2008, Atlas, Folio 2.60).——Fig. 302,*1d. C. insuetus* (Koren'), holotype, scale bar, 5 mm (Rickards, Hutt, & Berry, 1977, fig. 39).——Fig. 302,*1e. C. magnificus* (Averianow), holotype, scale bar, 5 mm (Obut, 1950, fig. 6).

Barrandeograptus Bouček, 1933, p. 62, *ex Monograptus* (*Barrandeograptus*) Bouček, 1933, p. 62; Münch, 1938, p. 53][**Cyrtograptus pulchellus* Tullberg, 1883, p. 36; OD]. Slender tubarium, strongly dorsally and/or ventrally curved proximally, less strongly curved distally; up to at least three orders of thecal cladia may be developed; thecae slender and axially elongated; proximally appearing hooked; distal thecae triangular tubes typically with pronounced notch between dorsal wall and ventral wall of succeeding protheca; apertures of distal thecae may be furnished with lateral lappets. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone)–*Wenlock* (*Sheinwoodian, Monograptus riccartonensis* Biozone): worldwide.——Fig. 302,*2a–c, d*?. **B. pulchellus* (Tullberg); *2a,* holotype, SGU 5684, complete specimen showing sicula, Röstånga, Scania, Sweden (Tullberg, 1883, pl. 3.*12*); *2b–c,* MGUH (MMH) 13497, fragments showing distal thecal style (Bjerreskov, 1975, fig. 27C–D); *2d,* proximal theca tentatively referred to *B. pulchellus,* inverted SEM photo (Loydell & Nestor, 2006, fig. 13C). Scale bars, 1 mm; 0.2 mm in *2d.*

Diversograptus Manck, 1923, p. 283 [**D. ramosus;* SD Bulman, 1929, p. 176] [=*Dibranchiograptus* Hundt, 1949a, p. 19 (type, *D. bibrachiatus,* OD), syn. by Loydell, herein]. Narrow tubarium comprising main stipe and one sicular cladium with or (usually) without thecal cladia; stipes straight or gently curved; thecae hooked, with retroflexed apertures flanked by small lateral lappets. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone–*Cyrtograptus lapworthi* Biozone): Germany, UK (Wales, Scotland), Estonia, Latvia, Czech Republic, Turkey, Morocco.——Fig. 302,*3a–c*. **D. ramosus; 3a,* lectotype (selected by Bouček & Pribyl, 1953, p. 489), repository unknown, scale bar, 5 mm (reconstruction from Bulman, 1970, fig. 102,*3a*); *3b,* specimen showing bipolar growth, MGM 146-S, Jabalón River section, central Spain, scale bar, 1 mm (Loydell & others, 2009, fig. 4J); *3c*, stipe fragment, MGM 419-52, Aizpute-1 drill core, Latvia, scale bar, 1 mm (Loydell & Nestor, 2006, fig. 11C).——Fig. 302,*3d–e. D.*? *pergracilis* (Bouček, 1931, p. 302), fragments showing thecal style, Ventspils D-3 drill core, 826.7 m, Latvia (Loydell & Nestor, 2006, fig. 12A–B). Scale bars, 1 mm (*d*); 0.1 mm (*e*).

Paradiversograptus Sennikov, 1976, p. 225, *ex Monograptus* (*Paradiversograptus*) Sennikov, 1976, p. 225; Loydell, 1993, p. 143 [**Rastrites capillaris* Carruthers, 1867b, p. 368; OD]. Gently ventrally or dorso-ventrally curved tubarium; sicular cladium; metathecae simply hooked; no thecal overlap. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone–*Telychian, Spirograptus guerichi* Biozone): worldwide.——Fig. 302,*4a–b*. **P. capillaris* (Carruthers); *4a,* holotype, NHMUK Q86, stipe fragments, Birkhill Shales, Moffat, Dumfriesshire, Scotland, UK (Strachan, 1969, fig. 6a); *4b,* proximal end, BB 696, Tmaň, Czech Republic (Štorch, 1998a, fig. 8,*3*). Scale bars, 1 mm.——Fig. 302,*4c–d. P. runcinatus* (Lapworth, 1876e), Glenkiln Burn, Dumfriesshire, Scotland, UK; *4c*, proximal end in relief; *4d,* specimen with sicular cladium (Strachan, 1952, fig. 1B–C). Scale bars, 1 mm.

Sinodiversograptus Mu & Chen, 1962a, p. 147 [**S. multibrachiatus;* OD; =*Streptograptus lientanensis* Mu, 1948, syn. by Loydell, 1990a, p. 847]. Tubarium with sicular cladium and thecal cladia; sicula small; both main stipe and sicular

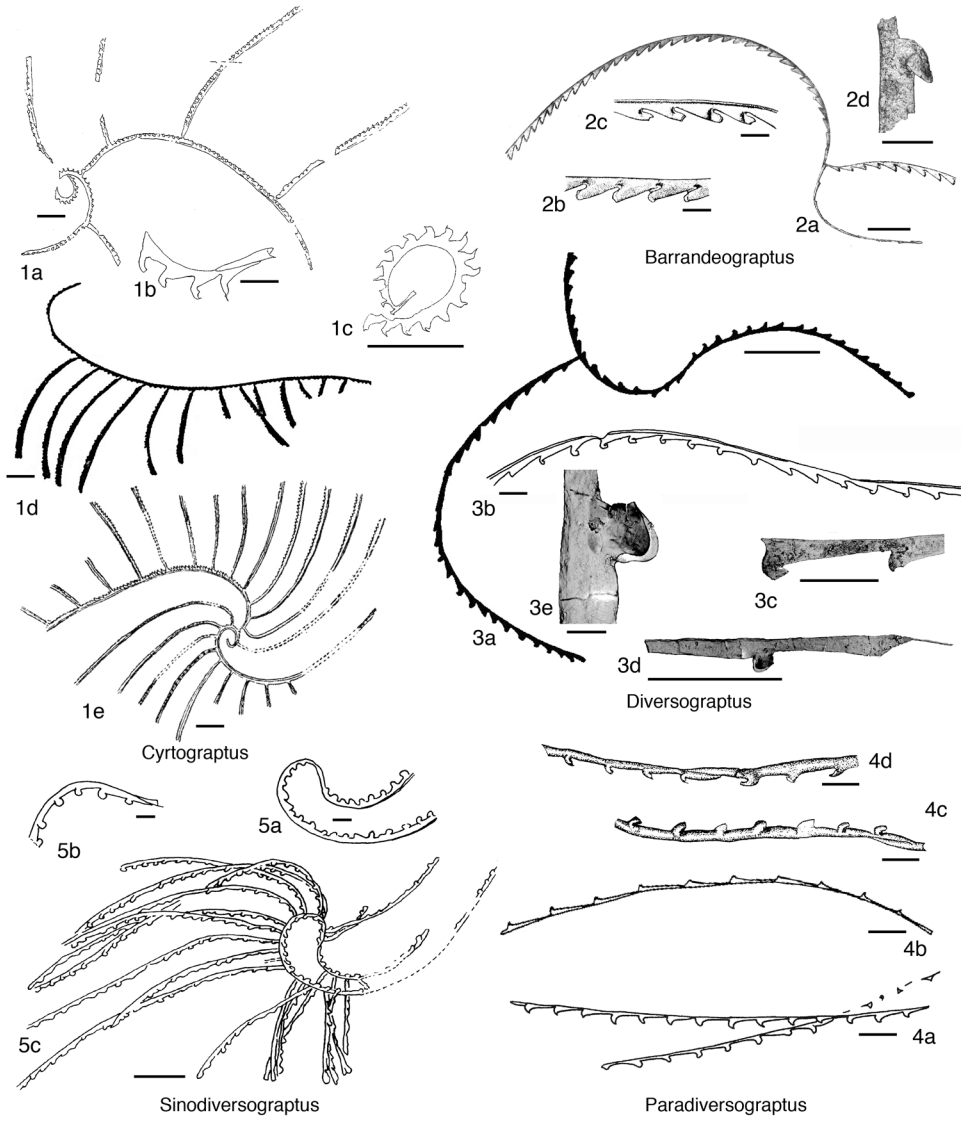


FIG. 302. Monograptinae with cladia (p. 447–448).

cladium ventrally curved, with curvature decreasing distally; tubarium developed through three stages: monograptid, diversograptid (with sicular cladium), and sinodiversograptid (with thecal cladia); metathecae hooked; gently ventrally curved cladia originated from almost all proximal and mesial thecae. *Silurian, Llandovery* (*Telychian*, *Spirograptus guerichi* Biozone): Australia, Canada, China.——FIG. 302,*5a–c*. *S. lientanensis* (MU); *5a,* holotype, specimen with sicular cladium, Lientan, Guandong Province, China, scale bar, 5 mm (LOYDELL, 1990a, fig. 2.*5*); *5b,* small proximal end, Lientan, Guandong Province, China, scale bar, 1 mm (Loydell, 1990a, fig. 2.*1*); *5c.* holotype of **S. multibrachiatus* (MU & CHEN), mature specimen with numerous cladia, NIGP 11580a, Qiaoting, Nanjiang District, Sichuan Province, China, scale bar, 5 mm (Loydell, 1990a, fig. 1).

Subfamily PRISTIOGRAPTINAE Gürich, 1908

[*nom. correct*. PŘIBYL, 1946, p. 277, *ex* Unterfamilie Pristiograptidi GÜRICH, 1908, p. 32] [=Heisograptinae TSEGELNJUK, 1976, p. 102; =Saetograptinae URBANEK, 1958, p. 50; =Uncinatograptinae TSEGELNJUK, 1976, p. 96; =Wolynograptinae TSEGELNJUK, 1976, p. 110; herein]

Tubarium straight or gently dorsally or ventrally curved proximally; thecal length increasing along first few thecae, later constant in most taxa, but may increase in others; sicula of medium length with low metasicular origin of th1; thecae usually straight, with straight or nearly straight, outward-inclined ventral wall; rarely, proximal thecae with isolation of metathecae; geniculum may be present; thecal aperture straight, outward-inclined to hooked, or provided with lateral lobes or spines; thecal style may be modified considerably in derived taxa. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone)–*Lower Devonian* (*Emsian, Uncinatograptus yukonensis* Biozone): worldwide.

The Pristiograptinae are difficult to define in the light of the numerous species included in the genus *Pristiograptus* and the independently derived lineages from this stem. Rickards, Hutt, and Berry (1977) provided an overview of the then identified taxa and their biostratigraphic ranges. Earliest taxa were considered close to *Atavograptus* by the authors. They differentiated the *Pristiograptus regularis* (Llandovery) and *Pristiograptus dubius* (upper Llandovery *Spirograptus turriculatus* Biozone and upward) lineages as having only short biostratigraphical overlap during the upper Llandovery.

Tsegelnjuk (1976) erected a number of subfamilies that are here referred to the Pristiograptinae. Tsegelnjuk (1998, p. 271) especially discussed the Uncinatograptinae and their stratigraphical value in the upper Silurian. Due to the incomplete knowledge of many tubarium characters, these subfamilies are not differentiated herein, awaiting a detailed phylogenetic analysis based upon well-preserved material. The Pristiograptinae are considered to derive from an ancestor in the genus *Atavograptus* during the Rhuddanian, early Silurian (see Rickards, Hutt, & Berry, 1977; Štorch, 1988). Evolutionary investigations of this clade, however, are largely restricted to the *Pristiograptus dubius* lineage. *Pristiograptus dubius* is a particularly long-ranging taxon from which a number of derived taxa originated, leading to iterative speciation and the evolution of new groups of monograptids (Urbanek & others, 2012; Whittingham, Radzevičius, & Spiridonov, 2020).

MORPHOLOGY

The morphology of early Pristiograptinae is fairly simple, with basically straight tubarium shapes and simple thecae having an angular, straight aperture, typically adorned only with a thickened rim (Fig. 303.1–303.2). Dorsal curvature is present in *Formosograptus*, *Slovinograptus,* and *Wolynograptus*, associated with thecal elongation and isolation of metathecae. Distally, the thecae possess increasing overlap in these taxa. Ventral curvature may be present and affects the sicula and very few proximal thecae. Regular ventral curvature is typical for *Pristiograptus paradoxus* Loydell & Walasek, 2019 and *Pristiograptus macrodon* Štorch, 1992, both of which exhibit only slight dorso-ventral curvature. Further examples of this are *Pseudomonoclimacis tetlitensis* Lenz, 1988b and *Monograptus banksi* Rickards & others, 1995.

The sicula is straight to somewhat curved ventrally and, in many species, bears a variable number of sicular annuli (Fig. 303.4). The number and position of the sicular annuli appears to have become stabilized during the uppermost Silurian during which most taxa possessed three or fewer annuli (Urbanek, 1997a).

The prosicula is small and slender and bears a small number of longitudinal rods (Fig. 303.6). The metasicula widens gradually, except in taxa with trumpetlike siculae such as *Colonograptus deubeli* (Jaeger, 1959) and a number of other taxa, including some Early Devonian forms (see Jaeger, 1988). Apertural modifications of the sicula are rare, but dorsal lappets are present in a number of taxa (Fig. 303.4), and slight lateral lappets or lobes appear to be present in *Uncinatograptus falcarius* (Fig. 303.6) and probably in other related taxa.

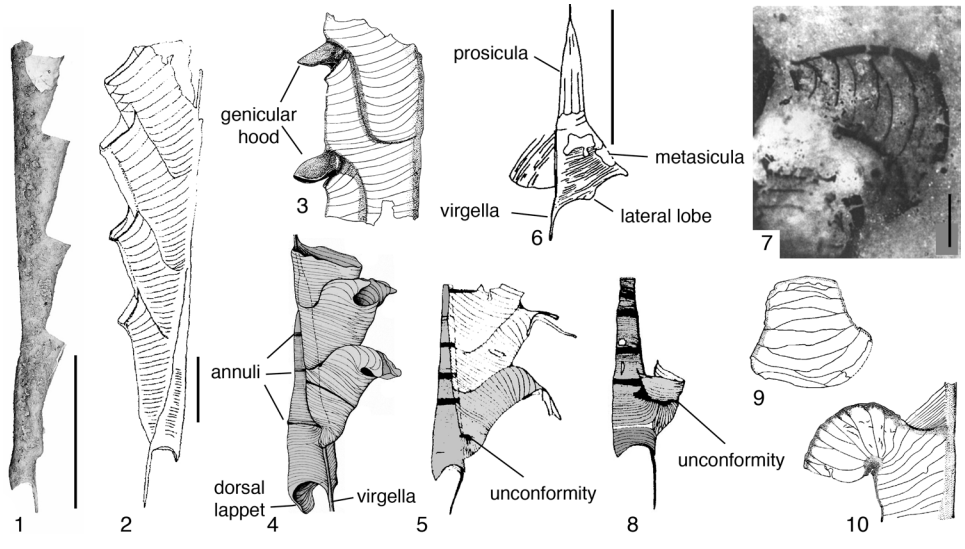


FIG. 303. Morphology of Pristiograptinae. *1, Pristiograptus* sp. cf. *Pristiograptus regularis* (TÖRNQUIST, 1899) (SEM photo inverted from Russel-Houston, 2001, pl. 12C); *2*, *Pristiograptus frequens* JAEKEL, 1889, proximal end in obverse view showing thecal shape (Maletz, 1999a, fig. 2R); *3*, *Heisograptus micropoma* (JAEKEL, 1889), development of microfusellar hoods (Urbanek, 1958, fig. 67); *4*, *Skalograptus lochkovensis* (PŘIBYL, 1940a), proximal end (adapted from Urbanek, 1997a, fig. 49); *5*, *Saetograptus chimaera* (BARRANDE, 1850), proximal end (adapted from Walker 1953, fig. 4G); *6–7*, *Uncinatograptus falcarius* (KOREN', 1969), showing sicular development and formation of dorsal hood (Koren', Kim & Walliser, 2007, fig. 4R, pl. 1.*9*); *8*, *Pristiograptus dubius* (SUESS, 1851), juvenile in reverse view, showing prothecal unconformity (Walker, 1953, fig. 2B); *9–10*, *Uncinatograptus uncinatus* (TULLBERG, 1883), development of thecal hood (Urbanek, 1958, fig. 21). Scale bars, 1 mm; reconstructions, no scale.

The origin of th1 may be through a sinus and lacuna development in all Pristiograptinae but has been verified from only a few taxa. It has been described in *Pristiograptus frequens* (EISENACK, 1942), *Heisograptus micropoma* (MALETZ, 1999a), *Wolynograptus acer* (URBANEK, 1997a), *Formosograptus* (URBANEK, 1997a), and *Skalograptus* (URBANEK, 1997a). LUKASIK and MELCHIN (1994) illustrated a possible primary porus in *Pristiograptus* sp. cf. *Pristiograptus regularis* from Arctic Canada. WALKER (1953) described in great detail the early growth of th1 in *Pristiograptus* and *Saetograptus* from glacial boulders found in northern Germany. The specimens show a distinct unconformity in the early growth on the reverse side but not on the obverse side in *Pristiograptus* (Fig. 303.8) and to a lesser extent in *Saetograptus* (Fig. 303.5).

Many taxa have a gradient in the development of thecal apertures, from low lateral lobes or spines to simple straight apertures distally. Geniculae are present in some taxa, rounded in *Heisograptus* but also angular as in *Uncinatograptus*. The details of the development of thecal hoods in the Pristiograptinae are known from a number of taxa (URBANEK, 1958, 1997a; KOREN', KIM, & WALLISER, 2007). *Heisograptus* has hoods formed from microfusellar material as secondary additions at the genicula (Fig. 303.3). In *Uncinatograptus*, apertural hoods are present at least on the proximal thecae but may be lacking in distal thecae. These hoods look similar to genicular developments but are true hoods formed as extensions of the dorsal thecal wall. In *Uncinatograptus falcarius* and related Early Devonian taxa, the initial part of the thecal hood is reduced in width, but distally a considerable lateral extension is visible forming a spatulate process (Fig. 303.7) and not a thecal hood as in *Uncinatograptus uncinatus* (Fig. 303.9–303.10). The thecal hood, thus, does not cover the thecal aperture.

Colonograptus PŘIBYL, 1943, p. 2, *ex Pristiograptus* (*Colonograptus*) PŘIBYL, 1943, p. 2 [**Graptolithus*

colonus Barrande, 1850; OD] [=*Ludensograptus* Tsegelnjuk, 1978, p. 88 (type, *Graptolithus Ludensis* Murchison, 1839, OD), syn. by Loydell, herein] [=*Conomograptus*, misspelling in Přibyl, 1983, p. 149]. Tubarium gently ventrally curved throughout or only proximally, being straight distally; sicula ventrally curved; biform thecae; proximal two or three thecae with ventrally projecting broad fusellar lappets; distal thecae simple tubes. *Silurian, Wenlock* (*Homerian, Colonograptus praedeubeli/deubeli* Biozone)–*Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——Fig. 304,*1a–b*. **C. colonus* (Barrande), lectotype, NMP L19771, Butovice-Nová-Ves, Czech Republic, *Neodiversograptus nilssoni* Biozone, proximal end and distal part of specimen preserved in relief, scale bars, 1 mm (new; drawing by Petr Štorch and Zuzana Strossova, 2021).

Dulebograptus Tsegelnjuk, 1976, p. 98 [**D. bresticus* Tsegelnjuk, 1976, p. 98; OD]. Tubarium straight or ventrally curved proximally and straight distally; proximal one to three thecae with complete fusellar hoods formed of dorsal walls of thecae; succeeding thecae have apertures with symmetrical lateral lobes which retreat distally; distal thecae becoming simple with straight margins, similar to those in *Pristiograptus*. *Silurian, Pridoli* (*Skalograptus lochkovensis* Biozone): Ukraine, Belarus, Poland.——Fig. 304,*2a–c*. *D. trimorphus* Tsegelnjuk, 1976; *2a,* specimen in ventral view; *2b,* sicula with first bud, showing presence of sicular annuli; *2c,* fragment showing style of thecal apertures (Urbanek, 1997a, pl. 14.A; text-fig. 42). Scale bars, 1 mm.

Formosograptus Bouček, Mihajlovic, & Vaselinovic, 1976, p. 84 [**Monograptus formosus* Bouček, 1931, p. 300; OD] [=*Tamplograptus* Tsegelnjuk, 1976, p. 114 (type, *Monograptus* (?*Spirograptus*) *convexus* Přibyl, 1940a, p. 73, OD), syn. by Přibyl, 1983, p. 150]. Dorsally curved tubarium; sicula straight or very gently ventrally curved, with dorsal process; proximal thecae non-overlapping, subtriangular with distinctly isolated apertural part; distal thecae overlap for approximately half their length with metathecae that are more adnate; thecal aperture overhung by laterally expanded lobe, with semitubular lateral processes terminating in auriculum. *Silurian, Ludlow* (*Ludfordian, Pseudomonoclimacis latilobus* Biozone)–*Pridoli* (*Neocolonograptus ultimus* Biozone): worldwide.——Fig. 304,*3a–c*. **F. formosus* (Bouček), Mielnik drill core, Poland; *3a,* proximal end showing shape of tubarium (adapted from Urbanek, 1997a, fig. 19B); *3b–c,* distal fragment showing increase of thecal overlap (Urbanek, 1997a, fig. 21). Scale bars, 1 mm.

Heisograptus Tsegelnjuk, 1976, p. 103 [**Pomatograptus micropoma* Jaekel, 1889, p. 682; OD]. Tubarium straight or nearly so; sicula ventrally curved, with dorsal tongue; thecae with sharp geniculae and supragenicular walls that are parallel to tubarium axis; apertural excavations semi-circular or semi-elliptical; aperture may be overhung by hood of microfusellar tissue. *Silurian, Ludlow* (*Gorstian*, *Neodiversograptus nilssoni* Biozone–*Lobograptus scanicus* Biozone): worldwide.——Fig. 304,*4a–d*. **H. micropoma* (Jaekel); *4a,* lectotype (selected by Jaeger, 1959, pl. 6,*7*), MB.G 470d, glacial boulder, Zölling bei Neusalz an der Oder, now Nowa Sól, Poland (Wilkinson, 2018b, Atlas, Folio 3.52); *4b–c,* juveniles in reverse (*4b*) and obverse (*4c*) views, showing presence of sicular annuli (Maletz, 1999a, fig. 2C,E); *4d,* specimen showing apertural hoods (Jaeger, 1959, fig. 20D). Scale bars, 1 mm.

Neomonograptus Mu & Ni, 1975, p. 18 [**N. himalayensis;* OD; =*Monograptus atopus* Bouček, 1966, syn. by Jaeger 1983, p. 250]. Tubarium straight throughout or with dorsal curvature proximally; first theca robust and strongly hooked, concealing aperture; subsequent thecae with dorsal hoods above semi-circular or semi-elliptical apertures, these becoming much less pronounced in mesial and distal thecae; thecae strongly geniculate throughout. *Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone)–*Emsian, Uncinatograptus yukonensis* Biozone): worldwide.——Fig. 304,*5a–b*. *N. atopus* (Bouček), holotype, proximal end (*5a*) and distal thecae (*5b*), scale bars, 1 mm (Bouček, 1966, fig. 1C); *5c,* holotype of **N. himalayensis,* scale bar, 1 mm (Chen & others, 2021, fig. 5F).

Pristiograptus Jaekel, 1889, p. 667 [**P. frequens;* OD]. Tubarium straight or gently dorsally or ventrally curved; thecal length increasing along first few thecae, later constant; sicula of medium length with low origin of th1; thecae straight, cylindrical, with straight or nearly straight ventral wall; thecal aperture without any supplementary structures except thickened apertural rim. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone)–*Pridoli* (*Skalograptus perneri* Biozone): worldwide.——Fig. 304,*8a–d*. **P. frequens; 8a,* neotype, MB.G 458.3.1, selected by Štorch, Manda, & Loydell, 2014, p. 1016 (Jaeger, 1991, fig. 26.*9*); *8b–d, P. dubius* (Suess, 1851), isolated specimens, glacial boulder, note the lack of sicular annuli (Maletz, 1999a, fig. 2Q-S). Scale bars, 1 mm.

Proteograptus Lenz, Senior, Kozłowska, & Melchin, 2012, p. 26 [**Monograptus opimus* Lenz & Melchin, 1991, p. 230; OD]. Gently ventrally curved tubarium that widens rapidly proximally; sicula straight with dorsal tongue; thecae appear hooked in profile view, but this hook is formed from paired lateral lappets that may fuse centrally, particularly in proximal part of tubarium to produce a pseudohood, the dorsal side of which has a consistently present laterally ovate opening onto the protheca. *Silurian, Wenlock* (*Sheinwoodian*, *Proteograptus opimus* Biozone–*Cyrtograptus perneri* Biozone): Arctic Canada.——Fig. 304,*6a–d*. **P. opimus* (Lenz & Melchin), GSC 134694, Cape Phillips, Arctic Canada; *6a–b,* reverse (*6a*) and ventral (*6b*) views of colony showing thecal style, (Lenz & others, 2012, pl. 12,*1–2*); *6c,* change in thecal style over first four thecae (Lenz & others, 2012, pl. 12,*3*); *6d,* development of distal thecae (Lenz & others, 2012, pl. 12.*6*). Scale bars, 1 mm.

Pseudomonoclimacis Mikhailova, 1975, p. 156 [**P. elegans*; OD]. Tubarium gently ventrally curved proximally and mesially, straight distally; sicula ventrally curved, with dorsal process; thecae moderately to strongly geniculate, generating a thecal excavation. *Silurian, Ludlow* (*Gorstian, Lobograptus progenitor* Biozone)–*Pridoli* (*Skalograptus perneri* Biozone): worldwide.——Fig. 304,*7a*. **P. elegans,* CNIGR 20/10290, holotype, scale bar, 1 mm (Mikhailova, 1975, pl. 38,*3*).——Fig. 304,*7b*. *P. dalejensis* (Bouček, 1936), specimen showing curvature of sicula, Všeradice section, Prague syncline, Czech Republic, scale bar, 1 mm (Štorch, Manda, & Loydell, 2014, fig. 6F).——Fig. 304,*7c–e*. *P. antiqua* Štorch, Manda, & Loydell, 2014; *7c*, slender specimen, Všeradice section, Prague syncline, Czech Republic (Štorch, Manda, & Loydell, 2014, fig. 6Q); *7d–e,* juvenile specimens in reverse (*7d*) and obverse (*7e*) view, glacial boulder, Bramsche, northern Germany (Maletz, 1999a, fig. 2M–N; identified as *Heisograptus* sp.). Scale bars, 1 mm.

Saetograptus Přibyl, 1943, p. 11 [**Graptolithus chimaera*, Barrande, 1850, p. 52; OD]. Straight or dorsally curved tubarium; sicula with variably developed dorsal apertural tongue; tubular thecae terminated by paired apertural spines developed on all or only proximal thecae; aperture of first theca has broad, triangular, spine-like lateral lappets; other thecal apertures have ventral notch and laterally to dorso-laterally situated spines separated by trough from ventral wall of next theca. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——Fig. 304,*10a–b*. **S. chimaera* (Barrande); *10a,* holotype, NMP L19973 (new; drawing by P. Štorch, 2021); *10b,* chemically isolated specimen (Přibyl, 1943, fig. 1, redrawn from original illustration in Münch, 1938, pl. 5,*1a*). Scale bars, 1 mm.

Skalograptus Tsegelnjuk, 1976, p. 100 [**Skalograptus vetus;* OD; =*Monograptus ultimus* Perner, 1899; Kříž & others, 1986, p. 322; Koren' & Sujarkova 1997, p. 87] [=*Istrograptus* Tsegelnjuk, 1988, p. 85 (type species not selected; illustrated as *Is*(*tr*)*ograptus transgrediens* [Perner, 1899] and *Istrograptus ultimus* [Perner, 1899]); =*Neocolonograptus* Urbanek, 1997a, p. 165 (type, *Monograptus lochkovensis* Přibyl, 1940a, OD, see Urbanek, 1997a, p. 128, table 1), syn. by Loydell, herein].Tubarium gently ventrally curved, gently dorso-ventrally curved or straight; sicula moderately to strongly ventrally curved; thecae with bilobate apertural elaborations, ranging from gentle undulations to strong lappets oriented antero-laterally; apertures of distal thecae may lack these elaborations; ventral walls of thecae sigmoidal or straight. *Silurian, Pridoli* (*Skalograptus parultimus* Biozone–*Skalograptus transgrediens* Biozone): worldwide.——Fig. 304,*9a–b*. *S. ultimus* (Perner); *9a*, lectotype (selected by Přibyl, 1948a, p. 77) Praha-Dvorce (formerly Dworetz), Czech Republic (Perner, 1899, fig. 14a); *9b,* chemically isolated specimen, Kosov Quarry, Czech Republic, *Skalograptus ultimus* Biozone, ~4 m above base of Pridoli (adapted from Kříž & others, 1986, fig. 36a). Scale bars, 1 mm.

Slovinograptus Urbanek, 1997a, p. 129 [**Monograptus balticus* Teller, 1966, p. 556; OD; Urbanek, 1997a, p. 128; =*Monograptus kallimorphus* Kraatz, 1958, p. 48, syn. by Jaeger 1978b, p. 514]. Tubarium slender and dorsally curved proximally, straight distally; sicula ventrally curved; thecal apertures provided with globose hoods, adnate to the ventral wall; substantial thecal overlap, especially distally. *Silurian, Ludlow* (*Ludfordian, Pseudomonoclimacis latilobus/Slovinograptus balticus* Biozone)–*Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone): worldwide.——Fig. 304,*11a–d*. *S. kallimorphus* (Kraatz); *11a,* holotype of **Monograptus balticus* (Koren' & Suyarkova, 1997, fig. 9G); *11,b,* CGM 26/12879, Peshkaut Valley, southern Tien Shan (Koren' & Suyarkova, 1997, fig. 9A); *11c,* proximal end, KR 58d, Mollenberg, Harz Mountains, Germany (new); *11d,* distal fragment, KR 58A, Mollenberg, Harz Mountains (new). Scale bars, 1 mm.

Uncinatograptus Tsegelnjuk, 1976, p. 96 [**Monograptus uncinatus* Tullberg, 1883, p. 30; OD] [=*Tirassograptus* Tsegelnjuk, 1976, p. 119 (type, *Monograptus* (*Pomatograptus*) *uncinatus* var. *uniformis* Přibyl, 1940a, p. 71; OD), syn. by Loydell, herein; =*Metamonograptus* Wang, 1977, p. 198 (type *Monograptus* (*Metamonograptus*) *qinzhouensis* Wang, 1977, p. 198; OD), syn. by Loydell, herein]. Tubarium straight or dorsally curved proximally and mesially, becoming straight distally; sicula straight or ventrally curved, aperture flaring with or without distal curving lappet; thecae with dorsal hoods, often best developed in proximal thecae but present throughout the tubarium; ventrolateral margin of aperture may be lobate and also spinose; thecal overlap increases distally. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone)–*Lower Devonian* (*Emsian, Uncinatograptus yukonensis* Biozone): worldwide.——Fig. 304,*12a–c*. **U. uncinatus* (Tullberg); *12a,* lectotype, selected by Přibyl, 1948a, p. 35 (Tullberg, 1883, pl. 1,*25;* ?LO collection, specimen not identified); *12b–c,* proximal end in lateral (*12b*) and ventral (*12c*) views (Urbanek, 1958, pl. 1,*3a–3b*). Scale bars, 1 mm.

Wandograptus Rickards & Jell, 2002, p. 118 [**W. wandovalensis;* OD]. *Pristograptus*-like tubarium but with more frequent and irregular curvature and development of thecal cladia. [The taxonomic position of the genus is uncertain. Rickards and Jell (2002) described it as related to *Pristiograptus,* but bearing cladia. The proximal end and thecae are very similar to those of early *Pristiograptus* and *Atavograptus*.] *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone–*Streptograptus crispus* Biozone): Australia (Queensland).——Fig. 304,*14a–b*. **W. wandovalensis,* fragments from the holotype slab, UQ 35968, Queensland, Australia;

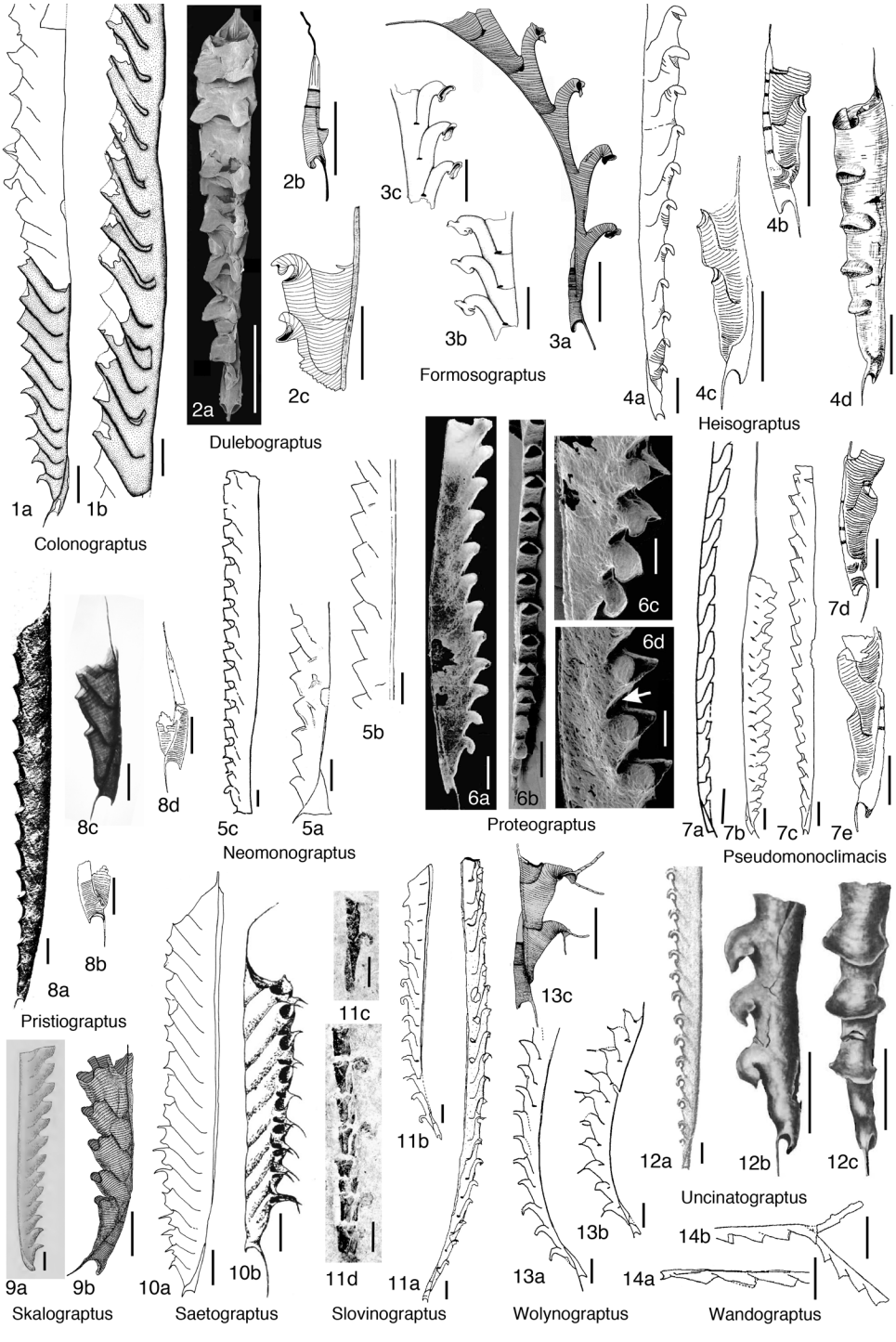


FIG. 304. Pristiograptinae (p. 450–454).

(Rickards & Jell, 2002, fig. 4I–J, L–M). Scale bars, 1 mm.

Wolynograptus Tsegelnjuk, 1976, p. 110 [**W. valleculosus;* OD) [=*Acanthograptus* Tsegelnjuk, 1976, p. 113 (type *A. spineus;* OD), syn. by Přibyl, 1983, p. 150, homonym of *Acanthograptus* Spencer, 1878 [Dendroidea]); =*Bugograptus* Tsegelnjuk, 1998, p. 272 (type, *A. spineus* Tsegelnjuk, 1976, OD), syn. by Loydell, herein]. Tubarium dorsally curved proximally and mesially, becoming straight distally; sicula straight or ventrally curved, bearing two annuli; thecae with extensive dorsal hoods; anterolateral margin of aperture may be lobate and also spinose; thecal overlap increases distally. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Wolynograptus spineus* Biozone): worldwide.——Fig. 304,*13a*. *W. aculeatus* Tsegelnjuk, 1976, proximal end, scale bar, 1 mm (Koren' & Suyarkova, 1997, fig. 8A).——Fig. 304,*13b–c*. *W. spineus* Tsegelnjuk, 1976; *13b*, proximal end (Koren' & Suyarkova, 1997, fig. 14H); *13c*, proximal end (Urbanek, 1995, fig. 1D). Scale bars, 1 mm.

Subfamily LINOGRAPTINAE Obut, 1957

[Subfamily Linograptinae Obut, 1957, p. 18; *nom. transl.* Teller, 1962, p. 153, *ex* Linograptidae Obut, 1957, p. 18] [=Cucullograptinae Urbanek, 1958, p. 62; herein; =Neocucullograptinae Urbanek, 1970, p. 265; herein; =Neolobograptinae Tsegelnjuk, 1976, p. 120; herein]

Variably straight to usually ventrally curved, slender to distally widening monograptids; thecal overlap from very low to extremely high; thecal apertures may be elaborated with paired lateral lobes, commonly with asymmetrical development; sicula slender to aperturally widening (trumpet-shaped), with variable number of annuli. *Silurian, Wenlock* (*Homerian, Colonograptus ludensis* Biozone)–*Lower Devonian* (*Lochkovian, Uncinatograptus hercynicus* Biozone): worldwide.

A number of small subfamilies have been erected for late Wenlock (Homerian) and Ludlow (Gorstian to Ludfordian) monograptids. Small-scale modifications of their thecae have been used to describe the evolutionary transformation of the species. Urbanek (1970, pl. 8) suggested a close phylogenetic relationship between the various groups. Urbanek (1958) did not provide a diagnosis of the Cucullograptinae and his description of the various species is based largely on small fragments. Urbanek (1966) discussed and described a number of additional species of the clade and suggested common roots with the Linograptinae and the '*Pristiograptus' bohemicus* group (Urbanek, 1966, pl. 8). Whittingham, Radzevičius, and Spiridonov (2020) supported these relationships when they discussed iterative evolution during the late Silurian graptolite faunas and indicated a possible sister-group relationship between the *Colonograptus* and *Lobograptus* clades, based on stratocladistics.

MORPHOLOGY

Most of the taxa included in the Linograptinae, as used herein, are characterized by a ventrally curved to straight tubarium with thecae having low inclination and often distally increasing thecal overlap. The sicula is small in most taxa and bears a variable number of sicular annuli. An elongated sicula is present in the genus *Urbanekia*. Cladial branching is present in a few taxa forming very large colonies.

The thecal apertures vary from simple (Fig. 305.3) to complex, often including a considerable asymmetry of the two lateral lobes (Fig. 305.12–305.17), but lacking torsion of the metathecae. The complex thecal apertures are formed either from normal fusellar development (Fig. 305.12–305.13) or from microfusellar additions (Fig. 305.16–305.17). The simple thecal apertures have a straight aperture, inclined to the ventral side of the tubarium. Lateral lobes are barely recognizable in some taxa (Fig. 305.6–305.8) but may be quite extensive in others. They may have strong lateral extensions and may be curved or coiled.

Bohemograptus cornutus (Urbanek, 1970) has an extreme development of lateral additions in the form of paired spatulate extensions formed from fusellar material (Fig. 305.2), and membranes with an internal branching system of rods have been documented in *Bohemograptus papilio* Kozłowska & Urbanek, 2013 (Fig. 305.1). A characteristic virgellarium ending with four finger-like extensions occurs in *Linograptus* and probably in *Abiesgraptus* (Urbanek, 1997b).

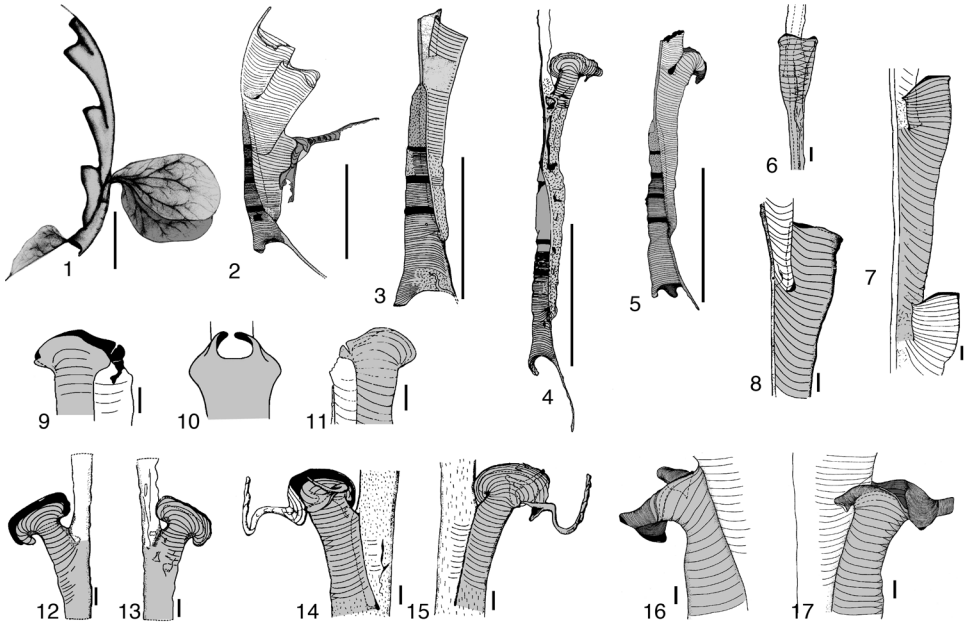


FIG. 305. Thecal morphology of the Linograptinae. *1, Bohemograptus papilio* KOZŁOWSKA & URBANEK, 2013, reconstruction showing patagia (Kozłowska & Urbanek, 2013, fig. 5); *2, Bohemograptus cornutus* URBANEK, 1970 with partly preserved lateral apertural processes (Urbanek, 1970, pl. 25); *3, 8, Lobograptus progenitor* URBANEK, 1966, proximal end (*3*) and thecal style (*8*) (Urbanek, 1966, pl. 14A); *4, 14–15, Lobograptus cirrifer* URBANEK, 1966, proximal end (*4*) and thecal style (*14–15*) (Urbanek, 1966, pl. 34); *5, Neocucullograptus kozlowskii* URBANEK, 1970, proximal end (*5*) and thecal style (*16–17*) (Urbanek, 1970, pl. 38); *6–7, Linograptus posthumus* (RICHTER, 1875), thecal style in ventral (*6*) and lateral (*7*) views (Urbanek, 1963, pl. 9); *9–11, Lobograptus simplex* URBANEK, 1960, thecal style (Urbanek, 1966, pl. 16); *12–13, Lobograptus scanicus* (TULLBERG, 1883), thecal style (Urbanek, 1966, pl. 27). All illustrations are modified from the original illustrations. Scale bars, 1 mm in *1–5;* all others 0.1 mm.

Taxa with cladial branching (URBANEK, 1997b) may possess a sicular cladium to form a bipolar tubarium as in *Neodiversograptus* or thecal cladia as in *Lenzograptus*. More complex tubaria are present in *Linograptus,* in which the sicula may form numerous sicular cladia but no thecal cladia. *Abiesgraptus* bears three sicular cladia and additional thecal cladia along the initial stipe and the first sicular cladium (JAEGER, 1959; URBANEK, 1997b).

Bohemograptus PŘIBYL, 1967b, p. 134 [**Graptolithus bohemicus* BARRANDE, 1850, p. 40; OD] [=*Fterograptus* TSEGELNJUK, 1976, p. 131 (type, *F. torsivus,* OD), syn. by LOYDELL, herein]. Tubarium ventrally curved; thecae tubular, with straight or gently elevated lateral apertural margins, either devoid of or provided with microfusellar additions forming broadly lobate, annular or tape-like apertural structures. *Silurian, Wenlock* (*Homerian, Colonograptus ludensis* Biozone)–*Ludlow* (*Ludfordian, Neocucullograptus kozlowskii* Biozone): worldwide.——FIG. 306,*1a–c*. **B. bohemicus* (BARRANDE, 1850); *1a–b,* NMP L17762, lectotype (Přibyl, 1948a, p. 68) and associated specimen with sicula (Štorch, 2000d, Atlas, Folio 1.9); *1c,* proximal end with sicular annuli, Mielnik drill core, 957.90 m, Poland (Urbanek, 1970, fig. 10B). Scale bars, 1 mm.

Crinitograptus RICKARDS, 1995b, p. 1107 [**Monograptus crinitus* WOOD, 1900, p. 480; OD]. Slender tubarium, straight or irregularly flexed; short sicula with annuli; simple tubular thecae, parallel to or inclined to tubarium axis at less than 10°; thecae increasing in lateral width toward aperture; only slight thecal overlap; thecal aperture simple, with overhanging hood formed by extension of dorsal wall of theca. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone)–*Pridoli* (*Neocolonograptus parultimus* Biozone): UK, Germany (erratics), Bulgaria, Arctic Canada, Australia, Russia.——FIG. 306,*2a–c*. **C. crinitus* (WOOD), Long Mountain, Shropshire, UK; *2a,* BU 1615, part of holotype (Rickards, 1995b, fig. 4.*1*); *2b,* BU 1618, syntype, proximal end showing

sicular annuli (Rickards, 1995b, fig. 1). *2c*, BU 1616, bipolar fragment (Rickards, 1995b, fig. 4,*3*). Scale bars, 1 mm.

Cucullograptus Urbanek, 1954, p. 291 [**C. pazdroi;* OD]. Narrow, straight, or gently ventrally curved tubarium; small sicula; first theca originated via a primary porus; thecae long, with elongate protheca and short metatheca; thecal aperture slit-like, with complex auriculate lateral apertural lobes, with increasing asymmetry distally; the left apertural lobe overlaps right lobe, restricting thecal aperture. *Silurian*, *Ludlow* (*Gorstian, Lobograptus parascanicus* Biozone–*Ludfordian, Cucullograptus rostratus/lower Bohemograptus tenuis* Biozone): Poland, Czech Republic, Germany, China (Yunnan).——Fig. 306,*3a–c*. **C. pazdroi;* three different views of holotype, glacial boulder, Gdansk-Wrzeszcz, Poland (Urbanek, 1954, fig. 2). Scale bars, 1 mm.

Egregiograptus Rickards & Wright, 1997b, p. 222 [**'Monograptus' egregius* Urbanek, 1970, p. 367; OD]. Tubarium strongly ventrally curved, almost circular; short sicula (usually less than 1.5 mm long); thecae adnate, tubular; proximal thecae extremely elongated and inclined at a very low angle to the tubarium axis; distal thecae with considerable overlap; thecal apertures straight or with paired lateral lobes. *Silurian, Ludlow* (*Gorstian, Lobograptus scanicus* Biozone–*Ludfordian, Saetograptus chimaera* Biozone–*Neocucullograptus kozlowskii* Biozone): Poland, Czech Republic, Kyrgyzstan, Canada (Yukon), Australia.——Fig. 306,*4a–c*. **E. egregius; 4a,* holotype (Urbanek, 1970, pl. 43D1); *4b,* proximal end showing sicular annuli (Urbanek, 1970, p. 42A); *4c,* proximal end, th1 reconstructed (Urbanek, 1970, pl. 42F). Scale bars, 1 mm.——Fig. 306,*4d. E. dimitrii* (Koren' & Suyarkova, 2004), CNIGR 13107/63, holotype, Tien Shan, Kyrgyzstan, scale bar, 1 mm.

Enigmagraptus Rickards & Wright, 2004, p. 192 [**Neocucullograptus? yassensis* Rickards & Wright, 1999a, p. 200; OD]. Very slender tubarium (up to 0.25 mm wide), straight or irregularly flexed; small sicula with virgella and dorsal apertural process; axially elongate prothecae usually developed from threadlike origin; metatheca up to half tubarium width comprising hood derived by retroversion of the dorsal metathecal wall, and variously enrolled ventrally to enclose simple ventral thecal margin. *Silurian* (*Pridoli, Neocolonograptus parultimus* Biozone): Australia (New South Wales).——Fig. 306,*5a–b*. **E. yassensis; 5a,* AMF 92343, holotype, proximal end; *5b,* AMF 92346, stipe fragment (Rickards & Wright, 2004, fig. 4B–C). Scale bars, 1 mm.

Korenea Rickards, Packham, Wright, & Williamson, 1995, p. 54 [**K. sherwini;* OD]. Tubarium ventrally curved, hook-shaped; sicula small; uniform overlapping tubular thecae with strongly developed paired symmetrical lateral apertural lappets resembling retroverted hooks in profile. *Silurian* (*Ludlow*): Australia.——Fig. 306,*6a–b*. **K. sherwini,* New South Wales, Australia; *6a*, holotype, AMF 89624 (Rickards & others, 1995, fig. 33B); *6b*, thecal detail (Rickards & others, 1995, fig. 38E). Scale bars, 1 mm.

Lobograptus Urbanek, 1958, p. 12 [**Monograptus scanicus* Tullberg, 1883, p. 26; OD] [=*Falcatograptus* Hundt, 1965, p. 48 (type, *F. rarus,* M), syn. by Loydell, herein]. Narrow, straight, dorsoventrally or gently ventrally curved tubarium, widening distally; thecae long, with elongate protheca and increasing distal overlap; thecal aperture with asymmetrical or symmetrical lateral lobes that may curve over central part of aperture. *Silurian, Wenlock* (*Homerian, Colonograptus praedeubeli* Biozone)–*Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——Fig. 306,*7a–b*. **L. scanicus* (Tullberg), *7a,* syntype, specimen not identified (Tullberg, 1883, pl. 2.*4*2); *7b,* proximal end (Urbanek, 1966, fig. 11). Scale bars, 1 mm.

Neocucullograptus Urbanek, 1970, p. 329 [**N. kozlowskii;* OD]. Tubarium strongly ventrally curved proximally, less strongly curved or nearly straight distally; sicula with dorsal apertural process and late astogenetic paired symmetrical lobes of microfusellar tissue situated on reverse and obverse apertural margins; first theca originated via a primary porus; complex metathecae, consisting of smaller right and larger left lobe, sometimes provided with gular, rostral, and lateral processes. *Silurian, Ludlow* (*Ludfordian, Neocucullograptus inexpectatus* Biozone–*Neocucullograptus kozlowskii* Biozone): Poland, Czech Republic, Kyrgyzstan, Kazakhstan.——Fig. 306,*8a–d*. **N. kozlowskii,* Mielnik drill core, Poland; *8a–b,* holotype in lateral (*8a*) and ventral (*8b*) views (Urbanek, 1970, fig. 20A); *8c*, distal theca (Urbanek, 1970, pl. 38A); *8d,* reconstruction (Urbanek, 1970, pl. 7C). Scale bars, 1 mm.

Neolobograptus Urbanek, 1970, p. 321 [**N. auriculatus;* OD]. Ventrally curved tubarium; straight sicula with prominent dorsal process; thecae slender and elongate; thecal apertures with lateral elevations and dorso-lateral incisions. *Silurian, Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone–*Neocucullograptus inexpectatus* Biozone): Poland, Kyrgyzstan.——Fig. 306,*9a–b*. **N. auriculatus,* Mielnik drill core, Poland; *9a,* holotype, sicula with incomplete first theca (Urbanek, 1970, pl. 29B); *9b,* reconstruction (Rickards & Wright, 1999b, fig. 3F, based on Urbanek, 1970, pl. 7A). Scale bars, 1 mm.

Polonograptus Tsegelnjuk, 1976, p. 124 [**P. podoliensis* Přibyl, 1983, p. 158; SD ICZN, Opinion 2023, 2003; Riva, Koren', & Rickards (2001) applied to the ICZN to change the type species from *Monograptus butovicensis* Bouček, 1936 to *Polonograptus podoliensis*, approved as Opinion 2023 (ICZN, 2003)]. Tubarium ventrally curved with proximally accentuated curvature; sicula small and straight; thecae subsequent to the short first theca exhibit considerable elongation and overlap; all thecae simple tubes; apertures have lateral elevations.

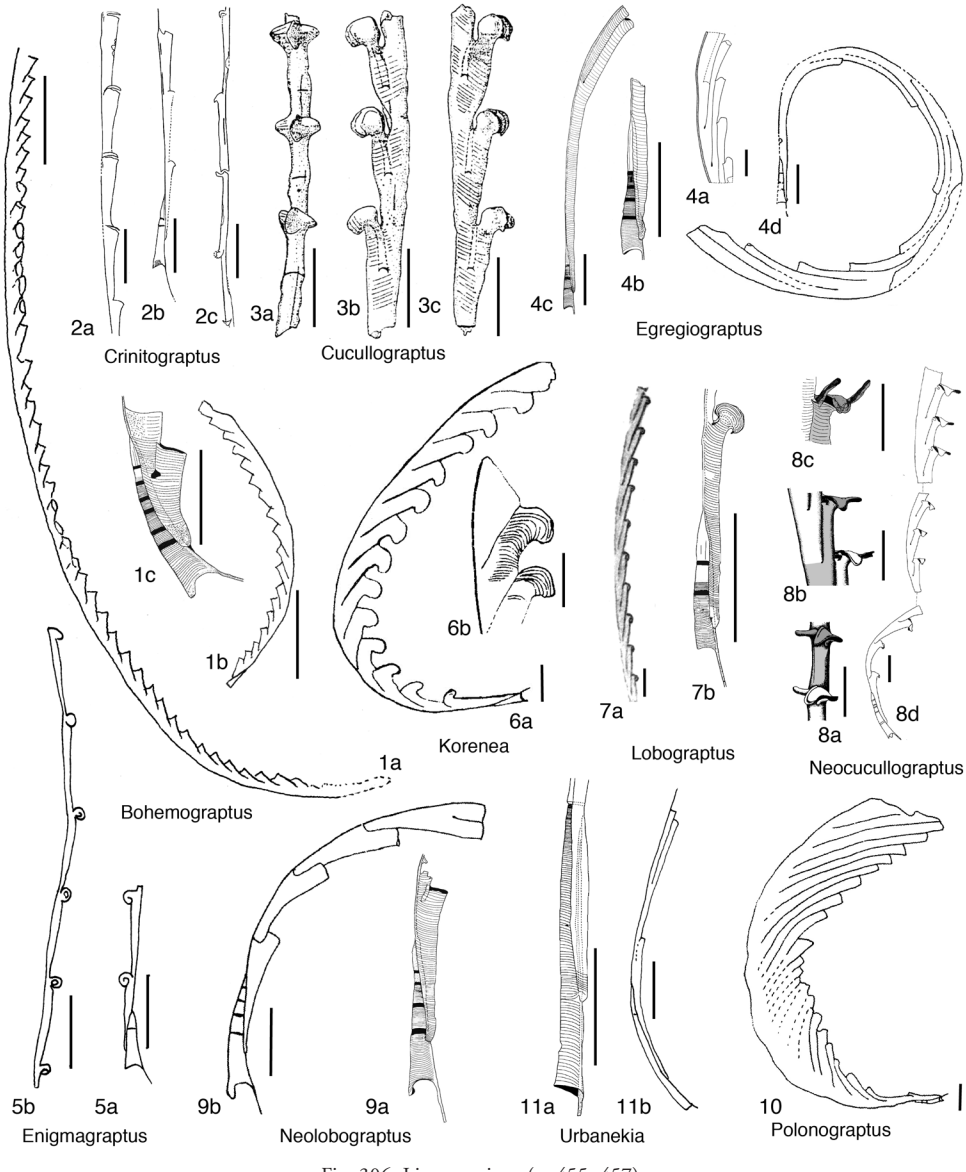


Fig. 306. Linograptinae (p. 455–457).

Silurian, Ludlow (*Ludfordian*, *Neocucullograptus inexpectatus* Biozone–*Neocucullograptus kozlowskii* Biozone): Czech Republic, Austria, Australia, Kyrgyzstan.——Fig. 306,*10*. **P. podoliensis,* CNIGR 13107/104, southern Tien Shan, Kyrgyzstan, scale bar, 1 mm (Koren' & Sujarkova, 2004, fig. 28B).

Urbanekia Rickards & Wright, 1999b, p. 319 [*'*Monograptus*' *proegregius* Urbanek, 1970, p. 364; OD]. Tubarium known from fragments only but appears narrow (less than 0.3 mm) and ventrally curved; sicula elongated (more than 3 mm long) and ventrally curved; sicular aperture lacks dorsal process; thecae very long (at least 7 mm), narrow and tubular, with ventral walls subparallel to the tubarium axis; thecal apertures simple, perpendicular to thecal axis and with slight lateral elevations. *Silurian, Ludlow* (*Gorstian, Lobograptus parascanicus* Biozone): Poland.——Fig. 306,*11a–b*. **U. proegregius* (Urbanek); *11a,* paratype, sicula with part of first theca (Urbanek, 1970, pl. 41.*C*); *11b,* reconstruction (Rickards & Wright, 1999b, fig. 2L). Scale bars, 1 mm.

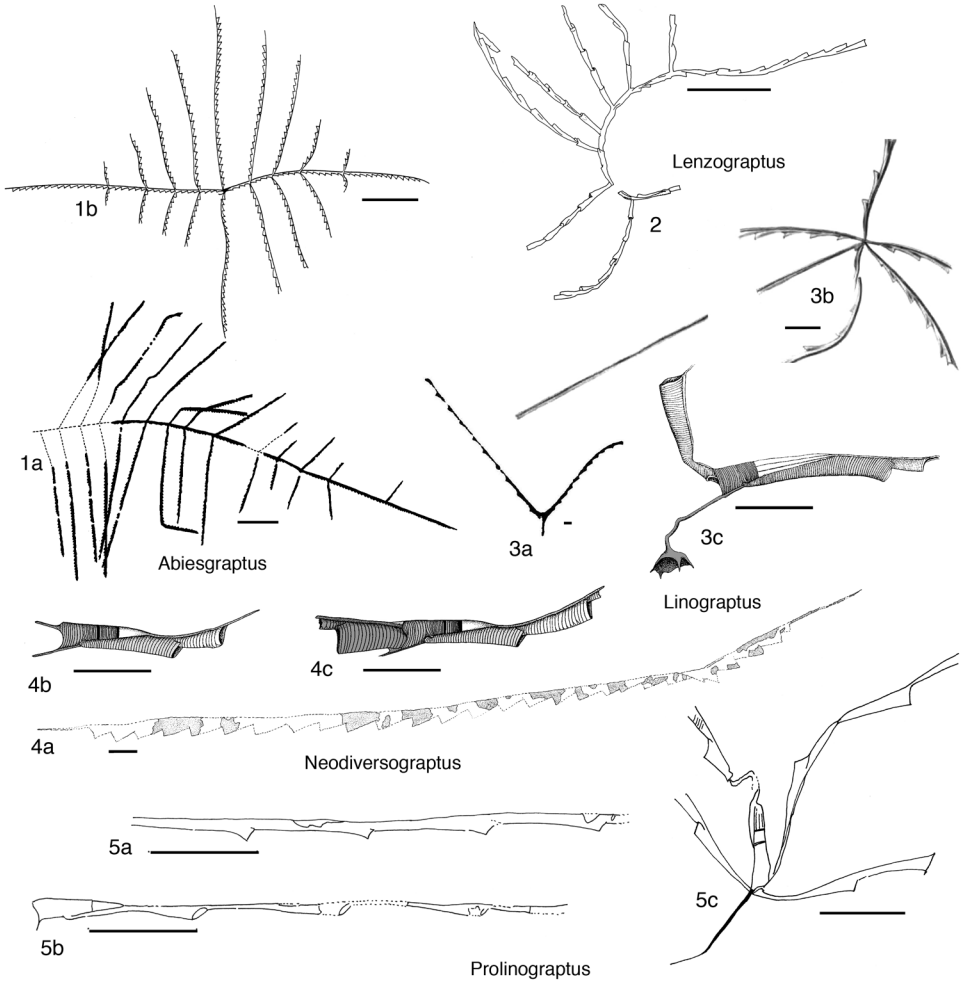


FIG. 307. Linograptinae (cladia-bearing) (p. 458–459).

LINOGRAPTINAE WITH CLADIA

URBANEK (1997b) discussed in some detail the evolution of the cladia-bearing linograptines from the genus *Lobograptus* (probably *Lobograptus sherrardae*) through the bipolar *Neodiversograptus* and, thus, indicated the independent origin of cladia-bearing taxa from older cladia-bearing forms during the early Silurian. URBANEK (1963, 1997b) included only three genera, *Neodiversograptus, Linograptus,* and *Abiesgraptus* in his subfamily Linograptinae and suggested that they represent an instance of a single line of descent forming sequential chronospecies. The relationship to the genus *Lenzograptus* remains uncertain. Thus, the cladia-bearing taxa, separated here from the other taxa for practical reasons, might not form a phylogenetically definable clade.

Abiesgraptus HUNDT, 1935a, p. 3 [**A. multiramosus;* SD BULMAN, 1938, p. 84] [=*Didymograptoides* HUNDT, 1953a, p. 40 (type, *D. liebei,* M), syn. by LOYDELL, herein; =*Gangliograptus* HUNDT, 1939, p. 119 (type, *G. hoppeianus,* SD MÜLLER, 1969, p. 919), syn. by LOYDELL, herein]. Tubarium complex, comprising the main stipe and three sicular cladia; the main stipe and central sicular cladium bear paired thecal cladia; thecae simple, without apertural modifications. *Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone–*Pragian, Uncinatograptus fanicus* Biozone): worldwide.——FIG.

307,*1a–b. *A. multiramosus* Hundt, *1a,* lectotype, selected by Müller, 1965, p. 5, BAF 73/H4151, Ramstal bei Creunitz, Thuringia, Germany (Müller, 1965, fig. 1); *1b,* reconstruction; scale bars, 10 mm (Jaeger, 1959, fig. 25).

Lenzograptus Loydell, 2021, p. 205 [**Lenzia lenzi* Rickards & Wright, 1999b, p. 319; OD] [*pro Lenzia* Rickards & Wright, 1999b; homonym of *Lenzia* Perry, Boucot, & Gabrielse 1981 (Devonian brachiopod)]. Cladia-bearing linograptid, with tubarium largely ventrally curved but twisting around its axis; thecae simple or with slight lateral apertural lobes, generating cladia every one or two thecae, directed to the dorsal side of main stipe. *Silurian* (*Ludlow*): Canada (Yukon).——Fig. 307,*2. *L. lenzi,* holotype, UWO 2664, Richardson Mountains, Yukon, Canada, scale bar, 5 mm (Lenz, 1984, fig. 1a).

Linograptus Frech, 1897, p. 662 [**Dicranograptus posthumus* Richter, 1875, p. 267; OD; =*Linograptus nilssoni* Frech, 1897, p. 662; syn. by Jaeger, 1959, p. 143] [=*Thuringiograptus* Hundt, 1939, p. 121 (type, *T. voigtii,* M), syn. by Loydell, herein]. Tubarium with narrow stipes comprising main stipe and, late in astogeny, several sicular cladia; main stipe and sicular cladia may be straight or more usually gently ventrally curved; virgella with virgellarium, a terminal four-pronged membranous structure; sicula with a long dorsal apertural spine that forms secondary nema for first sicular cladium; further cladia develop from reverse and obverse margins of the sicula; first theca of main stipe originated close to boundary of prosicula and metasicula; thecae simple tubes, apertures with lateral elevations which are more pronounced in distal thecae and may be somewhat introverted. *Silurian, Ludlow* (*Ludfordian, Bohemograptus tenuis* Biozone)–*Lower Devonian* (*Lochkovian, Uncinatograptus hercynicus* Biozone): worldwide.——Fig. 307,*3a–c. *L. posthumus; 3a,* lectotype, BGR 10370 (Richter, 1875, pl. 8.*3*); *3b,* specimen from Herzogswalde bei Silberberg, Schlesien (Frech, 1897, pl. A7); *3c,* isolated proximal end with virgellarium and one sicular cladium (adapted from Urbanek, 1997a, fig. 5D). Scale bars, 1 mm.

Neodiversograptus Urbanek, 1963, p. 149 [**Monograptus nilssoni* Lapworth, 1876c, p. 315; *sensu* Urbanek, 1954, p. 300; OD]. Proximally gently dorsally curved monograptid stipe, distally straight or dorso-ventrally curved, forming bipolar tubarium in mature specimens; sicula with long dorsal apertural spine, with its further prolongation producing secondary nema for sicular cladium; thecae tubular, with apertures either straight or with slightly elevated margins; ventral thecal wall at low angle to tubarium axis. [The problems of the identification of *N. nilssoni* were discussed in Palmer (1971a, 1971b) and Strachan (1973).] *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide (although only questionably from Arctic Canada).——Fig. 307,*4a–c*. **N. nilssoni* (Lapworth); *4a,* neotype (Palmer 1971b, p. 97), Long Mountain Shales, Welsh Borderlands, UK (Wilkinson, 2018c, Atlas, Folio 3.58); *4b–c,* proximal ends without (*4b*) and with (*4c*) sicular cladium, Silurian, Ludlow, Poland (Urbanek, 1997b, fig. 2A–B). Scale bars, 1 mm.

Prolinograptus Rickards & Wright, 1997b, p. 225 [**P. packhami;* OD]. Very slender tubarium with numerous sicular cladia; stipes straight or gently ventrally curved; sicula small; sicular cladia with secondary nemata; thecae with simple everted apertures. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Neocucullograptus inexpectatus/kozlowskii* Biozone): Australia, Poland, Arctic Canada.——Fig. 307,*5a–b*. **P. packhami; 5a,* AMF 81773a, distal thecae of holotype (Rickards & Wright, 1997b, fig. 9L); *5b,* AMF 91956b, proximal end with sicula (Rickards & Wright, 1997b, fig. 9K). Scale bars, 1 mm.——Fig. 307,*5c*. *P. orangensis* (Rickards & others,1995); AMF 81650, holotype, scale bar, 1 mm (Rickards & others, 1995, fig. 35d).

UNCERTAIN GENERA

Jörg Maletz and Michael Steiner

INTRODUCTION

The history of research on graptolites includes quite a number of genus-level taxa that have later been identified as belonging to other groups of organisms, even to trace fossils. Some genera have been described that cannot be identified at all. Bulman (1955, 1970) provided a list of unrecognizable taxa. That list is updated here with additional information to provide a better understanding of the current status of these genus-level names. In the future, some of these taxa will be properly identified and referred to other fossil groups or recognized as genuine graptolite taxa. Organic macrofossils can be very similar in fossil preservation to some graptolites, and differentiation may be difficult or impossible in poorly preserved material. Thus, some Neoproterozoic taxa identified as worms, algae, or other organisms have features that are strongly reminiscent of early graptolites and graptolitic tubaria. The organic-walled taxa of the Sabelliditidae may have distinct tubular structures with wrinkled surface ornamentation (Urbanek & Mierzejewska, 1977) similar to the fusellar construction of the graptolite tubaria. Maletz and Beli, 2018) and Maletz (2019a) identified material of the presumed sabelliditid *Sokoloviina costata* Kirjanov, 1968 as remains of early pterobranchs and referred them preliminarily to the Rhabdopleuridae.

GRAPTOLITIC (PTEROBRANCH) REMAINS OF UNCERTAIN VALUE

A number of genus-level taxa have been mentioned but never described or are based on inadequate material. These taxa are listed here if a graptolitic identity can be suggested. This possible graptolite identity is generally based on the preservation of organic material in the fossil specimens or in the concept of the described genus. In some cases, it may be that the publications with descriptions of those taxa have not been traced or are not currently identifiable. For example, many of the several hundred publications of Rudolf Hundt were in newspapers or in obscure or difficult-to-obtain local journals and are impossible to trace, especially if references to these are not correct. Other genera listed herein have been referred to a number of fossil groups but can be recognized as graptolitic in nature.

Alexandrograptus Přibyl, 1981, p. 373, *nom. dub.,* Urbanek & Teller, 1997, p. 43; rejected and invalid name, ICZN, Opinion 2023, 2003, p. 74 [**Monograptus butovicensis* Bouček, 1936, p. 4; OD]. Přibyl (1981, p. 375) recognized *Alexandrograptus* as a synonym of *Polonograptus,* based on the same types species in a postscript to his paper. Urbanek and Teller (1997) identified the type species *Monograptus butovicensis* as a *nomen dubium* and Riva, Koren', and Rickards (2001) applied to ICZN to replace *Monograptus butovicensis* with *Polonograptus podoliensis* Přibyl, 1983 as the type species of *Polonograptus,* granted, ICZN Opinion 2023 (2003).

Amansites Brongniart, 1828, p. 70, *nom. dub.,* herein, *ex Fucoides*, section *Amansites,* Brongniart, 1828, p. 70. The author of the genus *Amansites* is usually listed as Brongniart in d'Orbigny (1849), but it was introduced earlier by Brongniart (1828). The genus was listed as algal remains in d'Orbigny (1849, p. 145), based on the two species: *Amansites serra* Brongniart, 1828 (=*Tetragraptus serra*) and *Amansites dentata* Brongniart, 1828 (=*Levisograptus dentatus*). It was listed in Andrews (1970, p. 16), Burkhardt (2018), and most recently in the Guiry and Guiry (2020) algae database. A type species has never been designated for the genus, and it has never been discussed or revised. If these remains are not plant fossils, the genus *Amansites* would be a senior synonym of *Tetragraptus* Salter, 1863a or *Levisograptus* Maletz, 2011c. [The history of this taxon can be regarded as a good example of an unwarranted resurrection of a long-unused taxon name for recent interpretations (see Guiry & Guiry, 2020) and also of the difficulty of identifying organically preserved fossils.]

Ascograptus Ruedemann, 1925b, p. 18, *nom. dub.,* herein [**A. similis;* OD]. Small, conical thecae, arranged spirally along an unbranched axis.

[This taxon could represent a juvenile dendroid graptolite; herein.] *Silurian, Ludlow* (*Gorstian*): North America.——Fig. 308,*1a–b*. **A. similis; 1a,* holotype; *1b*, reconstruction (Ruedemann, 1925b, pl. 6,*6* and 6,*8*). Scale bars, 1 mm.

Birastrites Geinitz, 1866, p. 125, *nom. dub.,* herein. Remarks of Geinitz (1866) suggest, that he intended to include biserial forms with isolated thecal tubes in the genus, based on a theoretical concept, not on actual material.

Ceramograptus Hudson, 1915, p. 129, *nom. dub.*, herein [**C. ruedemanni;* OD]. The type specimen is preserved on the slab with the holotype of *Urasterella pulchella* (Billings, 1857) as stated by Hudson (1915, p. 129). The specimen is at the GSC, Ottawa, Canada. It is clearly an indeterminable biserial graptolite fragment. *Upper Ordovician:* Canada.——Fig. 308,*2*. **C. ruedemanni,* magnification unclear (Hudson, 1915, pl. 2).

Changyangograptus Shao, Jia, Liu, Fu, Zhang, Qin, Jiang, Tang, Wang, & Hu, 2018, p. 422, *nom. nud.*, herein [**Monograptus changyangensis* Sun, 1933, p. 43; OD]. *Silurian* (*Llandovery*). The taxon was listed in a range chart with a single species from the Aeronian (lower Silurian), here regarded as the type species, but there is no description available. Chen and Lin (1978) described and illustrated the Llandovery (lower Silurian) *Monograptus changyangensis* on which the genus may be based.

Coelograptus Ruedemann, 1947, p. 266, *nom. dub.,* herein [**Inocaulis problematicus* Spencer, 1878; OD]. Multiramously branching, encrusting colony; thecal style and development unknown. [This might be a benthic, encrusting graptolite] *Silurian, Ludlow* (*Gorstian*): Canada.——Fig. 308,*3a–b*. **C. problematica* (Spencer), Niagara Dolomite, Hamilton, Ontario, Canada. *3a,* holotype, scale bar, 10 mm (Ruedemann, 1947, pl. 91,*3*); *3b,* plesiotype, scale bar, 5 mm (Ruedemann, 1947, pl. 39,*12*).

Cystoturriculagraptus Hundt, 1953a, p. 40, *nom. nud.,* herein. It was cited as *Cystoturriculagraptus* Hundt, 1952, but a 1952 paper with such a citation has not been identified. The genus was listed under the heading Monograptidae without a description or illustration.

Demicystifer Hundt, 1959, p. 27, *nom. dub.,* herein [**Demicystifer cavernalis;* OD]. No description is included, but there is a single illustration of an unidentifiable distal fragment of a biserial graptolite bearing a nematularium. This is not a misspelling of the petalolithid *Demicystograptus* Hundt, 1950 (see Lenz & others, originally published in *Treatise Online,* 2018, p. 31). *Silurian, Llandovery* (*Rhuddanian, Parakidograptus acuminatus* Biozone–*Cystograptus vesiculosus* Biozone): Germany.——Fig. 308,*4*. **D. cavernalis,* holotype, Hohenleuben, Thuringia, Germany (Hundt, 1959, pl. 6.*1;* specimen not identified). Scale unclear.

Furkagraptus Hundt, 1959, p. 18, *nom. nud.,* herein [**F. furkatus;* OD]. The taxon was listed but neither described nor illustrated by Hundt, 1959. *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone): Germany.

Geminograptus Hundt, 1953a, p. 40, *nom. nud.,* herein). The taxon was listed in Hundt (1953a) as having been published in Hundt (1951), but a paper describing the taxon has not been identified. There is no illustration or description available. Hundt (1953a) also listed a family Geminograptidae.

Graptolites M'Coy, 1850, p. 270. M'Coy (1850) introduced the name as a genus name for monograptids and compared it to '*Diplograpsis*' (now *Diplograptus*) introduced for biserial graptolites. Nicholson (1868b) used the genus name, but it survives only as the common name for the group, as it was already used by Barrande (1850) and has never been accepted as a valid genus name.

Graptolithus Linnaeus, 1768, p. 173. Linnaeus (1768) listed the genus *Graptolithus* with a number of taxa that may have included plants (algae), dendrites, and other inorganic objects (In a note on the bottom of page 173: "Petrificatum, proprie dictum, non est Graptolithus, licet petrificaris communiter annumeretur"). The genus name was originally applied to inorganic marks simulating fossils (Linnaeus, 1735). Linnaeus (1751, p. 147) for the first time illustrated a *Graptolitus* (sic) in his account of his Scania visit. This illustration has been copied repeatedly and may remain the earliest illustration of a graptolite (see Maletz, 2017a, fig. 15,*1*), but a specific identification of the taxon is impossible and the original material is not preserved. Linnaeus (1768) listed among others *Graptolithus sagittarius* and *Graptolithus scalaris*. ICZN Opinion 197 (1954a) finally suppressed the genus name *Graptolithus* Linnaeus, 1768 and the species *Graptolithus scalaris* Linnaeus, 1768.

Halograptus Hundt, 1936, p. 36, *nom. nud.,* herein. Hundt (1936) stated that *Halograptus* can be compared to *Abiesgraptus* (Lower Devonian), but is from the Ordovician (lower Silurian at that time in Germany). It may be a misspelling of *Holograptus,* but Hundt never illustrated a specimen under this name in any of his papers.

Hippurograptus Ehlers & Wilson MS in Ehlers, 1973, p. 129, *nom. nud.*, herein [**H. ruedemanni;* OD] The name was provided in a faunal list from the Schoolcraft Member of the Manistique Dolomite, Clinton Group (Silurian) of Michigan, USA. A description or illustration is not available.

Janograptus Tullberg, 1880a, p. 314, *nom. dub.,* herein [**J. laxatus;* M]. Regenerated stipe fragments of expansograptid or acrograptid origin; see Albani & others, 2001, p. 390. *Lower Ordovician* (*Floian*)–*Middle Ordovician* (*Darriwilian*): worldwide.——Fig. 308,*5a*. **J. laxatus*, LO 413t, syntype, Scania, Sweden, scale bar, 1 mm (Tullberg, 1880a, fig. 5).——Fig. 308,*5b*. Janograptid specimen, GSC 119829, *Pterograptus elegans* Biozone, Mainland, western Newfoundland, Canada, scale bar, 1 mm (Albani & others, 2001, fig. 5D).

Labrumograptus Hundt, 1953a, fig. 122, *nom. dub.,* herein [**L. primigenius;* M]. The illustration shows a robust monograptid fragment preserved as an internal cast in pyrite. It is specifically indeterminable. *Silurian, Ludlow* (Zone 20): Germany.——

Fig. 308,*6*. **L. primigenius,* Ronneburg-Raitzhain, Thuringia, Germany, scale bar, 1 mm (Hundt, 1953a, fig. 122; specimen is not identified).

Lunatograptus Shao, Jia, Liu, Fu, Zhang, Qin, Jiang, Tang, Wang & Hu, 2018, p. 422, *nom. nud.,* herein. Three species from the Aeronian (lower Silurian) were listed under this genus name in a range chart, but there is no description available. The species are *Lunatograptus lunata* (Chen & Lin, 1978), *Lunatograptus variabilis* (Ni, 1978), and *Lunatograptus falcata* (Chen & Lin, 1978).

Mystiograptus Hundt, 1965, p. 45, *nom. dub.,* herein [**M. primus;* OD]. Proximally uniserial and distally biserial colony with triangular to hook-shaped thecae. [The holotype BAF 186/299 (Hundt, 1965, fig. 36.1) is based on an indeterminate tectonically deformed curved uniserial graptolite fragment. The locality is Arnsbach near Gräfenthal, Thuringia, Germany.] *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone): Germany.

Nereitograptus Hundt, 1953a, p. 40, *nom. dub.*, herein [type not selected; ?*N. linearis* Hundt, 1965; M]. The taxon was listed in Hundt (1953a) as having been published in Hundt (1951a), but a paper describing the taxon has not been identified. Hundt (1965, fig. 36,*2*) illustrated a single specimen as *N. linearis* Hundt, 1965 (BAF H225?). This is a non-identifiable graptolite fragment. Hundt (1953a) also used the family name Nereitograptidae.

Nodosograptus Hundt, 1965, p. 46, *nom. dub.,* herein [**N. pensilis* Hundt, 1965; M]. The genus was spelled *Nodosugraptus* in Hundt, 1953a, p. 40. The taxon was already listed in Hundt (1953a) as having been published in Hundt (1951a), but this paper has not been identified and may not exist. The illustration of *N. pensilis* in Hundt (1965, fig. 38) may be a dorsoventrally preserved fragment of a *Campograptus* or *Monograptus* specimen from the *Stimulograptus sedgwickii* to *Spirograptus turriculatus* Biozone interval at Steinpöhl, Vogtland, Thuringia, Germany.

Paradimorphograptus Hundt, 1953a, p. 40, *nom. nud.,* herein. The taxon was listed in Hundt (1953a) as having been published in Hundt (1951a), but a paper describing the taxon has not been identified.

Paragraptus Hundt, 1965, p. 47 [*P. *rhabdopleuraoides;* OD]. Hundt (1965, fig. 115, BAF H 2517, Weinberg bei Hohenleuben, Thuringia) compared the taxon with the extant *Rhabdopleura* and with *Rastrites*. Zone 13? (*Monograptus sedgwickii* Biozone?): Germany.

Phycograptus Gurley, 1896, p. 89, *nom. dub.,* herein [**P. brachymera;* OD]. Ruedemann (1908, p. 245) considered *P. brachymera* Gurley, 1896 from the Lower *Dicellograptus* Zone at Stockport, New York as a frontal view (ventral view) of a *Dicellograptus* stipe, based on his material, but he was unable to find the type specimen in the Gurley collection. Ruedemann (1908, p. 246) discussed *P. laevis* (Hall, 1847) as an undescribed sponge taxon. The type is from the Utica Shale of Turin, Lewis County, New York, USA, and is preserved at the AMNH.

Polygonograptus Bouček, 1957, p. 151, *nom. dub.,* herein [**Palaeodictyota sokolovi* Obut, 1953, p. 54; OD]. Irregular network of mainly pentagonal or hexagonal meshes; thecal structure completely unknown. [The genus is unrecognizable and may represent a fragment of a callograptid or dendrograptid graptolite.] *Upper Ordovician–Silurian* (*Wenlock, Testograptus testis* Biozone): Czech Republic, Russia.——Fig. 308,*7a*. **P. sokolovi* (Obut), holotype, Leningrad area, Russia, scale bar, 1 mm (Obut, 1953, pl. 11,*4a*).——Fig. 308,*7b*. *P. boncevi* Bouček, 1957, holotype, Czech Republic, scale bar, 10 mm (Bouček, 1957, pl. 38,*1*).

Praerhynia Hundt, 1949d, p. 45, *nom. dub.,* herein. Hundt (1949d) introduced the genus without diagnosis and illustrated two specimens. These can probably be recognized as *Cephalograptus cometa* juveniles (Hundt, 1949d, fig. 31; *Praerhynia*) and an unidentifiable biserial, most likely a *Normalograptus* fragment (Hundt, 1949d, fig. 30, identified as "Sporangien von *Praerhynia*"). The material originated from the Llandovery of Thuringia, probably from the *Lituigraptus convolutus* Biozone, but different biostratigraphic levels were given in Hundt (1949d, 1965) for the same specimen. The specimen initially identified as a sporangium of *Praerhynia* was later re-illustrated under the name *Triplograptus triangulatus* (Hundt, 1965, fig. 120; BAF 186/2296, Heinrichsruh/Schleiz, Zone 11/12).

Priodon Nilsson cited in Hisinger, 1831, p. 29, 37; homonym of *Priodon* (attributed to Cuvier) Quoy & Gaimard, 1825, p. 377 [**P. annulatus* Quoy & Gaimard; OD; =*Naso annulatus* (Actinopterygii, Acanthuridae)]. Some confusion arose over the naming of graptolites with the introduction of the genus name *Priodon*, apparently suggested but not published by Sven Nilsson (see Tullberg, 1882b, p. 7; cited also in Elles & Wood, 1902, p. vii) and used first by Bronn (1835, p. 56), who indicated the homonymy with the genus *Priodon* Quoy & Gaimard, 1825.

Prionotus Nilsson, cited in Hisinger, 1837, p. 113; homonym of *Prionotus* Lacépède, 1801, p. 20 (a fish genus of the family Triglidae, searobins). A note to the preoccupation of the name *Prionotus* is in Tullberg (1882b) and Bulman (1929). Regnéll (1991) discussed the influence of the Swedish scientist Sven Nilsson on graptolite research in Sweden and explained the reason for the reference of the genus names *Priodon* and *Prionotus* to Nilsson, even though Nilsson never published a single paper on graptolites.

Procyrtograptus Poulsen, 1943, p. 304, (*nom. dub.,* Bjerreskov, 1975, p. 46) [**P. garboei;* OD]. Bjerreskov demonstrated that this genus consists of a combination of specimens of *Coronograptus gregarius* and *Pernerograptus sudburiae* and is therefore not a valid genus.——Fig. 308,*8*. **P. garboei,* 2943, Bornholm, Denmark, scale bar, 1 mm (Poulsen, 1943, fig. 2).

Protograptus Matthew, 1886, p. 31, original spelling as *Protograpsus* changed in ICZN Opinion 650, 1963, *nom. dub.,* herein [**P. alatus;* M]. Peculiar

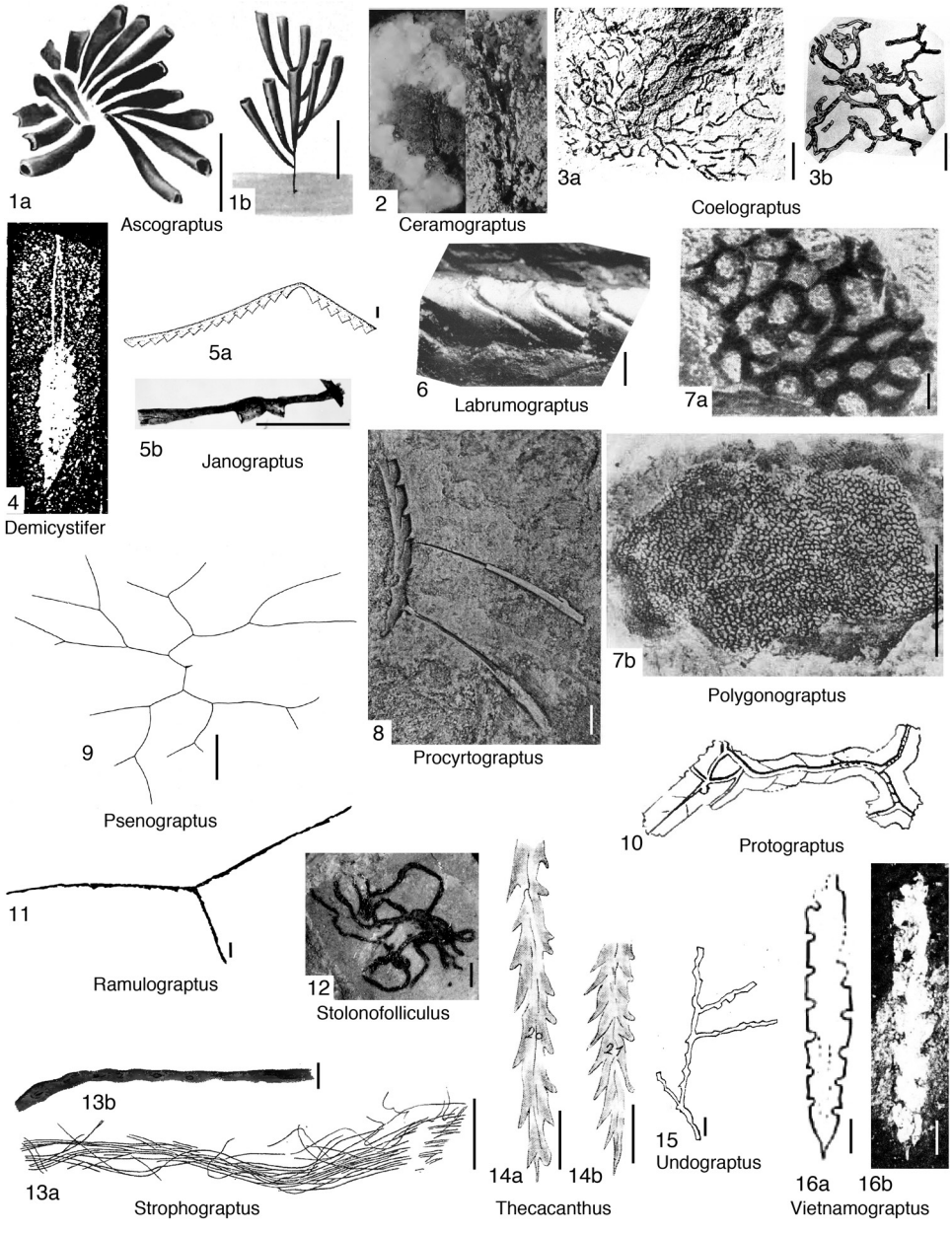


FIG. 308. Uncertain graptolitic remains (p. 461–466).

in its alation, which extends along the axis of the stipe, apparently without bearing cells at the margin. [This fragment looks like a late Tremadocian to Floian adelograptid or clonograptid but is specifically indeterminable. It is associated with *Dendrograptus*(?) *primordialis* MATTHEW, 1886. The material is supposed to come from the "highest *Paradoxides* horizon of the St. John Group" (MATTHEW, 1893a, p. 4), thus the middle Cambrian.] ?*Middle Cambrian:* Canada.——FIG. 308,*10*. **P. alatus,* Porter's Brook, St. Martin's, New Brunswick, Canada (Matthew, 1886, pl. 5,*6*).

Psenograptus VANDENBERG, 2019b, p. 47, *nom. dub.,* herein [* *P. costermansi;* OD]. Multiramous species with horizontal funicle, lacking visible thecae. *Lower Ordovician* (*Floian, Paratetragraptus approxi-*

matus Biozone): Australia. [The material is poorly preserved, does not show thecae, and therefore is unidentifiable even at the genus level. However, it may represent a multiramous sigmagraptine or dichograptine from the Floian Stage of Australia and is similar to *Clonograptus subtilis* Törnquist (1904) from the Floian of Sweden, in which low-inclined thecae are visible.]——Fig. 308,*9*. **P. costermani,* holotype, NMV P 327560, Campbelltown, Victoria, Australia, scale bar, 10 mm (new; drawing based on VandenBerg, 2019b, fig. 48).

Ramulograptus Ross & Berry, 1963, p. 84, *nom. dub.,* herein [**R. surcularis;* OD]. *Middle Ordovician* (*Dapingian–Darriwilian, Isograptus* Zone): USA. The specimen appears to be an indeterminable graptolite fragment of dichograptid or sigmagraptid origin.——Fig. 308,*11*. **R. surcularis,* holotype, USNM 138492, Vinini Formation, Nevada, USA, scale bar, 1 mm (Ross & Berry, 1963, pl. 5,*6*).

Sinograptus Shrubsole, 1880 (?), *nom. nud.,* herein. Münch (1931, p. 42) discussed the name, but a paper providing a description or illustration is not currently available. According to Münch (1931), "Mr. Korn initially compared the new species with a graptolite described in American literature under the name *Sinograptus* by Shrubsole (1880), but did not find a match" (Münch, 1931, p. 42, translated by J. Maletz). It appears that the name *Sinograptus* Shrubsole, 1880 was used to describe a retiolitid graptolite (see discussion in Münch, 1931, p. 42), but it might not have been published officially and has not been found in an unpublished manuscript. The genus cannot be identified with *Sinograptus* Mu, 1957 (see p. 277).

Spinosudiplograptus Hundt, 1953a, p. 40, *nom. nud.,* herein. The taxon was listed in Hundt (1953a) as published in Hundt (1951a), but a paper describing the taxon has not been identified. Hundt (1953a) included the genus in the Diplograptidae, but did not provide a diagnosis, description, or illustration.

Stenograptus Gurley, 1896, p. 296, *nom. nud.*, herein. *Lower Ordovician* (*Floian–?Dapingian*): Canada. The name was used in a manuscript sent from Charles Lapworth to R. R. Gurley (see Gurley, 1896, p. 303) but appears not to have been published by Lapworth subsequently. The only record is in a list in Gurley (1896, p. 296) in which the species *Stenograptus speciosus* "Lapworth, MS" is included.

Stolonofolliculus Zessin & Puttkamer, 1994, p. 570, *nom. dub.*, Mierzejewski & Urbanek, 2004, p. 521–522 [**Melanostrophus signum* Öpik, 1930; OD]. Zessin & Puttkamer (1994) even erected a new family, Stolonofolliculidae, for the genus. Mierzejewski (1988) stated that the type material of *M. signum* was lost but referred the taxon to *Graptovermis intestinalis* Kozłowski, 1949. *Ordovician.*——Fig. 308,*12*. **S. signum* (Öpik), holotype, TUG 1053-17, Kukruse Stage, (lower Sandbian) Kohtla, Estonia, scale bar, 1 mm (new; provided by Ursula Toom).

Strophograptus Ruedemann, 1904, p. 716, *nom. dub.,* herein [* *S. trichomanes;* OD]. Bundles of long thin flexuous carbonaceous fibers, subparallel and not bifurcating; thecae indistinct, perhaps represented by minute pores along the stipes. [The genus has to be regarded as graptolite indet. at the moment. It is not even clear whether the material represents graptolite remains. The few known specimens were collected from graptolitic shales and are apparently comprised of organic material.] *Middle Ordovician* (*lower Darriwilian, Levisograptus dentatus* Biozone): USA.——Fig. 308,*13a–b*. **S. trichomanes,* holotype (*a*) and enlargement (*b*) of single stipe; scale bar, 10 mm (*a*); 1 mm (*b*) (Ruedemann, 1904, pl. 4,*17,20*).

Thecacanthus Hernández Sempelayo, 1960, p. 35, *nom. dub.*, herein, *ex Glossograptus* (*Thecacanthus*) Hernández Sempelayo, 1960, p. 35 [**Glossograptus* (*Thecacanthus*) *loxos;* OD]. This taxon was introduced for biserial forms where the interthecal septa "are not precisely marked inside the fossil" and whose "thecae are individualized and prolongate to end in spines with proximal inclination" (Hernández Sempelayo, 1960, p. 35). The material originated from the Almadén syncline and the Almadén mine and may instead represent distal fragments of *Parapetalolithus* or *Glyptograptus*. (information and translation, J. C. Gutiérrez-Marco, May, 2020).] *Silurian:* Spain.——Fig. 308,*14a–b*. **T. loxos,* two examples, scale bars, 1 mm (Hernández Sampelayo, 1960, pl. 16,*20–21*).

Triplograptus Hundt, 1965 (listed in Hundt, 1959, p. 19) *nom. dub.*, herein [*non Triplograptus* Richter, 1871, p. 251 (type, *T. nereitarum,* OD, trace fossil *Protovirgularia*, see p. 9)]. Tubaria with three rows of thecae. [Hundt (1965, in explanation to fig. 39,*1–3*) listed a family Triplograptidae. Hundt (1965) listed a number of species that may belong to the genera *Cystograptus*, *Petalolithus,* and *Normalograptus*.] *Silurian, Llandovery* (*Aeronian*): Germany.

Undograptus Nindel, 1949, p. 24, *nom. dub.,* herein [**U. nodosus;* OD]. Undulating stipes with ?alternate thecae, branching observable. [This is certainly a strongly tectonized monograptid graptolite but is too poorly preserved for identification. Nindel (1949, p. 24) indicated that the genus was already described by Hundt (1946), but this paper is unknown]. *Silurian, Llandovery* (*Telychian*).——Fig. 308,*15*. **U. nodosus,* Raitzhain, Ronneburg, Thuringia, Germany, Zone 15 (*Monograptus exiguus* Zone of Eisel, 1903; =*crispus/griestoniensis* Zone), scale bar, 1 mm (Nindel, 1949, fig. 21,*4*).

Vietnamograptus Van Phuc, 1998, p. 286, *nom. dub.*, herein [**V. thamhocensis;* OD]. According to the author, the new genus is small and short, slender and undulated. The rhabdosome has two types of thecae: monograptid type on one side, but glyptograptid type with the star thecal apertures on the other side (Van Phuc, 1998). [No illustrations of Vietnam material are available, but Jaeger (1988) illustrated a single specimen, which is not mentioned in the abstract in

which the genus was introduced. It appears to be a secondarily? biserial taxon, originating from a monograptid ancestor (comparable to the abnormal, partly biserial specimen of *Slovinograptus balticus* in Urbanek, 1997a, fig. 10).] *Lower Devonian* (*Lochkovian, Uncinatograptus hercynicus* Biozone): Austria, Vietnam.——Fig.308,*16a–b*. **V. thamocensis,* Obere Bischoffsalm, Carnic Alps, Austria; *16a,* drawing (Jaeger, 1988, fig. 1K); *16b,* photo (Flügel, Mostler, & Schönlaub, 1993). Scale bars, 1 mm.

TAXA OF UNCERTAIN ORIGIN

The genera listed here do not represent graptolitic remains, but cannot currently be assigned to any fossil group. They were initially described as graptolites.

Acanthastus Kozłowski, 1949, p. 226 [**A. luniewskii;* OD]. Bulman (1970) included the order Acanthastida Kozłowski, 1949 with its single genus *Acanthastus* under the heading Graptolithina *incertae sedis*. Kozłowski (1949) suggested a chitinous composition and a possible secretion of the features as evidence of a possible graptolite relationship, which has not been verified. The complex development of the specimens and the lack of any recognizable pterobranch features may render doubtful the assignment to the Pterobranchia. *Lower Ordovician* (*Tremadoc*): Poland.——Fig. 309,*1a–c*. **A. luniewskii,* holotype, dorsal (*a*), ventral (*b*), and lateral (*c*) views; scale bars, 1 mm (Kozłowski, 1949, pl. 40,*2*).

Conograptus Ruedemann, 1947, p. 267 [**C. simplex;* OD]. Simple, conical tube that contains bundles of filiform thecae within the outer periderm; thecal apertures circular, scattered on surface of rhabdosome. *Cambrian:* USA (Colorado).——Fig. 309,*2a–b*. **C. simplex,* drawings of two fragmented specimens; scale bars, 1 mm (Ruedemann, 1947, pl. 40,*26–27*).

Crinisdendrum Dzik, Baliński, & Sun, 2016, p. 327 [**C. sinicum;* M]. Mature colony with lateral branches (thecae?) distributed along axis. [Dzik, Baliński, and Sun (2016) erected the family Crinisdendridae for the genera *Crinisdendrum* and *Webbyites* Kraft, Kraft, & Prokop, 2001 and suggested a pterobranch affinity as the most likely hypothesis. There is no evidence of fusellar construction in these taxa to support a pterobranch affinity.] *Lower Ordovician* (*Floian,* ?*Tetragraptus approximatus* Biozone): China (Hubei Province).——Fig. 309,*10a–b*. **C. sinicum,* Fenxiang Formation, Hubei Province, China; *10a,* juvenile colony, scale bar, 0.5 mm; *10b,* part of mature colony; scale bars 5 mm (Dzik, Baliński, & Sun, 2016, fig. 5).

Hunanodendrum Mu, Li, Ge, Chen, Ni, Lin & Mu, 1974, p. 220 [**H. typicum;* OD]. It is impossible to relate the material to any known graptolite taxon. *Silurian, Llandovery* (*Telychian*): China.——Fig. 309,*3a*. **H. typicum,* syntype, scale bar, 10 mm (Mu & others, 2002, pl. 33,*5*).——Fig. 309,*3b*. *H. irregulare* Ni, in Li & Ni, 1979, holotype, scale bar, 10 mm (Mu & others, 2002, pl. 33,*9*).

Protistograptus McLearn, 1915, p. 55 [**Creseis corrugata* Matthew, 1892, p. xviii & Errata (listed as *Cyrtotheca* on p. xviii, revised in Errata; no page number); OD; see Bulman, 1929, p. 181 (referred to *Styliola* by Bassler, 1915b, p. 1242)]. Arched or straight cone, formed from carbonaceous material; probably representing a sicula comparable to the genus *Corynoides*. [The graptolitic assignment is based on the presence of carbonaceous material and the interpretation as a large sicula, but the identification is uncertain. Matthew (1893b, p. 105) described it as "a horny consistency, or of thick chitenous substance." The specimens may be comparable with carbonaceous problematica from the Martinsburg Formation of Pennsylvania (Meyer & others, 2018) (see Fig. 309,*5b*).] *Lower Ordovician* (?*Floian*)–*Upper Ordovician* (*Sandbian*): ?Australia (Tasmania), Canada, USA.——Fig. 309,*5a*. **P. corrugata* (Matthew), St. John, New Brunswick, Canada, scale bar, 1 mm (McLearn, 1915, fig. 2).——Fig. 309,*5b*. Carbonaceous problematica, Martinsburg Formation, USA, scale bar, 1 mm (Meyer & others, 2018, fig. 5D).

Quadruplograptus Haupt, 1878, p. 51 [**Q. rhomboidalis;* M]. The identity of this material is uncertain and it might not be a graptolite. Haupt's paleontological collection may be at the University of Wrocław, Poland (formerly Breslau) (Schönwälder, 1882), but the specimen has not been identified. *Silurian* (*Wenlock–Ludlow*).

Undagraptus Hemmann, 1951, p. 75 [**U. stolzenbergensis;* OD]. The identification is based on the undulating shape of the specimen. The original was said to be in the collection of the author. The counterpart is at Paläontologisches Institut, Martin Luther Universität Halle, Germany (Nr. 48015). The available photo is too poor for an identification or re-illustration. *Silurian, Ludlow* (*Gorstian*).

ARTHROPODS

A few taxa were described initially as graptolites but can be recognized as arthropods. Pieces of phyllocarids, in particular, have been identified as graptolites in the past, either as colonies (rhabdosomes; tubaria), floats, or ovarian capsules due to their representing organically preserved material in graptolitic shales. Manck (1927) described a number of examples as gonothecae and float structures of graptolites from the Silurian of Germany. Gürich (1928) strongly opposed this view and recognized some of the specimens as phyllocarid remains. The most prominent example may be *Megalograptus* Miller, 1874, now recognized as fragments of an eurypterid.

Coronagraptus Hundt, 1951a, p. 60 [**C. singularis;* OD]. Bulman (1970) considered the genus as unrecognizable. It is clearly a phyllocarid frag-

ment, possibly belonging to the genus *Peltocaris* Salter, 1862 as described by Salter (1862). The species may be common in the Unterer Graptolithenschiefer in Germany. The genus should not be confused with *Coronograptus* Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968, a Silurian monograptid. *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone): Germany.——Fig. 309,*6*. **C. singularis,* holotype, not identified, Hässlich near Weckersdorf, Thuringia, Germany, scale bar, 5 mm (Hundt, 1951a, fig. 16).

Dawsonia Nicholson, 1873, p. 139 [**D. campanulata;* SD Miller, 1889, p. 184] [*non Dawsonia* Hartt in Dawson, 1868 (Trilobita, Eodiscina); Axheimer, 2006]. The genus is a junior homonym to *Dawsonia* Hartt in Dawson, 1868, thus invalid. Rolfe (1969, p. 316) stated that *Dawsonia* Nicholson, 1873 is a junior synonym of *Caryocaris* Salter, 1862, but Page and others (2009) discussed *D. campanulata* as a fossil of uncertain origin, a flat problematicum, but recognized that a number of unrelated fossil remains were described under this name, including linguliform brachiopods and crustacean tail pieces. *Silurian, Llandovery.*——Fig. 309,*7*. **D. campanulata,* lectotype NHMUK Q253, Silurian, Llandovery, Dob's Linn, Scotland, scale bar, 1 mm (Page & others, 2009, fig. 1a).

Megalograptus Miller, 1874, p. 343 [**M. Welchi;* OD]. Ruedemann (1908, p. 247) discussed the genus as "fragments of a crustacean" and compared it with *Echinognathus clevelandi* Walcott, 1882. Clarke and Ruedemann (1912a, 1912b) referred the material to the Eurypterida. Lamsdell and others (2015) included it in the family Megalograptidae (see Størmer, 1955, p. 36) and recognized the members of the family as the oldest known eurypterids. Tollerton (1989) elevated the family to the superfamily Megalograptoidea. *Upper Ordovician, Katian.*

HYDROIDS

Quite a number of dendroid graptolites have been identified as hydroids in the past (see Maletz & Beli, 2018). Due to their poor preservation, it is often difficult or impossible to determine the true affinity of such taxa. For example, Muscente, Allmon, and Xiao (2015) recognized the hydroid genus *Archaeoantennularia* Decker, 1952 as a benthic graptolite, and there might be more such taxa that could be identified as graptolites in the fossil record. Conversely, other taxa regarded as graptolites may belong to the hydroids, as was verified for the genus *Plumalina* (see Muscente & Allmon, 2013).

Archaeodendrum Obut, 1974, p. 9 [* *A. bulmani;* OD] Colony slender, flexuous, shape unknown; thecae tubular, elongate, isolated distally, slightly widening toward the aperture, arranged in triad groups on alternate sides of stem. [According to Rickards & Durman (2006, p. 58), this taxon belongs to the Hydroida. It does have an unusual grouping of the thecae and a flexing of the axis. No fusellar features or stolons are known.] *Cambrian, Miaolingian* (*upper Drumian, Anomocaroides* Zone): Russia (Siberian Platform).——Fig. 309,*8a–b*. **A. bulmani,* holotype (*a*) and paratype (*b*), scale bars, 1 mm (Rickards & Durman, 2006, fig. 47).

Dyadodendrum Sennikov, 1998, p. 18., *ex Archaeodendrum* (*Dyadodendrum*) Sennikov, 1998, p. 18, herein [**A.* (*D.*) *obuti;* OD]. According to Rickards and Durman (2006, p. 58), this taxon belongs to the Hydroida. The authors did not recognize much difference from *Archaeodendrum* but did not synonymize the two taxa, which they regarded as subgenera. *Cambrian, Miaolingian* (*Drumian*).

Plumalina Hall, 1858, p. 143 [**P. plumaria;* OD]. Hall (1858) included the taxon in his family Graptolitidae. Ruedemann (1916) and Bayer (1956) referred *Plumalina* to the Gorgoniidae (Alcyonaria). Sass and Rock (1975) suggested a possible inclusion in the Hydrozoa but were uncertain. Muscente and Allmon (2013) identified the genus *Plumalina* as a hydroid of the superfamily Plumularioidea McCrady, 1859. Dzik, Baliński, and Sun (2016) rejected the hydrozoan affinity of *Plumalina* and suggested an algal relationship. *Silurian* (*Wenlock)–Devonian* (*Famennian*).

Protohalecium Chapman & Thomas, 1936, p. 203 [**P. hallianum;* M]. Erect, multiramous tubarium, with isolated tubular thecae, formed in bundles. [Rickards and Durman (2006) regarded the genus *Protohalecium* from the Middle Cambrian of Australia as a hydroid. However, there is a chance that the taxon belongs to the Dithecodendridae if the presence of fusellar construction can be proven.] *Cambrian, Furongian* (*Paibian, Olenus* Biozone): Australia.——Fig. 309,*9a–c*. **P. hallianum; 9a*, holotype, Victoria, Australia (Rickards & Durman, 2006, fig. 50a); *9b–c*, counterpart specimens from Que River, Tasmania (Rickards & Durman, 2006, fig. 50). Scale bars, 1 mm.

ECHINODERMS?

Planctograptus Yakovlev, 1933, p. 979 (misspelled as *Planktograptus* in Bulman, 1955, 1970) [**P. rastritoides;* M]. Hexagonal central body (also identified as a central disk, 7.3 × 10 mm) and cirrus rays emanating from its corners. [Based on the original illustration, the genus may represent an unusual echinoderm but needs to be re-investigated. It is certainly not a graptolite.] ?*Upper Silurian*——Fig. 309,*11*. **P. rastritoides,* holotype, Kazakhstan, scale unknown (Yakovlev, 1933, pl. 2,*2b*).

TRACE FOSSILS

Due to an incomplete understanding of graptolites, early researchers often included unrelated fossils in the group. Thus, a number

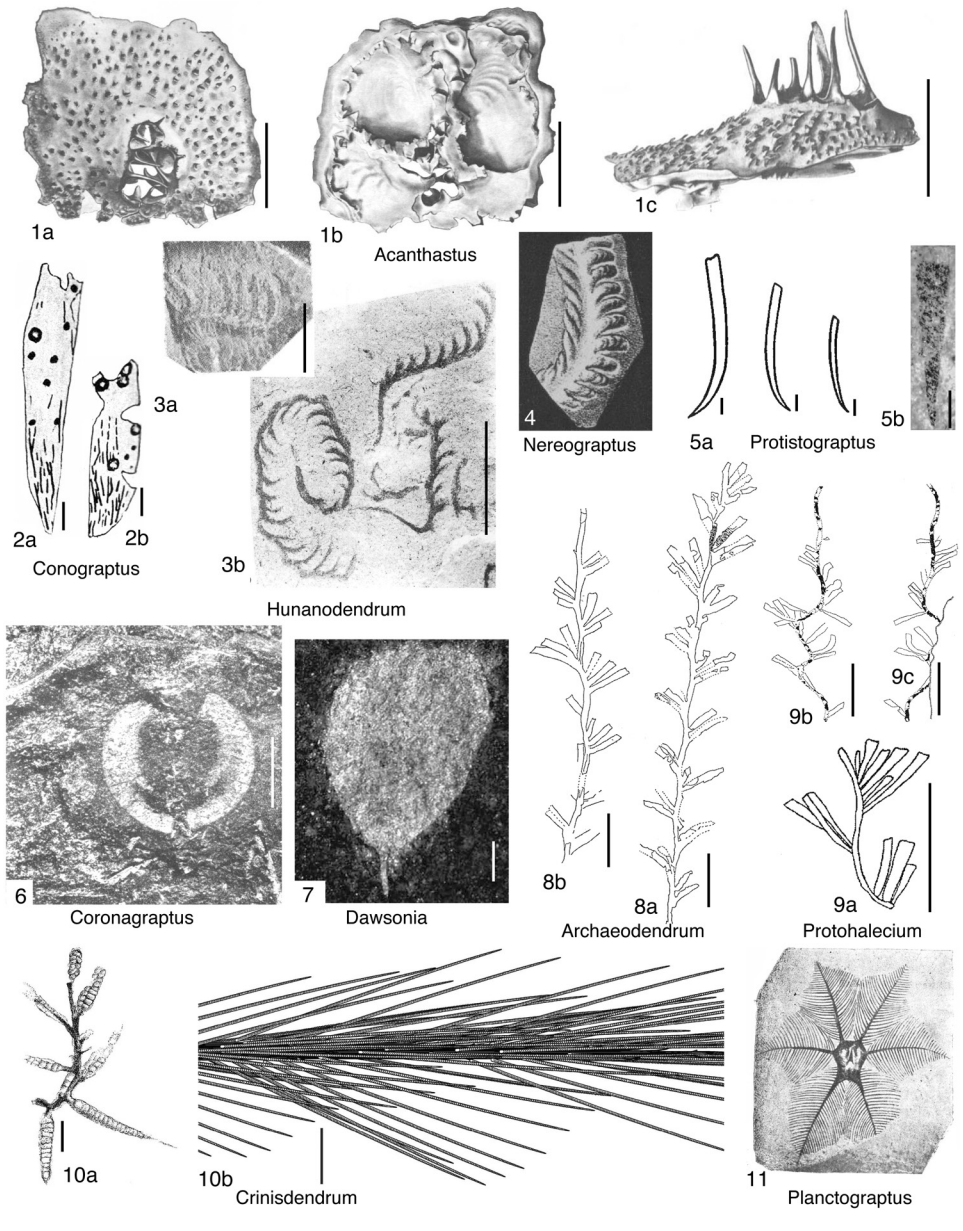


FIG. 309. Genera of uncertain affinity and genera possibly assignable to arthropods, hydroids, echinoderms, or trace fossils (p. 466–469).

of genera were initially described as graptolite remains but later recognized as trace fossils. HALL (1865, p. 51) included—with a question mark—the genus *Oldhamia* FORBES, 1848 in his Graptolitidae and listed the species *Oldhamia fruticosa* HALL 1865 but did not describe or illustrate the species. WHITFIELD (1894) described fossil material as the marine alga *Callithamnopsis fruticosa* (HALL, 1865). The taxon was regarded as a noncalcified dasycladacean alga by LODUCA, KLUESSENDORF, and MIKULIC (2003), who

referred to WHITFIELD (1894) as the author of the species. This example illuminates the difficulty of understanding graptolite remains during the early stages of investigation.

Humiligraptus HUNDT, 1940, p. 244 [**H. attenuatus;* SD herein]. HUNDT (1940) referred three species from the Phycodes Group (late Tremadocian–Floian) of Thuringia to this new genus. *H. attenuatus* may represent a poorly preserved trace fossil. There are no good illustrations of the specimens referred to this genus available, and the material has never been revised and was not identified in the Hundt collection at FU Bergakademie Freiberg Thuringia, Germany. *Ordovician* (*late Tremadocian–Floian*): Germany (Thuringia).

Nereograptus GEINITZ, 1852, p. 27, *nom. correct. pro Nereograpsus* GEINITZ, 1852, p. 27; GEINITZ, 1866, p. 125 [**Nereites cambrensis* MURCHISON, 1839; OD]. GEINITZ (1852) clearly identified *Nereograptus* as giant graptolites (zum Teil gigantische Graptolithinen) from the Ordovician (lower Silurian at the time) of Thuringia, Germany. It seems he wanted to introduce the name *Nereograptus* to demonstrate his interpretation of these fossils as graptolites, because he synonymized the genus *Nereites* with his *Nereograptus*. RICHTER (1849) had previously described *Nereites cambriensis* from Thuringia, even though at the time he did not identify it as a trace fossil but as a kind of fossil worm. There is no doubt that *Nereograptus* GEINITZ, 1852 is a trace fossil and the name is a synonym of *Nereites* MACLEAY, 1839.——FIG. 309,*4*. **Nereograptus cambrensis* (MURCHISON), Ordovician, Saalfeld, Thuringia, Germany, scale uncertain (Geinitz, 1852, pl. 5,*20*).

Protovirgularia M'COY, 1850, p. 272 [**P. dichotoma;* M] [=*Triplograptus* RICHTER, 1871, p. 251 (type, *Cladograpsus Nereitarum* RICHTER, 1853, p. 450; M); HAN & PICKERILL, 1994, p. 203]. M'COY (1850) referred the genus *Protovirgularia* to the family Gorgonidae and compared it with some biserial graptolites. HAN and PICKERILL (1994) revised the genus, and SEILACHER and SEILACHER (1994) identified it as a bivalve trace fossil.

MACROALGAE

The identification of fossil algae as graptolites has been common in the past. The reasons for this may be 1) the preservation as organic remains and 2) the general similarity of algal shapes to the shapes of dendroid graptolite tubaria. The taxonomy of fossil noncalcified macroalgae is very difficult due to the typically poor preservation as thin films of carbonaceous material in shales, siltstones, and limestones. Furthermore, many have been transported and, thus, fragmented and rarely preserved as complete specimens in their original growth position (see LODUCA & BRETT, 1997; LODUCA, MELCHIN, & VERBRUGGEN, 2011).

In a number of genera, the phylogenetic relationships to other macroalgae have been proposed in the literature, but for many forms, an algal origin can only be inferred from the shape of the fossil. The material invariably does not have the typical fusellar structure of the Pterobranchia (graptolites) but is preserved as structureless, dark carbonaceous material. MALETZ and CAMERON (originally published in *Treatise Online,* 2016, p. 12) identified the Cambrian alga *Yuknessia* WALCOTT, 1919 as a pterobranch, based on the presence of fusellar construction (LODUCA & others, 2015). MALETZ and BELI (originally published in *Treatise Online,* 2018, p. 1–2) listed the Cambrian algae *Dalyia* WALCOTT, 1919 and *Malongitubus* HU, 2005 as Graptolithina *incertae sedis* and recognized the presumed hydroids *Archaeolafoea* CHAPMAN, 1919 and *Sphenoecium* CHAPMAN & THOMAS, 1936 as rhabdopleurid pterobranchs.

LODUCA, MELCHIN, and VERBRUGGEN (2011) provided the description of a number of dasycladacean algae associated with graptolites from Cornwallis Island in the Canadian Arctic, explaining the usual preservation of these floras. LODUCA (1990) identified the genus *Medusaegraptus* RUEDEMANN, 1925b from the Silurian of New York State as a noncalcified dasycladacean, based on the type material and additional specimens from a variety of localities in New York State, USA, and Ontario, Canada. This may have been the start of a more cautious approach to some so-called dendroid graptolite remains and the recognition that some genera may better be referred to as algal remains of various types.

LODUCA and BRETT (1997) described the so-called *Medusaegraptus* epibole of the Lockport Group (Silurian) of western New York and southern Ontario, in which thallophytic algae and dendroid, benthic graptolites were a common constituent of the fauna and flora. Many specimens of these were

found *in situ* because they had grown on the sea floor, associated with other algae, brachiopods, conularids, corals, mollusks, annelids, and arthropods. The authors suggested a water depth of approximately 10–15 m for the environment in which the *Medusaegraptus* epibole flourished.

No attempt is made to differentiate the discussed genera and refer them to any taxonomic units within the Dasycladales herein; therefore the genera are listed in alphabetical order. Only taxa with uncertain, but possible, algal affinity are illustrated through their type material (Fig. 310). Otherwise, the most current revisions of the taxa are referenced below.

Boucekocaulis Obut, 1960, p. 148 [**Acanthograptus jubatus* Obut, 1953, p. 53; OD]. This taxon may represent an alga but needs to be re-investigated.——Fig. 310,*1*. **B. jubatus* (Obut, 1953), fragment, Russia, scale unclear (Obut, 1953, pl. 12,*5a*).

Buthograptus Hall, 1861b, p. 18 [**B. laxus;* M]. Hall (1861b) described *Buthograptus* as a benthic graptolite from the Upper Ordovician of Wisconsin, but Whitfield (1894, p. 352) first identified the taxon as an alga. LoDuca (2019) more recently revised the genus and referred it to the green algal order Bryopsidales. *Upper Ordovician:* USA.

Calyptograptus Spencer, 1878, p. 459, original spelling as *Calyptograpsus* changed in ICZN, Opinion 650, 1963 [**C. cyathiformis;* OD]. The genus is herein identified as a possible alga. The type may, however, represent a poorly preserved callograptid or dendrograptid, but there is no evidence of thecae or fusellar construction.——Fig. 310,*2*. **C. cyathiformis,* 1878), holotype, scale bar, 10 mm (Bassler, 1909, fig. 48).

Crinocaulis Obut, 1960, p. 148 [**C. flosculus;* OD]. The identity of this strange taxon is uncertain, but an algal relationship cannot be excluded.——Fig. 310,*3*. **C. flosculus,* scale unclear (Obut, 1960, pl. 3, fig. 1A).

Diplospirograptus Ruedemann, 1925b, p. 34 [**D. goldringae;* OD]. Bulman (1938) expressed doubts about the graptolitic nature of this taxon and suggested an algal affinity. Mierzejewski (1986) discussed *D. goldringae* as a possible alga of the class Chlorophyceae, essentially rejecting an inclusion in the graptolites. This interpretation is supported by the assignment of LoDuca (1990) and LoDuca, Kluessendorf, and Mikulic (2003).

Estoniocaulis Obut & Rotsk, 1958, p. 137 [**E. jaervensis*; OD]. Mierzejewski (1991) investigated the type material and recognized solid, roller-like elements that he compared with the melanosclerites and preliminarily referred the taxon to the order Melanoskleritoidea, a clade of possible algae from the lower Silurian.

Inocaulis Hall, 1852, p. 176 [**I. plumulosa;* M] ?*Ordovician–Silurian:* worldwide. The genus has long been identified as a dendroid graptolite and in the family Inocaulidae, established by Ruedemann (1947). Furthermore, Bouček (1957) referred to the group as the order Inocaulida Bouček, 1957. Mierzejewski (1986, p. 166) doubted the graptolitic nature of *Inocaulis* and discussed the genus as a hydroid. Maletz (2014b) suggested that *Inocaulis plumulosa* is an alga, but LoDuca and others (2017, p. 599) illustrated *I. plumulosus* as a "hemichordate with an alga-like tubarium." Because fusellar construction has not been identified in the type species of the genus, its inclusion in the graptolites is uncertain, and the preference herein is to keep it as an alga. However, most species referred to *Inocaulis* may represent species of the Callograptidae and should be referred to a number of other genera. Muir, Zhang, and Lin (2013) discussed a single fragment as *Inocaulis* sp., in which fusellar construction was detected.——Fig. 310,*4a–b*. **I. plumulosa; 4a*, illustration of type (Hall, 1865, fig. 26); *4b–c*, commonly illustrated typical specimens; scale bars, 10 mm (Bassler, 1909, fig. 59, 61).

Leveilleites Foerste, 1923, p. 62 [**L. hartnageli;* M]. The taxon was originally described as a possible alga but referred to the graptolites by Ruedemann (1947). An alga with similar form has been illustrated in Tinn and others (2009) from the Llandovery (Aeronian) of Estonia, suggesting an algal relationship of *Leveilleites*.

Medusaegraptus Ruedemann, 1925b, p. 29 [**M. mirabilis;* OD]. Bulman (1938) already expressed his doubts on this taxon and suggested an algal affinity. Mierzejewski (1991) discussed *Medusaegraptus* as an alga, and LoDuca (1990) referred the taxon to the noncalcified dasycladacean algae.

Palmatophycus Bouček, 1941, p. 3 [**P. kettneri;* OD]. *P. kettneri* was originally described as a dendroid graptolite from the Silurian (Wenlock/Ludlow) of the Czech Republic. LoDuca and others (2017) illustrated the taxon from the Eramosa Formation of Canada as a non-calcified marine alga.

Rhadinograptus Obut, 1960, p. 151 [**R. jurgensonae;* OD]. Mierzejewski (1991) did not find evidence of a graptolitic relationship and suggested that the taxon should be regarded as a fossil alga.

Thallograptus Ruedemann, 1925b, p. 35 [**Dendrograptus? succulentus* Ruedemann, 1904; OD] [*non Thallograptus* Öpik, 1928, p. 35 (type, *T. sphaericola,* OD [Wimanicrustidae, Graptolithina]); =*Hormograptus* Öpik, 1930 (Wimanicrustidae)]. Ruedemann (1925b) discussed a close similarity in shape to marine algae and reported that the thecal apertures appear as pores on the surface. Hewitt and Birker (1986) discussed the type specimens of *Buthotrephis grantii* Dawson, 1890 and *Inocaulis vegetabilis* Gurley in Bassler, 1909 from the Silurian Eramosa Member of the Lockport Dolomite of Ontario, Canada. Both types represent fragments of a single specimen referred now to *Thallograptus grantii* (Dawson, 1890) and interpreted as a possible alga, supporting the algal origin of some but not all taxa referred to the genus *Thallograptus* in the past. Bulman (1970) interpreted *Thallograptus* as a member of the Acanthograptidae

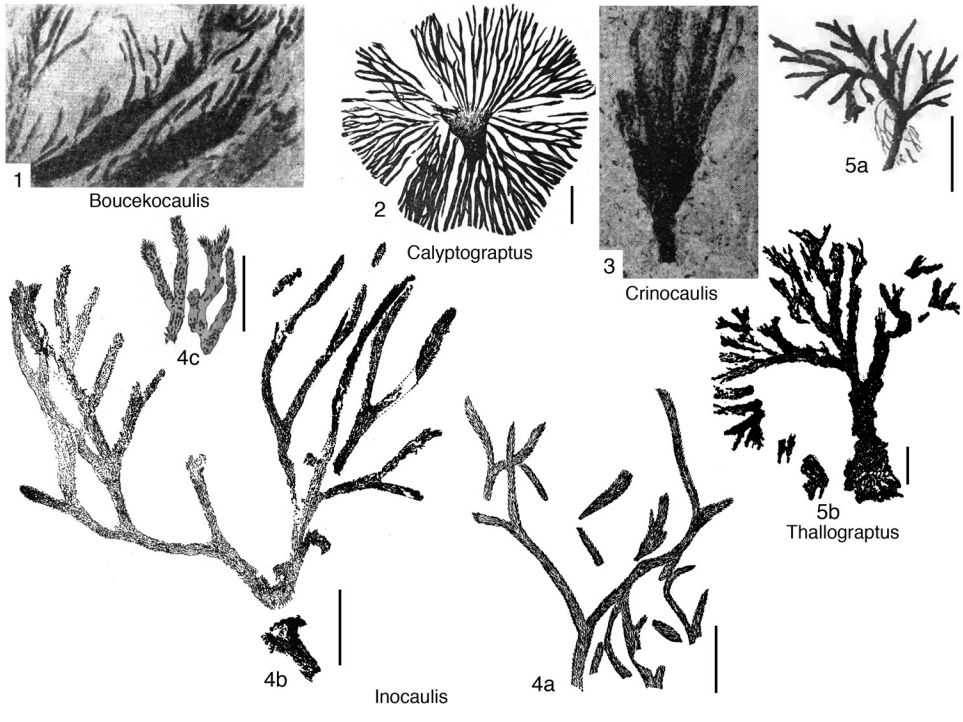


FIG. 310. Possible algae identified as graptolites (p. 470–471).

(now Callograptidae). Many taxa assigned to the genus in the past may need to be re-evaluated and referred to other genera of the Callograptidae.—— Fig. 310,*5a*. **T. succulentus* (RUEDEMANN), syntype, scale bar, 10 mm (Ruedemann, 1904, pl. 4,*4*).—— FIG. 310,*5b*. *T. phycoides* (SPENCER, 1884), specimen illustrated as *Thallograptus cervicornis* in BULMAN (1970, fig. 22,*2*). RUEDEMANN (1925b, fig. 23) illustrated the specimen as characteristic of the genus *Thallograptus*, scale bar, 10 mm.

LAND PLANTS

It should not be forgotten, that Rudolf HUNDT identified graptolite remains as early land plants. HUNDT (1949d, fig. 29) illustrated fragments of a biserial graptolite as "*Praerhynia* spec. Sporangien" and re-illustrated the specimen as *Triplograptus triangulatus* HUNDT in HUNDT (1965). Also, material he identified as *Baragwanathia oelheyi* HUNDT, 1952b (HUNDT, 1952b, fig. 30) might represent graptolite fragments. Uncertain fossils are also the "Praepsilophyten mit Sporangien" (HUNDT, 1952a). Unfortunately, the material illustrated by HUNDT in these papers has not been identified in his collection.

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