TREATISE ON
INVERTEBRATE PALEONTOLOGY

Part T

ECHINODERMATA 2

Revised

Crinoidea

Volume 3

by HANS HESS and CHARLES G. MESSING

WILLIAM I. AUSICH
Coordinating Author

Prepared under Sponsorship of

The Paleontological Society
The Palaeontographical Society
SEPM (Society for Sedimentary Geology)
The Palaeontological Association

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THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL INSTITUTE
LAWRENCE, KANSAS
2011

Library of Congress Catalogue Card Number 53-12913
ISBN 978-0-9833599-1-3

Distributed by the Paleontological Institute, The University of Kansas, 1475 Jayhawk Blvd., Room 119, Lawrence, Kansas 66045-7594, USA, www.paleo.ku.edu, from which current price lists of parts in print may be obtained and to which all orders and related correspondence should be directed. Editorial office of the *Treatise:* Paleontological Institute, The University of Kansas, 1475 Jayhawk Blvd., Room 119, Lawrence, Kansas 66045-7594, USA, www.paleo.ku.edu.

Citation information: Selden, P. A., ed. 2011. Treatise on Invertebrate Paleontology. Part T, Echinodermata 2, Revised, Crinoidea, vol. 3. The University of Kansas Paleontological Institute. Lawrence, Kansas. xxix + 261 p., 112 fig.

The *Treatise on Invertebrate Paleontology* has been made possible by (1) funding principally from the National Science Foundation of the United States in its early stages, from The Geological Society of America through the bequest of Richard Alexander Fullerton Penrose, Jr., and from The Kansas University Endowment Association through the bequest of Raymond C. and Lillian B. Moore; (2) contribution of the knowledge and labor of specialists throughout the world, working in cooperation under sponsorship of the Paleontological Society, the SEPM (Society for Sedimentary Geology), the Palaeontographical Society, and the Palaeontological Association; (3) acceptance by The University of Kansas of publication without any financial gain to the University; and (4) generous contributions by our individual and corporate sponsors.

PART T
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Revised
CRINOIDEA, vol. 3

By HANS HESS and CHARLES G. MESSING
WILLIAM I. AUSICH, Coordinating Author

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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 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 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.

Part O, Revised. ARTHROPODA 1 (Trilobita: Introduction, Order Agnostida, Order Redlichiida), xxiv + 530 p., 309 fig., 1997.

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 U. ECHINODERMATA 3 (Asterozoans, Echinozoans), xxx + 695 p., 534 fig., 1966.

Part V. GRAPTOLITHINA, xvii + 101 p., 72 fig., 1955.

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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.

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Part T, Revised. ECHINODERMATA 2 (Crinoidea), Volume 3. xxix + 261 p., 112 fig.

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 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 V, Revised. GRAPTOLITHINA.
Part W, Revised. TRACE FOSSILS.

EDITORIAL PREFACE

Paul A. Selden
[The University of Kansas]

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 T, Echinodermata 2, Crinoidea, Revised, Volume 3, is an exception to recent trends and has been prepared by two authors: Hans Hess and Charles Messing, and guided by Coordinating Author William Ausich. 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 1999 in the *International Code of Zoological Nomenclature,* hereinafter referred to as the *Code,* provide procedures for answering such questions. The prime objective of the *Code* is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding unwarranted restrictions on freedom of thought and action of systematists. Priority of names is a basic principle of the *Code;* but, under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Commission, ever aware of the changing needs of systematists, revised the *Code* in 1999 to enhance further nomenclatorial stability, specifying that the revised *Code* should take effect at the start of 2000. Among other requirements, the revised *Code* is clear in Chapter 14 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 upon all systematists, therefore, at the outset of their work to pay careful attention to the *Code* to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise,* especially in this volume. Terminology is explained, and examples are given of the style employed in the nomenclatorial parts of the systematic descriptions.

GROUPS OF TAXONOMIC CATEGORIES

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

FORMS OF NAMES

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

ORIGINAL SPELLINGS

If the first form of a name to be published is consistent and unambiguous, the original is defined as correct unless it contravenes some stipulation of the *Code* (Articles 11, 27 to 31, and 34) or unless the original publication contains clear evidence of an inadvertent error in the sense of the *Code,* or, among names belonging to the family-group, unless correction of the termination or the stem of the type genus is required. An original spelling that fails to meet these requirements 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 are classifiable into groups that have been recognized in previous volumes of the *Treatise,* although not explicitly differentiated in the *Code.* Among names that are available, these groups include inviolate names, perfect names, imperfect names, vain names, transferred names, improved or corrected names, substitute names, and conserved names. Kinds of unavailable names include naked names (see *nomina nuda* below), denied names, impermissible names, null names, and forgotten names.

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the *Code,* which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition, or indication (*Code,* Article 12) and names published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen novum*) of a preexisting available name (*Code,* Article 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 upon which the preparation of massive, electronic databases is predicated.

GENUS-GROUP NAMES

Conditions warranting change of the originally published, valid form of generic and subgeneric names are sufficiently rare that lengthy discussion is unnecessary. Only elimination of diacritical marks and hyphens in some names in this category and replacement of homonyms seem to furnish basis for valid emendation. Many names that formerly were regarded as homonyms are no longer so regarded, because two names that differ only by a single letter or in original publication by the presence of a diacritical mark in one are now construed to be entirely distinct (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 established 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 stemof 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,* since 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 -idae or -inae, which terminations are reserved for family-group taxa. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (*e.g.,* order Decapoda LATREILLE, 1803, crustaceans, and order Decapoda LEACH, 1818, cephalopods; suborder Chonetoidea MUIR-WOOD, 1955, and genus *Chonetoidea* JONES, 1928). Worthy of notice is the classificatory and nomenclatorial distinction between suprafamilial and family-group taxa that, respectively, are named from the same type genus, since one is not considered to be transferable to the other (*e.g.,* suborder Bellerophontina ULRICH & SCOFIELD, 1897 is not coordinate with superfamily Bellerophontacea MCCOY, 1851 or family Bellerophontidae MCCOY, 1851).

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

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

Order CORYNEXOCHIDA
Kobayashi, 1935

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

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

Order DISPARIDA
Moore & Laudon, 1943

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

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

Order HYBOCRINIDA
Jaekel, 1918

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

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

Subclass ENDOCERATOIDEA
Teichert, 1933

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

Order ENDOCERIDA
Teichert, 1933

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

TAXONOMIC EMENDATION

Emendation has two distinct meanings as regards zoological nomenclature. These are alteration of a name itself in various ways for various reasons, as has been reviewed, and alteration of the taxonomic scope or concept for which a name is used. The *Code* (Article 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.].

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

OTHER EDITORIAL MATTERS

BIOGEOGRAPHY

Purists, *Treatise* editors among them, would like nothing better than a stable world with a stable geography that makes possible a stable biogeographical classification. Global events of the past few years have shown how rapidly geography can change, and in all likelihood we have not seen the last of such change as new, so-called republics continue to spring up all over the globe. One expects confusion among readers in the future as they try to decipher such geographical terms as 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 have used *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 a Chinese author has used in each of his publications rather than attempting to adopt a common spelling of an author's name to be used in all citations of his work. It is entirely possible, therefore, that the publications of a Chinese author may be listed in more than one place under more than one name in the bibliography.

Second, most but by no means all Chinese list their family name first followed by given names. People with Chinese names who study in the West, however, often reverse the order, putting the family name last as is the Western custom. Thus, for example, Dr. Yi-Maw Chang, formerly of the staff of the Paleontological Institute, was Chang Yi-Maw when he lived in Taiwan. When he came to America, he became Yi-Maw Chang. In the *Treatise,* authors' names are used in the text and listed in the references as they appear in the source being cited.

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 ranges of taxa listed in the systematic descriptions herein have been compiled from the ranges of lower taxa. In all instances, we have used the *range-through* method of describing ranges. In instances, therefore, where the work of paleontology is not yet finished, some ranges of higher taxa will not show gaps between the ranges of their subtaxa and may seem to be more complete than the data warrant.

ACKNOWLEDGMENTS

The Paleontological Institute's Assistant Editor, Jill Hardesty has faced admirably the formidable task of moving this volume through the various stages of editing and into production. In this she has been ably assisted by other members of the editorial team, including Denise Mayse, Office Manager, with her excellent attention to detail while checking the references and various other items, and Mike Cormack with his outstanding computer skills. Three students also worked very hard on this volume: Sarah Jensen and James Lamsdell helped prepare figures, and Amanda Parker helped with checking and formatting references.

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. I am indebted to them for preparing earlier prefaces and for the leadership they have provided in bringing the *Treatise* project to its present status.

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Paul A. Selden
Lawrence, Kansas
May 16, 2011

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well established throughout the world, but minor divisions (e.g., subseries, stages, and substages) are more likely to be provincial in application. The stratigraphic units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to the revision of Part T (any provincial terms are presented in brackets in taxonomic descriptions). They are adapted from the International Stratigraphic Chart, compiled by the International Commission on Stratigraphy (ICS; ©2009).

- **Cenozoic Erathem**
  - **Quaternary System**
    - Holocene Series
    - Pleistocene Series
  - **Neogene System**
    - Pliocene Series
    - Miocene Series
  - **Paleogene System**
    - Oligocene Series
    - Eocene Series
    - Paleocene Series
- **Mesozoic Erathem**
  - **Cretaceous System**
    - Upper Cretaceous Series
    - Lower Cretaceous Series
  - **Jurassic System**
    - Upper Jurassic Series
    - Middle Jurassic Series
    - Lower Jurassic Series
  - **Triassic System**
    - Upper Triassic Series
    - Middle Triassic Series
    - Lower Triassic Series
- **Paleozoic Erathem**
  - **Permian System**
    - Lopingian Series
    - Guadalupian Series
    - Cisuralian Series
  - **Carboniferous System**
    - Pennsylvanian Series
      - Gzhelian Stage
      - Kasimovian Stage
      - Moscovian Stage
      - Bashkirian Stage
    - Mississippian Series
      - Serpukhovian Stage
      - Visean Stage
      - Tournaisian Stage
  - **Devonian System**
    - Upper Devonian Series
    - Middle Devonian Series
    - Lower Devonian Series
  - **Silurian System**
    - Pridoli Series
    - Ludlow Series
    - Wenlock Series
    - Llandovery Series
  - **Ordovician System**
    - Upper Ordovician Series
    - Middle Ordovician Series
    - Lower Ordovician Series
  - **Cambrian System**
    - Furongian Series
    - Series 3
    - Series 2
    - Terreneuvian Series

AUTHOR'S PREFACE

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1978 saw the publication of the 3 volumes on the Crinoidea. Volume 3 dealt with the post-Paleozoic and living forms, grouped in the subclass Articulata. This volume was written by H. Wienberg Rasmussen, with input on classification by Hertha Sieverts-Doreck. Since then, knowledge on both fossil and living forms has progressed enormously. Two developments merit special attention. (1) In the 1978 edition, the Triassic forms led a modest existence. *Encrinus liliiformis,* one of the most common and popular crinoids, was listed with a Paleozoic clade in Volume 2, and relationships with related taxa were not discussed. This has greatly changed, largely due to the work of Hans Hagdorn. (2) The advent of SCUBA diving, but especially the ever-increasing use of deep-sea submersibles, has led to a continuing increase in knowledge of stalked crinoids from the deep sea. As a consequence, the present revision contains much additional information on living forms that are diagnosed and illustrated accordingly.

More than ten years ago, William I. Ausich asked if I would cooperate on the revision of the crinoid *Treatise.* Being an amateur paleontologist, I agreed to undertake this difficult task only with the agreement of Charles G. Messing to coauthor the section on comatulids, the living representatives of which constitute nearly half the genera of Articulata. Needless to say, the task was immensely helped by the excellent collaboration of the editors.

As in other fossil groups, a cladistic approach for classification could not be applied for this volume. The reasons for this are manyfold: (1) many taxa are based on fragmentary material, greatly restricting the choice of characters; (2) convergent development and intraspecific variability is common in certain environments that are rich in crinoid remains; (3) scarcity of specimens prevents ontogenetic studies and recognition of heterochronies. Nevertheless, molecular studies on some living forms are now available and are discussed in the present volume. It may be expected that molecular phylogenetic studies on living forms will be of increasing importance for classification of related fossil taxa.

DEDICATION

The present volume is dedicated to the memory of H. Wienberg Rasmussen.

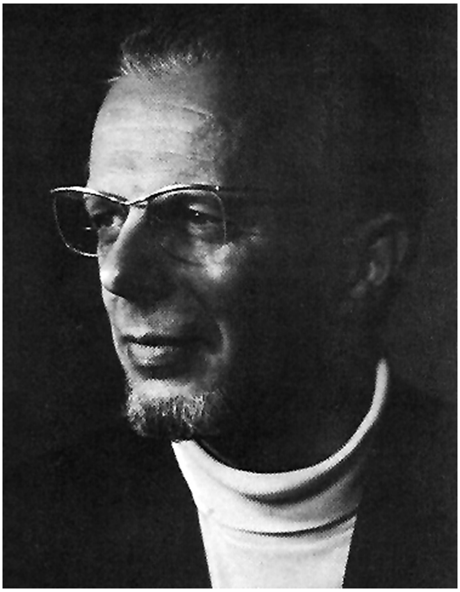
HENNING WIENBERG RASMUSSEN

June 20, 1920–June 27, 1980
(based on an article by Flores & Koch, 1984)

Henning Wienberg Rasmussen was born in Silkeborg, Denmark, the son of a master cabinetmaker. He died in Copenhagen. He attended school in Silkeborg and studied geology at the University of Copenhagen, where he received his doctorate in 1950, with a thesis on Cretaceous Asteroidea and Ophiuroidea. During his studies, he did field work with the Geological Survey of Denmark and was an assistant at the Mineralogical Museum of Copenhagen University. In the summer of 1946, he participated in an expedition to eastern Greenland with the Geological Survey of Greenland. In 1949, he was employed as university instructor at the Mineralogical Museum of the University of Copenhagen. He began teaching field courses at Mols (especially on the Quarternary), and later he taught evolution. From 1961 to 1966, he held a lectureship in geology, and from 1966 to 1972, his lectorship was in invertebrate paleontology. H. Wienberg Rasmussen was a good-humored and inspiring teacher.

He was a passionate paleontologist, collecting large numbers of fossils, which he described in compendia and textbooks, such as *Danmarks Geologi and Palæontologi—Fossile invertebrater* (Rasmussen, 1969). He also wrote popular science books and articles, and he translated and adapted foreign popular science books for Danish readers. He was an encyclopedia assistant for geological issues, an editorial committee member, and an author for the great work *Danmarks Natur*. His scientific career began with the study of Foraminifera. His study of echinoderms began with his thesis. In 1961, his monumental monograph on the Cretaceous Crinoidea was published (Rasmussen, 1961). This paper was followed in 1972 by an important paper on Paleogene echinoderms from northern Europe and Greenland (Rasmussen, 1972a). Last, but not least, he wrote the volume on Articulata of the crinoid *Treatise on Invertebrate Paleontology* (Part T) that appeared in 1978 (Rasmussen, 1978).

H. Wienberg Rasmussen was a kind person, liked by all who knew him. His work was outstanding for its accuracy and clarity. The present revision would have been much more difficult without the foundation he laid. He saw himself as a disciple of Christian Poulsen and Theodor Mortensen, of echinoid fame. He greatly admired the work of Charles Darwin, who was his lifelong inspiration.



H. Wienberg Rasmussen, 1920–1980 (courtesy of the *Bulletin of the Danish Geological Society*).

ACKNOWLEDGMENTS

I wish to thank H. Hagdorn for his invaluable contributions to Triassic crinoids, including photographs. C. G. Messing reviewed the whole manuscript and coauthored the section on Comatulidina; his profound knowledge of extant forms was essential for proper treatment of these taxonomically difficult animals. M. Roux contributed his extensive knowledge of Hyocrinida to this section. Photographs were kindly provided by N. Améziane, D. Berthet, C. Bright, L. Cavin, C. N. Ciampaglio, N. Hauschke, J. W. M. Jagt, S. L. Jakobsen, A. Kroh, C. Neumann, M. Nose, J.-M. Pacaud, A. Prieur, A. Schumacher, H. Thybo, A. Smith, and A. Weissmüller. Parts of the manuscript were reviewed by S. K. Donovan (Bourgueticrinina); J. W. M. Jagt (Isocrinina, Comatulidina, Roveacrinida); B. Ferré (Roveacrinida); M. Jäger (various taxa); T. Oji (Isocrinina); M. J. Simms (Isocrinina); and J. Žítt (Cyrtocrinida). A. N. Mironov provided information on Bourgueticrinina and Hyocrinida, with translations by S. Rhoznov; M. A. Salamon helped with some Russian texts. Information on specimens was furnished by N. Améziane, G. Breton, C. Bright, A. Cabrinovic, L. Cavin, G. Dietl, M. Florence, G. Heumann, M. Kölbl-Ebert, A. Kroh, D. Levin, R. Marchant, A. N. Mironov, J. Nebelsick, C. Neumann, J.-M. Pacaud, G. Pavy, D. Pemberton, A. Prieur, E. Robert, G. Schweigert, A. Smith, F. Stiller, N. Voss, and W. Weitschat. The author is greatly indebted to William I. Ausich for his critical review and editing of the manuscript. Special thanks are due to Jill Hardesty for her meticulous editing of the final volume.

REPOSITORIES AND THEIR ABBREVIATIONS

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

AK: Auckland War Memorial Museum, Auckland, New Zealand
AM, AMF: Australian Museum, Sydney, Australia
AMNH: American Museum of Natural History, New York, USA
ANU: Australian National University, Canberra, Australia
AU: Geology Department, Auckland University, Auckland, Australia
Auxerre Coll.: Collection ville d'Auxerre, France
BAU: Buenos Aires University, Buenos Aires, Argentina
BGS, GSM, IGS: British Geological Survey (formerly Geological Survey Museum; Institute of Geological Sciences, London) Keyworth, Nottinghamshire, United Kingdom
Bishop Museum: Bishop Museum, Oahu, Hawaii, USA
BMNH: The Natural History Museum, London, United Kingdom [formerly British Museum (Natural History)]
BMR: see CPC
Br: see TAGI Br
BSM: Bavarian State Museum, Munich, Germany
BSP: Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
BU: Department of Geology, Birmingham University, Birmingham, United Kingdom
BUM: Bristol University Museum, Bristol, United Kingdom
CAGS: Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China
CAMSM: Sedgwick Museum, Cambridge, England
CAS: California Academy of Sciences, Types Collections, San Francisco, California, USA
CB: Muséum d'Histoire Naturelle, Geneva, Switzerland
CEGH: see CORD-PZ
CFP UA: Compagnie Française Petroles, Paris, France
CGS: Czech Geological Survey, Prague, Czech Republic
CIGMR: Chengdu Institute of Geology and Mineral Resources, Chengdu, China
CKB: Collection Walter Koch, Grossenlüder-Bimbach, Germany
CM: Zoological Museum, Copenhagen, Denmark
CMB: City Museum and Art Gallery, Bristol, UK
CMNH: Carnegie Museum, Pittsburgh, USA
CNIGR: Central Scientific Geological Exploration Museum (Tschernyshev Museum), St. Petersburg, Russia
CORD-PZ: Universidad Nacional de Córdoba, Argentina
CPC: Commonwealth Palaeontological Collections, Australian Geological Survey Organisation, Canberra, Australia
CRMGE: Central Research Museum of Geological Explorations, St. Petersburg, Russia
CRRF: Coral Reef Research Foundation, Koror, Palau
CSG: Collection Manfred Schulz, Grossenlüder, Germany
D, EM, ENSM, FSI, FSL, SSL, TA: Université Claude Bernard, Lyon I, Villeurbanne, France
DNGM: Servicio Nacional Minero Geológico, Buenos Aires, Argentina
DP, DPO: Departamento de Geología, Oviedo University, Oviedo, Spain
DPO: see DP
DPUCM: Departamento de Paleontologia, Universidad Complutense, Madrid, Spain
EM: Ecole des Mines, Université Claude Bernard Lyon, France
EM: see D
ENSM: see D
ETH: Erdwissenschaftliche Sammlungen der ETH, Zürich, Switzerland
FD: Geological College of Eastern China, Fuzhou, China
FGM: Fakse Geological Museum, Denmark
FSI: see D
FSL: see D
GB: Xian Institute of Geology and Mineral Resources, Xian, China
GBA: Geologische Bundesanstalt Museum, Vienna, Austria
GIB: Geological Institute, Bonn, Germany
GIBAS: Geological Institute, Bulgarian Academy of Sciences, Sofia, Bulgaria
GIN KAZ: Institute of Geology, Kazakh Academy of Sciences, Alma-Ata, Kazakhstan
GIN TAD: Institute of Geology, Dushanbe, Tadzhikistan
GIN UZ: Institute of Geology, Uzbek Academy of Sciences, Tashkent, Uzbekistan
GIP: Geological Institute of the Czech Academy of Sciences, Prague, Czech Republic
GIUS: Laboratory of Paleontology and Stratigraphy, Department of Earth Sciences, Silesian University, Sosnowiec, Poland
GLAHM: Hunterian Museum, Glasgow University, Scotland, United Kingdom
GMC, IV: Geological Museum of China, Beijing, China
GMG: State Museum of Georgia (named after S. N. Djanashia), Academy of Sciences of the Georgian SSR, Tbilisi
GMUT: see TUG
GM YaRGTS: Geological Museum of the Regional Geological Centre, Yakutsk, Yakutia
GPIBo: Palaontological Institute, Bonn, Germany
GPI Kiel: Geologisch-Paläontologisches Institut der Universität Kiel, Germany

GPIT: Institut für Geowissenschaften, Tübingen, Germany
GPZ: Department of Geology and Palaeontology, Zagreb, Croatia
Grenoble: Collections géologiques, Observatoire des Sciences, Université Joseph Fournier, Grenoble, France
GSC: Geological Survey of Canada, Ottawa, Ontario, Canada
GSE: see IGS GSE
GSI: Geological Survey of India, Calcutta, India
GSM: see BGS
GSQ: Geological Survey, Queensland, Australia
GSV: Geological Survey of Victoria, Australia
GSWA: Geological Survey of Western Australia, Perth, Australia
GS YA: see CGS
GZG: Geowissenschaftliches Zentrum der Universität Göttingen, Germany
Hamburg: Geologisch-Paläontologisches Institut, Universität Hamburg, Germany
Hauff: Hauff Museum, Holzmaden, Germany
HB: Bureau of Geology and Mineral Resources of Hunan Province, Hunan, China
HGD: Geologisch-Paläontologisches Institut der Universität Heidelberg, Germany
HGI: Hungarian Geological Institut, Budapest, Hungary
HIGS: Hangzhou Institute for Geological Science, Hangzhou, China
HM: see GLAHM
HNHMB: Hungarian Natural History Museum, Budapest, Hungary
HUB: see MB
I: New York State Geological Survey, Albany, New York, USA
ICPSB: Institute of Geology, University of Padua, Italy
IG: Palaeontological Collections of L'Institut Royal des Sciences Naturelles de Belgique, Brussels
IGAS: Institute of Geology, Chinese Academy of Sciences, Beijing, China
IGiG: Institute of Geology and Geophysics, Siberian Branch, Academy of Sciences, Akademgorodok, Russia
IGM: Instituto de Geología, Universidad Autónoma de México, Ciudad Univesitaria, México City, Mexico
IGN: Institute of Geological Sciences, Kiev, Ukraine
IGNA: Geological Museum of the Institute of Geological Sciences, Almaty, Kazakhstan
IGN SO RAN: Geological Museum of the Institute of Geological Sciences of Yakutia Sakha Scientific Centre, Siberian Division, Russian Academy of Sciences, Yakutsk, Yakutia
IGPT: Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany
IGR: Institute of Geology, University of Rennes, Rennes, France
IGS GSE: Institute of Geological Sciences, Edinburgh, United Kingdom
IGS GSM: see BGS
IMGPT: Geological-Paleontological Institute and Museum of Tübingen University, Germany
Inst. Geol.: Geological Institute, Bishkek, Kyrgyzstan
IO: P. P. Shirshov Institute of Oceanology, Moscow, Russia
IOAS: Institute of Oceanology, Academia Sinica, Qingdao, China
IO RAS: Instutute of Oceanology, Russian Academy of Sciences, Moscow
IPB: Institut für Paläontologie der Universität Bonn, Germany
IPW: Institut für Paläontologie der Universität (Geozentrum), Vienna, Austria
IRScNB: Palaeontological Collections of L'Institut Royal des Sciences Naturelles de Belgique, Brussels
IV: see GMC
JCF: James Cook University, Townsville, Queensland, Australia
JME: Jura Museum, Eichstätt, Germany
KAS, MANK: Geological Museum of Institute of Geological Sciences, Almaty, Kazakhstan
KHGU: Kharkov State University, Ukraine
KIGLGU: Geology Faculty of Leningrad State University, Paleontology-Stratigraphy Museum, St. Petersburg, Russia
Kr-To: Collection Kristan-Tollmann, Senckenberg Museum, Frankfurt, Germany
L: National Museum, Prague, Czech Republic, Barrande specimens
LGE: St. Petersburg State University, St. Petersburg, Russia
LGI: Leningrad (formerly St. Petersburg) Geological Institute, Department of Structural and Sea Geology, Russia
LM: see LO
LMT: Loodus Museum, Tallinn, Estonia
LO (formerly LM): Lund University Museum, Sweden
LPB: Laboratoire de Paléontologie, Université de Bretagne Occidentale, Brest, France
LS: Linnean Society of London, United Kingdom
MANK: see KAS
MB (formerly HUB): Humboldt University, Berlin, Germany
MBHR: Museum of Dr. B. Horák, Rokycany, Czech Republic
MCA: Museo di Cortina d'Ampezzo (Coll. Zardini), Cortina d'Ampezzo, Italy
M.Ch: Museum Chabarovsk, Verkhoyan, eastern Siberia, Russia
MCMB: Department of Geology, University of Beijing, Beijing, China
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MDSGF: Museo del Dipartimento di Scienze Geolgiche dell'Università di Ferrara, Ferrara, Italy
MDTF: see MDSGF
MFLV: Museo dei Fossili della Lessinia, Verona, Italy
MFMGB: Museum of the Faculty of Mining and Geology, Belgrade University, Belgrade, Yugoslavia
MG: Institute of Geology, Ashkhabad, Turkmenistan
MGBW: Museum of the Geologische Bundesanstalt of Wien, Austria
MGL: Musée cantonal de géologie UNIL, Lausanne, Switzerland
MGRI: Moscow Geological Prospecting Institute, Moscow, Russia

MGSB: Museo Geológico del Seminario de Barcelona, Barcelona, Spain
MGU: Moscow State University, Russia
MGUH: Geological Museum, University of Copenhagen, Denmark
MGUP: Museum of Geology, University of Palermo, Sicily, Italy
MHI: Muschelkalkmuseum Hagdorn, Ingelfingen, Germany
MHNG: Muséum d'histoire naturelle de Genève, Switzerland
MHNH: Muséum d'histoire naturelle du Havre, France
MHNL: Muséum d'histoire naturelle de Lyon, France
MIP: see MLP
MLP: Invertebrate Paleontology Department, La Plata Natural Sciences Museum, La Plata, Argentina
MM: Geological Survey, Prague, Czech Republic
MM: Moravian Museum, Brno, Czech Republic
MMF: Geological and Mining Museum, Department of Mines, Sydney, Australia
MNB: see MB
MNHB: Museum für Naturkunde der Humboldt-Universität zu Berlin, Geologisch-Paläontologisches Museum, Germany
MNHN: Muséum National d'Histoire Naturelle, Paris, France
MONZ: see NMNZ
MPL: see MLP
MPM: Milwaukee Public Museum, Milwaukee, Wisconsin, USA
MPUM: Museo di Paleontologia del Dipartimento di Scienze della Terra dell'Università degli Studi di Milano, Italy
MRC: Museo Regoles Cortina d'Ampezzo, Italy
MUGT: see GIN TAD
Muz IG: Geological Museum of the Geological Institute, Warsaw, Poland
MV: see NMVP
NCSM: North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA
NHM: Natural History Museum, London, UK
NHMB: Natural History Museum, Basel, Switzerland (Naturhistorisches Museum Basel)
NHMM: Natuurhistorisch Museum Maastricht, the Netherlands
NHMW: Natural History Museum in Vienna, Naturhistorisches Museum, Wien, Austria
NIGP, NIGPAS: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NIWA: National Institute of Water and Atmosphere, Wellington, New Zealand
NLfB: Niedersächsisches Landesamt für Bodenforschung, Hannover, Germany
NM: National Museum, Prague, Czech Republic
NMB: Naturhistorisches Museum Basel, Switzerland
NMBi: Naturkundemuseum Bielefeld, Germany
NMC: Naturkundemuseum Coburg, Germany
NMING: National Museum of Ireland, Dublin, Ireland
NMNH: Newfoundland Museum of Natural History, Canada
NMNZ: Te Papa, Museum of New Zealand, Wellington, New Zealand
NMVP: Victoria Museum, Melbourne, Victoria, Australia
NMV P: Department of Invertebrate Palaeontology, Museum of Victoria, Australia
NMW: National Museum of Wales, Cardiff, United Kingdom
NS: Northeastern Institute of Geology, Inner Mongolia
NSM: National Science Museum, Tokyo, Japan
NSU: Nova Southeastern University Oceanographic Center, Dania Beach, Florida, USA
NUF: Department of Geology, University of Newcastle, New South Wales, Australia
NYSM: New York State Museum, Albany, USA
NZGS: New Zealand Geological Survey, Lower Hutt, New Zealand (presently called Institute of Geological and Nuclear Sciences)
NZOI: New Zealand Oceanographic Institute, National Institute of Water and Atmospheric Research, Wellington, New Zealand
OKGS: Oklahoma Geological Survey, Norman, Oklahoma, USA
OMR: District Museum, Rokycany, Czech Republic
OMR VH: see OMR
OSU: Orton Geological Museum, Ohio State University, Columbus, Ohio, USA
OU: University of Oklahoma, Norman, USA
OUM: Oxford University Museum, United Kingdom
OU NZ: Geology Department, Otago University, Dunedin, New Zealand
PAN: see PIN
PCZCU: Department of Biology, Západočeská univerzita, Plzeň, Czech Republic
PIN: Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia
PIN RAS: see PIN
PIW: Paleontological Institute, Würzburg University, Würzburg, Germany
PKUM: Geological Museum of Beijing University, China
PM (formerly PMU): Palaeontological Museum, Uppsala University, Uppsala, Sweden
PMNUF: Paleontological Museum, University of Naples 'Federico II', Naples, Italy
PMO: Paleontologisk Museum, University of Oslo, Norway
PMU: see PM
PRI: Paleontological Research Institute, Ithaca, New York, USA
PUC: Princeton University Collections, Princeton, New Jersey, USA
PUM: Geology, Peking University, Beijing, China
QMF: Queensland Museum, South Brisbane, Australia
RCCBYU: Research Center for the Chengjiang Biota, Yunnan University, Yunnan, China
RGF VR: Institute of Regional Geology and Paleontology, Faculty of Mining and Geology, University of Belgrade, Belgrade, Serbia
RGM: Nationaal Natuurhistorisch Museum, Leiden

(formerly Rijksmuseum van Geologie en Mineralogie), the Netherlands
RM, RMS: Swedish Museum of Natural History, Stockholm, Sweden
ROM: Royal Ontario Museum, Toronto, Ontario, Canada
RSM: Royal Scottish Museum, Edinburgh, England
RX: Rowley Collection, University of Illinois, Urbana, Illinois, USA
SAM.P: South Australian Museum, Adelaide, South Australia
SBNML: National Museum, Prague, Czech Republic
SGU: Geological Survey of Sweden, Uppsala, Sweden
SIGM: Shenyang Institute of Geology and Mineral Resources, Shenyang, Liaoning, China
SM (formerly SMA): Sedgwick Museum, University of Cambridge, United Kingdom
SMF: Senckenbergische Museum, Frankfurt, Germany
SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany
SMO: Silesian (Slezské) Museum, Opava, Czech Republic
SNM: Slovakian National Museum, Bratislava, Slovakia (Slovenské Narodné Múzeum, Bratislava)
SSL: see D
SUI: University of Iowa, Department of Geology, Iowa City, USA
SUP: Palaeontological collections, University of Sydney, New South Wales, Australia
T: Paleontological Museum, University of Naples, Naples, Italy
TA: see D
TAGI BR: Geological Museum, Institute of Geology, Tallinn Technical University, Tallinn, Estonia
TBR: see TF
TF: Geological Survey Division, Department of Mineral Resources, Bangkok, Thailand
TsGM: see CNIGR
TsNIGRA: see CNIGR
TUBr: Paläontologische Sammlung, Institut für Geowissenschaften, Universität Tübingen, Germany
TUG: Museum of Geology, University of Tartu, Tartu, Estonia
UA: University of Amsterdam Zoological Museum, Amsterdam, the Netherlands
UA: Geology Department, University of Alberta, Edmonton, Canada
UC: Field Museum of Natural History, Chicago, Illinois, USA
UCF: The University, Calgary, Canada
UCLA: University of California at Los Angeles, Los Angeles, California, USA
UCM: University of Canterbury, Christchurch, New Zealand
UCMP: University of California, Museum of Paleontology, USA
UD: University of Dijon, Dijon, France
UHR: Hokkaido University, Sapporo, Japan
UI: University of Illinois, Urbana, Illinois, USA
UJF: Université Joseph Fournier, Grenoble, France
UL: Department of Geology and Palaeontology, University of Ljubljana, Slovenia
UM: Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, USA
UM, UMC (formerly UMO): University of Missouri, Columbia, Missouri, USA
UMMF: Department of Geology, University of Montpellier, Montpellier, France
UMUT: University Museum of the University of Tokyo, Tokyo, Japan
UND: University of Notre Dame, Indiana, USA
U.N.E: University of New England, Armidale, Australia
UPS: Université de Paris-Sud, France
UQF: University of Queensland, Department of Geology, Brisbane, Australia
UR: Museo di Paleontologia, Dipartimento di Scienze della Terra, Università “La Sapienza,” Rome, Italy
USNM: United States National Museum (Smithsonian Institution), Washington, D.C., USA
UT: Department of Geology, University of Texas, Austin, Texas, USA
UTC: Department of Geology, University of Toronto, Canada
UTGD: University of Tasmania Geology Department, Hobart, Tasmania, Australia
U.W.A.: University of Western Australia, Nedlands, Western Australia
VH: see OMR
VSEGEI: Russian Geology Institute, St. Petersburg, Russia
XAGM: Xi'an Institute of Geology and Mineral Resources, Shaanxi, China
XB: Palaeontological Collections of the Xi’an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, Xi’an, Shaanxi Province, China
XIGMR: Xi’an Institute of Geology and Mineral Resources, Shaanxi, China
YaTGU: Geological Museum, Yakutsk, Yakutia
YIGM, YIGMR: Yichang Institute of Geology and Mineral Resources, Yichang, China
YIGMR: Yichang Institute of Geology and Mineral Resources, Yichang, China
YPM: Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA
ZI: Zhejiang Institute of Geology and Mineralogy, Zhejiang, China
ZMM: Zoological Museum, Moscow State University, Moscow, Russia
ZPAL, ZPAL Br: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland

ARTICULATA: INTRODUCTION

HANS HESS

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INTRODUCTION

Articulate crinoids originated from perhaps a single form of advanced cladid that survived the end-Permian extinction event, when the crinoids were nearly driven to complete extinction. During Mesozoic times, articulates radiated extensively, producing forms that rival Paleozoic crinoids in morphological disparity, although not in generic richness and abundance. KAMMER and AUSICH (2006) reported 606 genera from the Early Devonian to Late Pennsylvanian; in comparison, articulates comprise approximately 340 genera, including 150 or so exclusively extant comatulid genera. The Mesozoic had tiny pelagic forms, classified as Roveacrinida, and extremely large pseudoplanktonic forms attached to driftwood, classified in the orders Encrinida and Isocrinida. The encrinid *Encrinus liliiformis* formed thick beds composed largely of columnals (HAGDORN, 1999a). Unique to crinoid history was the appearance during the Middle Jurassic of single species of intact, shallow-water, benthic crinoids forming thick beds or lenses composed of several generations (HESS, 1999b). In Upper Cretaceous chalk sediments, lenses contain intact colonies of the large, stalkless *Uintacrinus* (HESS, 1999d). In contrast, the highly variable and at times bizarre-looking cyrtocrinids colonized hardgrounds and lived under conditions of slow sedimentation. Cyrtocrinids are hardly ever preserved intact as fossils, but a few forms still live today. The millericrinids, with some of the largest and best-known fossil articulates, are characteristic of Jurassic reefal settings. In comparison with the Mesozoic, the Cenozoic fossil record is poor in intact crinoids and is dominated by fragmentary material, composed mostly of comatulids (HESS, 1999e). During the later Paleogene, the habitat of stalked crinoids shifted from shallow to deeper water; unfortunately, deep-water sediments are nearly inaccessible to sampling. Thus, knowledge of post-Mesozoic stalked crinoids from deeper habitats, such as the delicate hyocrinids, is based largely on living forms. Today's seas are dominated by the free-moving comatulids, a group that is still diversifying and presents major unresolved taxonomic problems (MESSING, 1997).

In the present volume, eight orders are recognized (Holocrinida, Encrinida, Isocrinida, Comatulida, Millericrinida, Hyocrinida, Cyrtocrinida, and Roveacrinida). In comparison with the first crinoid *Treatise* (RASMUSSEN, 1978), much additional information is available, and many new taxa have been proposed, although many of them are based on fragmentary material. The exclusively Triassic encrinids now include 9 genera. The important cyrtocrinids first appeared during the Early Jurassic and now include 46 genera, 4 of which are living. For more information on the nearly 150 extant genera of comatulids proper (suborder Comatulidina), the reader should consult CLARK's monumental monograph (A. H. CLARK, 1915–1950; A. H. CLARK & A. M. CLARK, 1967).

Wherever possible and meaningful, new illustrations are included herein for genera described in RASMUSSEN (1978); in particular, the number of figured cup plates, brachials, and articulation facets is increased for better understanding of articulate morphology. In view of the somewhat inconsistent terminology in even recent literature, a short introductory chapter on the morphology of articulate crinoids and a glossary of terms used herein is included (p. 11).

MORPHOLOGY OF ARTICULATE CRINOIDS

Comprehensive discussions of crinoid morphology are in MOORE and TEICHERT (1978) and in Volume 1 of the ongoing *Treatise* revision. Below is a brief discussion pertinent to the present volume.

COLUMN AND ATTACHMENT

The column (syn., stem, stalk used in the term stalked crinoids) supports the cup or calyx and fixes it to the substrate. It is composed of columnals that may be circular, pentagonal, or stellate in cross section and range from low and discoidal to high and cylindrical. They may also be barrel shaped or constricted (spool shaped). Columns vary widely in length; they may consist of only a few or hundreds of columnals. A noncirriferous topmost columnal or fused topmost columnals may be enlarged and permanently attached to the cup, and then called the proximale. Some forms are unstalked, with the cup attached directly to the substrate by an expanded base. The free-living comatulids include a group of early forms, the paracomatulids, with a much-reduced column composed of a few fused pieces (see Fig. 37,*1a*), whereas all true comatulids shed all but the uppermost columnal (called centrodorsal) following a stalked postlarval stage. Columnals have an axial canal, so that the column contains a central tubular cavity with extensions of the coelom and nervous systems. Columnals are bound together by elastic ligament fibers, which occur in a characteristic pattern (muscles are absent in columns). Heteromorphic columns are composed of dissimilar columnals, commonly classifiable as nodals (with or without cirrus sockets) and internodals. The proximal column is called the proxistele, the middle part the mesistele, and the distal part the dististele. A column with different morphologies in the proxistele, mesistele, and dististele is referred to as xenomorphic column. Two or more columnals preserved united are termed pluricolumnals.

Stalked crinoids may be attached to hard substrates by an encrusting terminal disk (Fig. 1,*1*) that may be rootlike (Fig. 1,*2*). Such holdfasts occur in cyrtocrinids and millericrinids that lack cirri. Attachment by branching roots is more common in bourgueticrinids living on unconsolidated sediments or on soft bottoms (see Fig. 74*c*), and branching cirri also occur in millericrinids (Fig. 1,*3*). Stalked isocrinids are attached by cirri, flexible appendages arising at intervals from modified columnals (cirrinodals or nodals) that occur at intervals along the column. Cirri typically occur in a whorl of five around a nodal, but their number may be less. Among internodals, only infranodals can be recognized, because their two articular facets are different, a lower (distal) symplectial facet and an upper (proximal) cryptosymplectial or synostosial facet articulating to the nodal above. A noditaxis is a segment of the column including a nodal and all internodals on the proximal side until and excluding the next nodal (Fig. 1,*4*). New nodals are formed just below the cup, so the short proximal region is the immature column. Near the cup, the developing internodals are completely hidden by the nodals (Fig. 2,*1*), but internodals are successively introduced between nodals as the column matures. Proximal columnals are lower (thinner) than distal ones. The term nodal is also used in columns without cirri, where nodals (nudinodals) at regular intervals are distinguished by maximum height and/or width. Cirri attached to a centrodorsal also serve to anchor comatulids (see Fig. 44,*1a*). Cirri are attached to the nodal by a cirrus socket whose morphology may be quite distinctive. Cirrus sockets may be confined to sides of one nodal or may project onto the next columnal, occupying a notch in the supranodal. A shallow furrow on this columnal is called a cupule (Fig. 1,*4*). The central part of the socket, also called the cirral scar, may be supported by a lip and has two ligament areas separated by a transverse or fulcral ridge. The ossicles of cirri are cirrals and are connected by ligaments

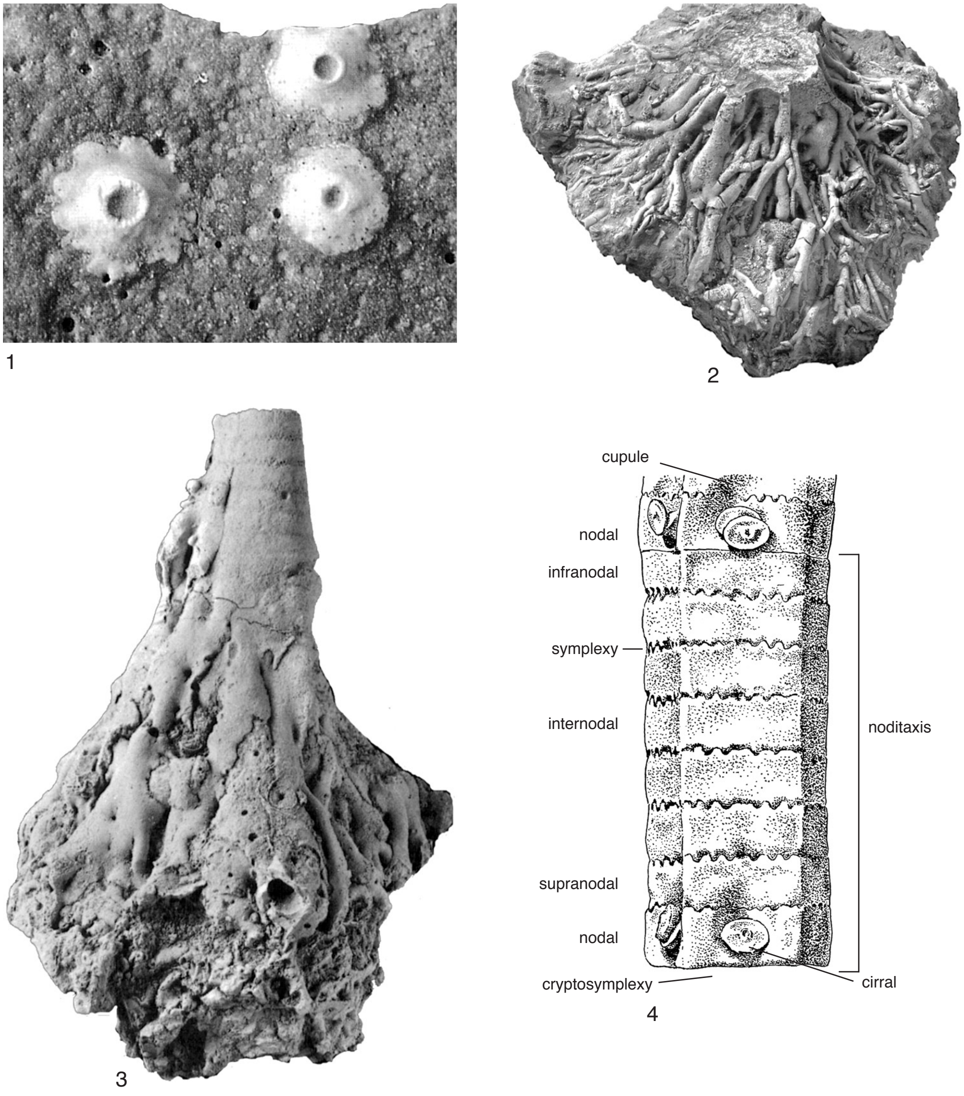

FIG. 1. *1, Carnallicrinus carnalli* (Beyrich); attachment disks on hardground with *Trypanites*, Anisian, Middle Triassic, Germany, MHI 1555/1, ×1.3 (Hagdorn, 1999b); *2, Liliocrinus munsterianus* (d'Orbigny); root previously attached to dead microsolenid coral, Oxfordian, Upper Jurassic, Switzerland, NMB M10615, ×0.3 (Hess, new); *3, Angulocrinus* sp.; root from marlstone, Oxfordian, Upper Jurassic, Switzerland, NMB M9887, ×0.75 (Hess, 1975); *4, Chariocrinus wuerttembergicus* (Oppel); lateral view of column, Bajocian, Middle Jurassic, Switzerland, NMB M9275, ×10 (Hess, 1972a).

composed of collagen fibrils. True cirri, as they occur in isocrinids and comatulids, have synarthrial articulations (Fig. 2,*2*). At each articulation, there is an adoral and an aboral ligament separated by a fulcral ridge. The cirrals are pierced by an axial canal. In living isocrinids, distal cirri are used to anchor the column. In living comatulids and isocrinids, cirri may grasp the substrate with a terminal claw or hook, aided by an opposing spine on the penultimate segment (Fig. 3,*1*).

Columnal articulations may be divided into several categories. In symplexy (adj., symplectial, also symplexial), ridges (culmina) on one joint face interlock with grooves (crenellae) on the joint face of the adjacent columnal, marked externally by crenulate suture. The combination of ridge and adjacent groove is called a crenula (pl., crenulae). Crenulae may be radially arranged as in millericrinids and cyrtocrinids; in isocrinids, the crenularium (entire area of columnal articular facet bearing crenulae) is arranged in a petaloid pattern (Fig. 2,*3*). A petal is formed by a loop of crenulae that enclose an areola of mostly droplike or elliptical shape. In describing an isocrinid crenularium, the number of crenulae refer to the lateral (radial) border of a petal. Petals are directed interradially, and adradial crenulae meet at the radius. Crenulae between petals in the interradius are called marginal crenulae. Cryptosymplexies are tight articulations of symplectial pattern but with much lower relief. They are developed between nodals and internodals of isocrinids (Fig. 2,*4a*). Breakage of the column at this juncture guarantees that segments always end with a whorl of cirri for better attachment. Breakage is facilitated by interruption of the through-going ligaments at this juncture, where the facets are held together by only short, intercolumnar ligaments (Ausich & others, 1999, fig. 12). Disintegration after death occurs more rapidly along cryptosymplexies than along symplexies, and this is the reason for the occurrence of pluricolumnals (several articulated columnals) in sediments. Synostoses are rigid and united by short ligament fibers; apposed facets are flat or shallow concave, yielding an externally straight suture. Cryptosymplexies and synostoses may be difficult to distinguish, as exemplified by articulations between nodals and infranodals (Fig. 4,*2*), where both serve as preformed rupture points. True synostoses, as defined by Moore (1978, p. 242), appear to be rare in columnals of articulate crinoids, where even flat facets have some kind of weak relief. Such facets, with marginal crenulae and inner granules, have been called zygosynostosial (Moore, 1978, p. 242). Columnal synarthries are restricted to juvenile isocrinids (see Fig. 30,*1f*), thiolliericrinids, and bourgueticrinids. The synarthry is characterized by two opposing bundles of long ligaments that are separated by a fulcral ridge. Synarthrial-type articulations are also present in the cirri. The term syzygy has been used for columnal articulations of non-isocrinid crinoids such as *Guillecrinus*, hyocrinids, and bourgueticrinids by Roux (1974, 1980a, 2002, 2004), Holland, Grimmer, and Wiegmann (1991), Bourseau and others (1991), Roux and Pawson (1999), and Améziane and Roux (2005). In these cases, ridges or tubercles of mostly dense stereom on one facet oppose the corresponding structure on the other facet (see Fig. 78,*1c;* Fig. 87,*1c*). A similar type of articulation occurs in *Cyclocrinus* (see Fig. 110,*1a,e–f*) (see also Hess, 2008, fig. 10). Herein, the term syzygy is reserved for brachial articulations. Another type of facet is developed in *Traumatocrinus,* where intercolumnal pore canals (fossulae) reach the latus, giving it a perforated appearance (see Fig. 17*g–h*).

Columnals are pierced by an axial canal with a lumen that varies in width and shape. The lumen may be surrounded by an empty space, the areola, or by a ring of smooth, granular, or vermicular surface (perilumen) (Fig. 5,*1*).

CROWN

The crown is composed of cup and arms. The cup (aboral cup, calyx) represents the link between the column (stem) and the arms and is the site of the main organs of the digestive, haemal, and nervous systems. The adoral surface of the visceral mass of the cup and proximal ossicles of the rays is called the disk, and it may be covered by a tegmen composed of small tessellate plates or a membrane studded with calcareous granules. The anal opening may be located at the apex of a small anal papilla (Fig. 3,*3*; and see Fig. 43,*3*) or on a raised cone (Fig. 2,*5;* and see Fig. 47*b*). The mouth, with its radiating ambulacra, is typically central on the disk, and the anal opening is displaced toward the

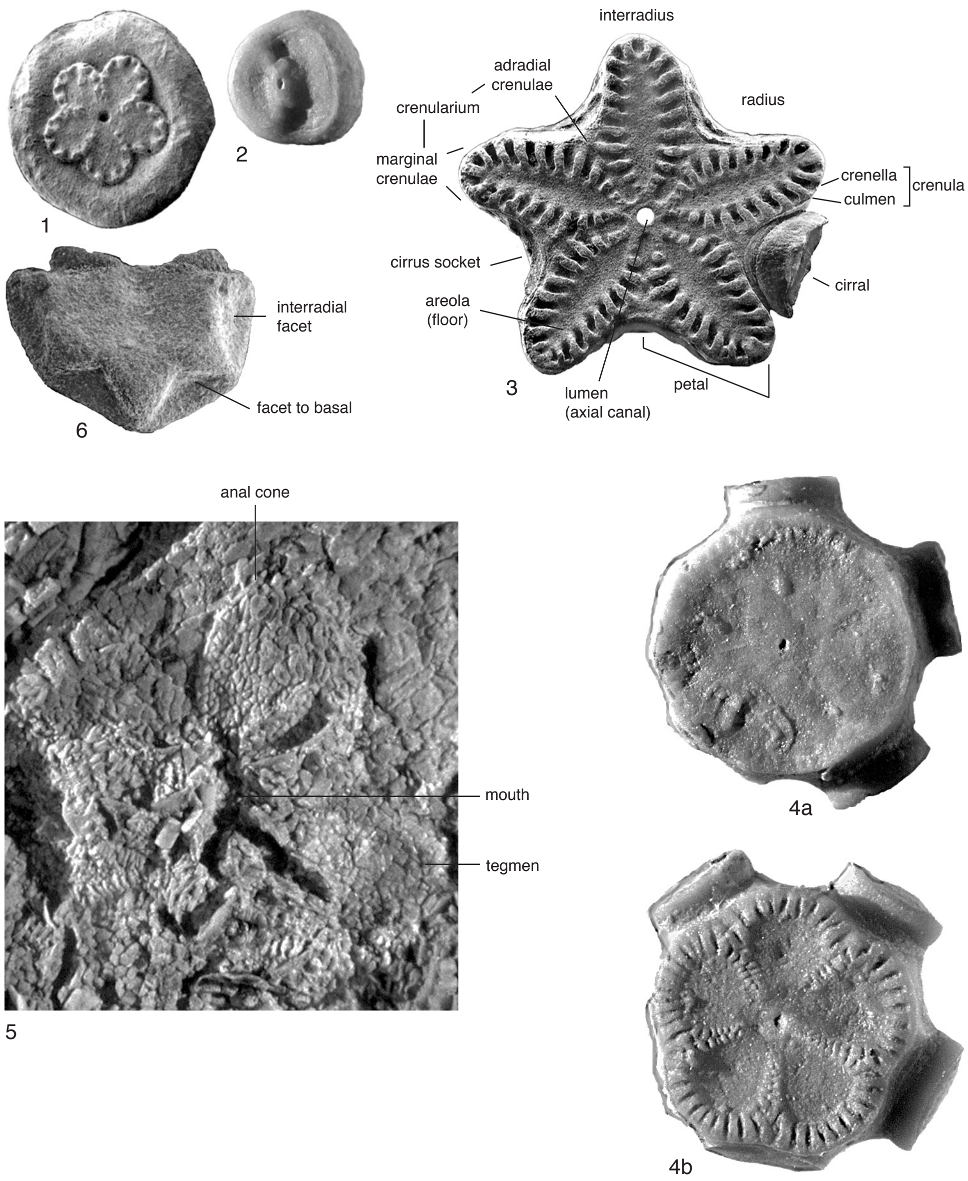

FIG. 2. *1, Encrinus liliiformis* (Lamarck), nudinodal with pentalobate internodal from proximal column, Ladinian, Middle Triassic, SMNS 26628, ×4.5 (Hagdorn, 1983); *2, Solanocrinites gresslyi* (Étallon); facet of proximal cirral, Oxfordian, Upper Jurassic, France, NMB M10621, ×5 (Hess, new); *3, Isocrinus desori* (Thurmann); proximal facet of nodal with cirral, Oxfordian, Upper Jurassic, France, NMB M10597, ×10 (Hess, 1975); *4a–b, Balanocrinus subteres* (Goldfuss); nodal with cirrals, *a,* cryptosymplectial distal facet, *b,* proximal symplectial facet, Oxfordian, Upper Jurassic, Switzerland, NMB M10613, ×5 (Hess, new); *5, Pentacrinites dargniesi* (Terquem & Jourdy), tegmen with anal cone, Bajocian, Middle Jurassic, Switzerland, NMB M10620, ×4 (Hess, new); *6, Dadocrinus gracilis* (Buch); adoral view of radial, interradial facets and facets to basals are synostosial with deep ligamentary pit, Anisian, Middle Triassic, Italy, MHI 1283/13, ×25 (Hagdorn, 1996b).

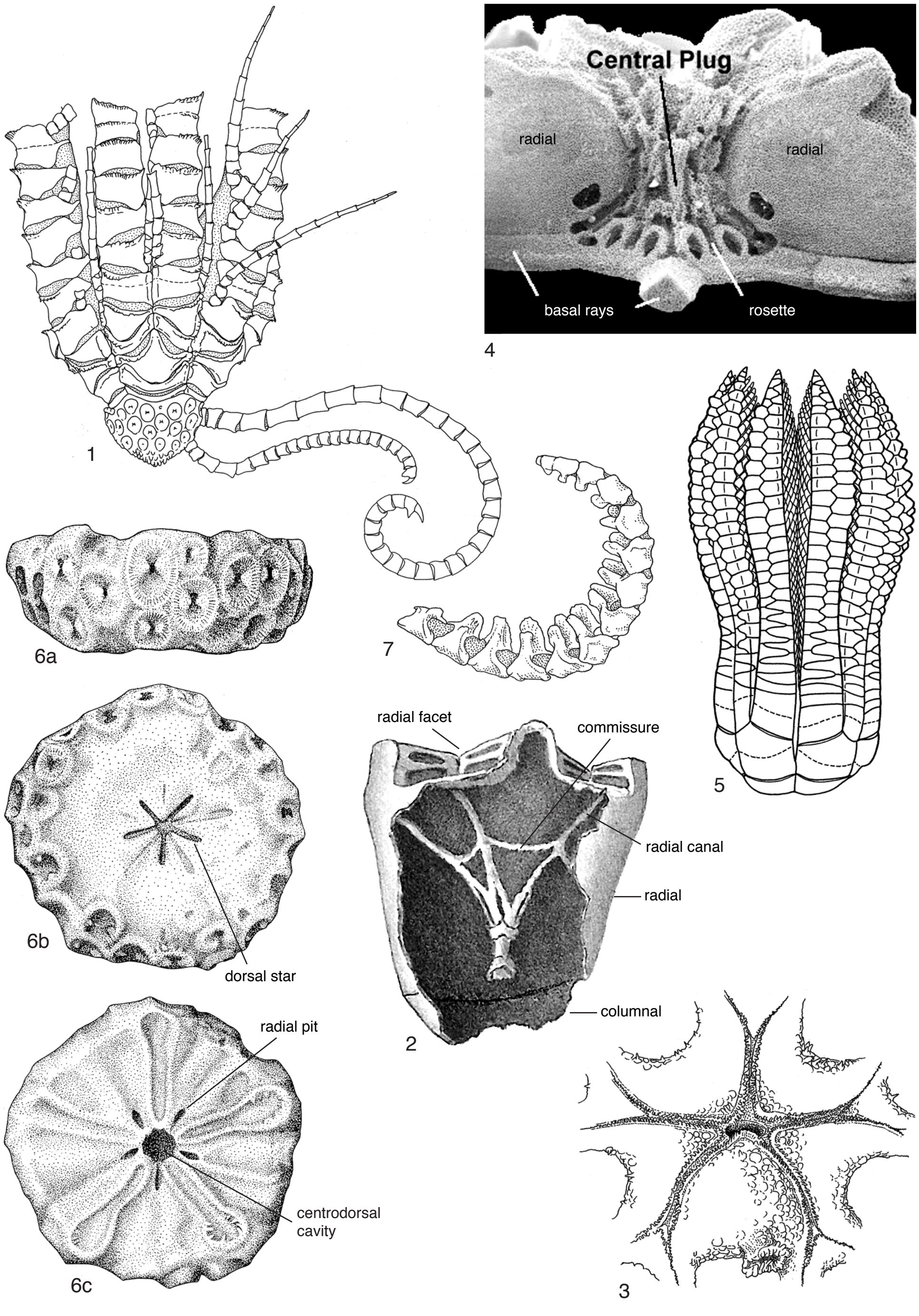

FIG. 3. *1, Trichometra cubensis* (POURTALÈS); centrodorsal, small apical and large peripheral cirrus (note opposing spine on penultimate cirral) and bases of three rays with the first three pinnules, syzygy between secundibrachials 3 and 4 and 9–10 indicated by *broken line,* Holocene, USNM, ×5 (Messing & Dearborn, 1990); *2, Eugeniacrinites cariophilites* (VON SCHLOTHEIM); partly silicified and corroded cup with nerve canals exposed, Oxfordian, Upper Jurassic,

(Continued on facing page.)

margin (Fig. 3,*3*). However, in some crinoids the anal opening may be more central and the mouth excentric (see Fig. 43,*3;* Fig. 47*b*). In its simplest form, the cup is composed of two circlets of five plates each (basals and radials) that may be fused; or alternatively, the cup may consist of only radials that may also be fused. Radials are the uppermost plates of the cup; they typically define the five-part symmetry of crinoids and give rise to the arms. Each radial represents the first, or proximalmost, ossicle of a ray. They align with the five internal water vascular canals that radiate from the ring canal that circles the esophagus. Thus, any feature associated with a radial plate or arranged in line with one has a radial orientation. Basal plates are beneath the radials. The center lines of each basal fall between radials, so the basals and anything arranged in line with them are interradial. Basals may form the base of the cup and, thus, articulate with the column (Fig. 4,*1*). In fossil comatulids, basals may be only partly visible (basal tubercle, see Fig. 40,*1a*), or they may be hidden entirely (see Fig. 41,*1d*). Basals are reduced in nearly all extant comatulids (exceptions include *Sibogacrinus*, *Atelecrinus*, and *Atopocrinus*) to a delicate internal rosette that roofs the centrodorsal cavity (Fig. 5,*2*). Five narrow, interradial rods (basal rays) may radiate from the rosette (Fig. 3,*4*); they are sometimes visible as tubercles at the proximal corners of the radials (interradial angles). Because the basals are typically reduced, the centrodorsal lies directly against and at least partly covers the five radial plates that may have a more or less exposed surface aborally. In the deep-water Atelecrinidae and in the Jaekelometridae, the basals remain a complete circlet between the centrodorsal and radials. Radial and basal ossicles are immovably joined to one another. In other crinoids, an additional circlet of plates, called infrabasal plates, may be present between the basals and the column. A cup composed of radials and basals is termed monocyclic, and a dicyclic cup is one that also has infrabasals (mono- and dicyclic refer to the one or two circlets of plates, respectively, beneath the radials). In cryptodicyclic cups, the infrabasals are hidden in the adult form or present only in immature growth stages. All of these plates are immovably joined to one another by synostosis or may even be fused. In some stalkless articulates, such as *Uintacrinus* and *Saccocoma*, the cup or calyx may contain a centrale inside the lowermost (infrabasal or basal or radial) circlet. In most articulate crinoids, the arms become free above the radials, and the cup is equivalent to the calyx. Cup plates are pierced by axial (nerve) canals. The axial canal of each ray penetrates into a radial, where it divides into two branches, one of which proceeds to the basal on the right, the other to the basal on the left. Within the radials, the axial canals of the five rays are connected to a commissural canal that generally forms a ring (ring commissure) all around the cup (Fig. 3,*2*). The position of individual rays and interrays has been designated using the position of the anus as explained by Ubaghs (1978, p. 61), but these methods are not used herein, because the anus (and corresponding plates) is rarely preserved in fossil articulates.

ARM BRANCHING

Arms are articulated to the radial plates, which form the base of a ray. Each ray consists

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Fig. 3. *Continued from facing page.*

Germany, ×4 (Jaekel, 1891); *3,* oral surface of disk of *Phanogenia gracilis* (Hartlaub), with central mouth and marginal anal papilla, Holocene, NSU, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*); *4,* lateral view of radial circlet (cut away) and basals of a comatulid, showing rosette with basal rays and central plug, enlarged (http://nova.edu/ocean/messing/crinoids); *5, Encrinus liliiformis* (Lamarck); crown with biserial brachials, Ladinian, Middle Triassic, ×0.8 (Ausich & others, 1999); *6a–c, Remesimetra discoidalis* (Gislén); centrodorsal, *a,* lateral, *b,* aboral, *c,* adoral, Cenomanian, Upper Cretaceous, Czech Republic, BMNH E14897, ×4 (Rasmussen, 1961); *7,* oral pinnule comb of *Davidaster rubiginosus* Pourtalès, oral pinnule comb with paired teeth, Holocene, NSU, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Soceity of Washington*).

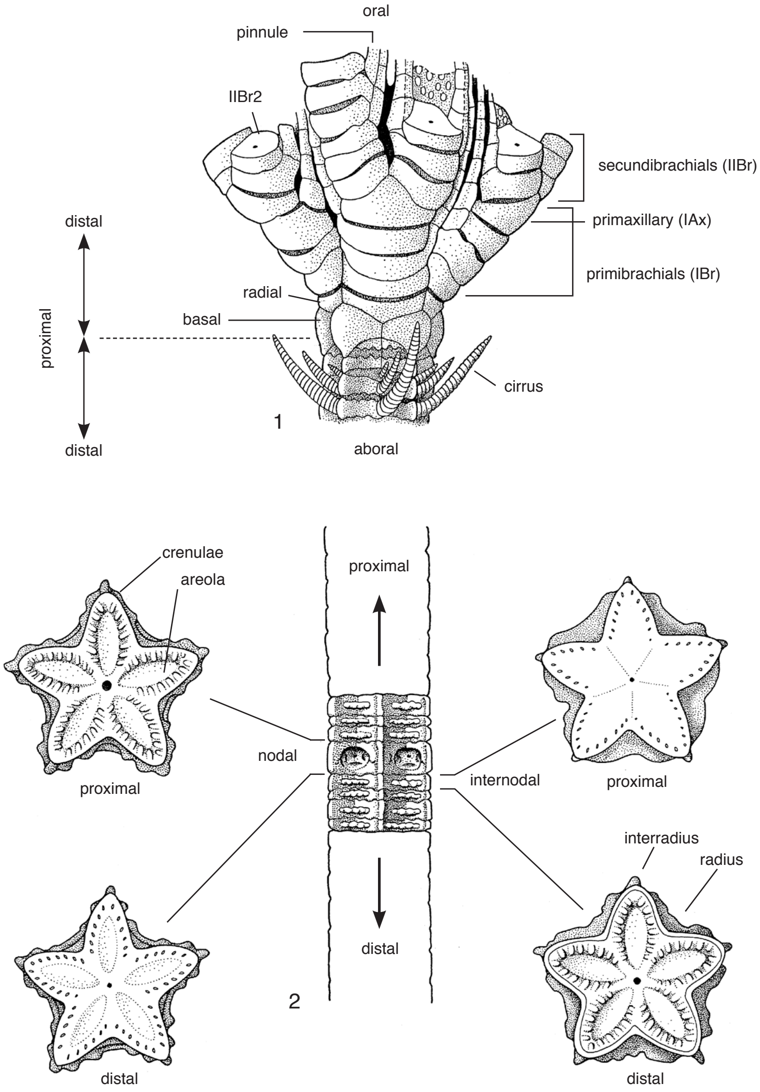

FIG. 4. *1, Metacrinus angulatus* CARPENTER; proximal column, cup, and base of crown, Holocene, ×2 (Ausich & others, 1999); *2,* column with facets of nodal and internodal, Holocene, ×2.1 (Ausich & others, 1999).

of a series of brachials. In its simplest form, a single unbranched (atomous) arm is inserted on each ray. In rays with arm branching, each series of brachials leading either from the radial to and including the first bifurcation plate (axillary), or from a subsequent axillary, to and including another axillary, is called a division series or brachitaxis. A division series terminates in an axillary with two distal articular facets. In most articulate crinoids, the first brachitaxis is composed of two brachials (the primibrachials). The second primibrachial is typically an axillary and supports the secundibrachials, followed by tertibrachials after the next axillary, and so on. Regular branching is called isotomous; in heterotomous arms, an axillary supports branches of unequal width, so the main branch, or ramus, carries smaller branches called armlets or ramules. In uniserial arms, brachials are

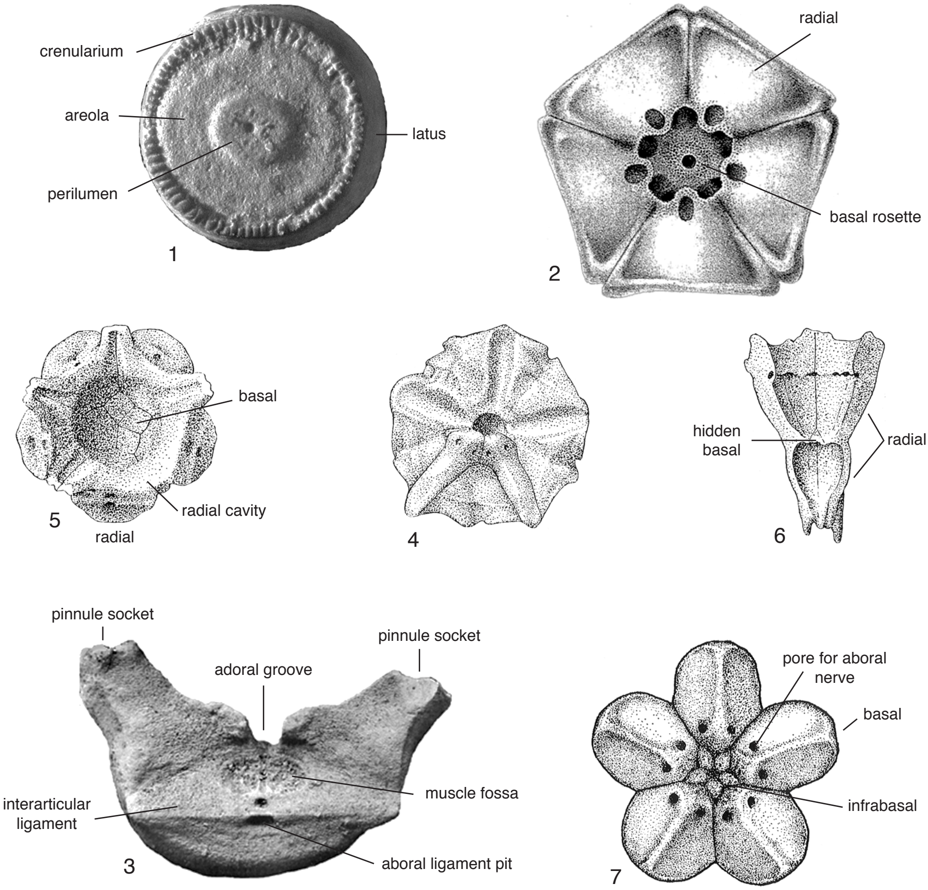

Fig. 5. *1, Cyclocrinus rugosus* (d'Orbigny); columnal facet, Oxfordian, Upper Jurassic, Switzerland, NMB M10484, ×4 (Hess, 2008); *2, Antedon bifida* (Pennant); lower (proximal) side of radial circlet with basal rosette, Holocene, ×15 (Carpenter, 1866); *3, Cyrtocrinus nutans* (Goldfuss); muscular facet of brachial with two pinnule sockets (bipinnulate condition), Oxfordian, Upper Jurassic, Switzerland, NMB M9292, ×5 (Hess, 1975); *4, Bruennichometra parvicava* (Gislén); centrodorsal with basals, Danian, Lower Tertiary, Denmark, holotype, MGUH 1215, ×10 (Rasmussen, 1961); *5–6, Roveacrinus communis* Douglas, Coniacian, Upper Cretaceous, England; *5,* adoral view of cup, BMNH E25712, ×15; *6,* broken cup, BMNH E15484, ×15 (Rasmussen, 1961); *7, Cainocrinus tintinnabulum* (Forbes); distal view of basal circlet with infrabasals, Danian, Lower Tertiary, England, MGUH 12763, ×10 (Rasmussen, 1972a).

arranged in a single row; in biserial arms, brachials are arranged in double rows, with interlocking sutures along the junction of the rows (Fig. 3,*5*). All articulates, except some encrinids, have uniserial arms. Pinnulation is a special type of arm branching. Pinnules are small, usually unbranched offshoots of the arm that arise from most brachial plates. In articulates, pinnules developed on alternate sides of successive brachials, except axillary brachials. Brachial pairs united by syzygy or synarthry invariably give rise to a pinnule from their distal component. Thus, epizygals are pinnule bearing, whereas hypozygals lack pinnules. Exceptionally, a brachial may carry a pinnule on each side; such a situation is called bipinnulate (Moore, 1978, p. 237, used the term hyperpinnulation for two or more pinnules on a single brachial) and occurs in some cyrtocrinids (Fig. 5,*3*). Brachials generally are wedge shaped, with the pinnules arising from the high side of the brachial. Hence, lowering the height of the opposite side of the brachial significantly reduces the spacing of the pinnules. Individual pinnulars are connected by muscular articulations, but muscles are mostly rather weak.

ARTICULATIONS IN CUP AND ARMS

Cup plates are joined in the large majority of articulates by flat, ligamentary articulations. In synostoses, as defined by Moore (1978, p. 242), the apposed facets are more or less concave, and thus slightly flexible. Such facets rarely occur between cup plates (Fig. 2,*6*) and interradial facets of primibrachials (see Fig. 38*k–l*) of articulates, and they seem to be exceptional between brachials. Brachial articulations are important for the classification of many articulates, especially the Isocrinina, where columnal articulations tend to be conservative. Synarthries in arms are ligamentary articulations superficially similar to those in the column. They have a fulcral ridge running adorally-aborally and separating two bundles of ligaments (Fig. 6,*2*). This structure allows limited movement. Synarthries are confined to the proximal parts of the arms and occur commonly between the first and second primibrachial and the first and second secundibrachial. In contrast to many extant forms (see Fig. 37,*2d*), synarthries in fossil articulates commonly are not strongly concave but have rather shallow ligament pits (Fig. 6,*3–4*). Nearly flat synarthries are called cryptosynarthries and may be recognized by their weak fulcral ridge (Fig. 6,*5*). Trifascial articulations have three ligament bundles and occur in bourgueticrinids. Muscular articulations combine collagenous ligament fibers with muscles. They possess a transverse or diagonal fulcral ridge, to the aboral side of which is a typically distinct ligament fossa with a pit for the attachment of the aboral ligament. Immediately to the adoral side of the fulcral ridge are two typically smaller areas for the interarticular ligaments (also called interarticular ligament fossae if depressed). Farther adorally, there are two flanges or fossae for the attachment of the adoral muscles (muscle fossae) (Fig. 5,*3;* Fig. 6,*1*). Syzygies are immovable articulations with radiating ridges on otherwise flat surfaces (Fig. 6,*6;* and see Fig. 37,*1f;* Fig. 78,*1e*). Instead of interlocking as in column symplexies so that the suture is crenulate, in syzygies, the ridges of one facet appose the ridges of the other (Fig. 6,*7*). Ridges may vary in number. The proximal element of a syzygial pair is called hypozygal, the distal element having a pinnule socket epizygal. Cryptosyzygies resemble syzygies, but the ridges are finer and are typically along the aboral edge (Fig. 6,*8a–c;* and see Fig. 36,*2b*); in side view, such junctions are continuous and appear to be tight. Cryptosyzygy was considered by Roux, Améziane, and Eléaume (2009) to be an inappropriate term, because during isocrinid ontogeny, a cryptosyzygy is an intermediate stage between a synostosis and a syzygy. However, the term is retained herein because it has been widely used in different taxa. Syzygies and cryptosyzygies are irregularly spaced along the arms and are preferred breaking points, similar to the cryptosymplexies or synostoses of the column. Symmorphies are immovable ligamentary articulations, where a general depression of one brachial facet corresponds to complementary relief on the other (Fig. 6,*9–11*; and see Fig. 31*i,k*). The aboral and adoral ligament areas are at an angle, and peripheral crenulae may occur on parts of a facet (see Fig. 24*d*). Brachials that combine flat faces with some kind of calcareous deposits have been called zygosynostoses by Moore (1978, p. 242). Zygosynostoses may be difficult to distinguish from cryptosyzygies (Fig. 6,*8a–c*). Symplectial articulations in the arms are not known from articulate crinoids.

SYMBOLS FOR CRINOID MORPHOLOGY

Br = brachial(s), used for all brachials if arms are undivided.
ax = axillary brachial, e.g., IIBr2ax.

IBr = primibrachial(s); IBr1 = first primibrachial, IBr2 = second primibrachial, and so on.

IIBr = secundibrachial(s); IIBr1 = first secundibrachial, and so on.

IIBr3–4 = articulation between secundibrachials 3 and 4; for example, syzygial articulation between secundibrachials 3 and 4. The type of articulation is spelled out herein. [MESSING (1997) used a different scheme for extant comatulids. He indicated each successive brachitaxis by a roman numeral followed by br; an Arabic number following indicates the number of component ossicles (for example, Ibr2 is the first brachitaxis, always composed of two ossicles in comatulids; IIIbr4 is the fourth ossicle of the third brachitaxis. A + sign indicates a syzygy, a type of articulation almost exclusive to comatulids. For example, IIbr4(3+4) is a second brachitaxis of four ossicles, with the third and fourth joined by syzygy; br9+10 indicates brachials 9 and 10 joined by syzygy. These symbols are not adopted herein.]

P = pinnule; P1 = first pinnule. For comatulids, Arabic numbers (e.g., P1, P2, P3) have been used for successive exterior pinnules, and letters (e.g., Pa, Pb, Pc) have been used for successive interior pinnules (MESSING, 1997).

GLOSSARY OF IMPORTANT TERMS

GENERAL TERMS

aboral (syn., dorsal). Applied to surface of body opposite adoral surface (syn., ventral); directed away from mouth. The free aboral surface of radials is called exposed surface (Fig. 4,*1*).

adoral (syn., ventral). Applied to surface of body that contains mouth and ambulacra; direction toward mouth; the term oral is reserved for plates on tegmen; it is also used in oral pinnules (Fig. 4,*1*).

adoral groove. Furrow along adoral surface of free brachials and pinnules (syn., ventral groove, ambulacral groove) (Fig. 5,*3;* Fig. 6,*1*).

arm facet. Articulation surface for attachment of free arm to cup, calyx, or theca, corresponds in most cases to radial articular facet.

articulum. Same as articular facet (or face).

brachial pair. Two brachials united by ligamentary articulation, for example, by synostosis in hyocrinids. Brachial pairs are followed by muscular articulation.

central plug. Generally spongy calcareous deposit within radial pentagon of comatulids (Fig. 3,*4*).

centrodorsal. Commonly cirriferous columnal or semifused or fused columnals attached to cup of comatulids.

centrodorsal cavity (Fig. 3,*6c*). Depression on adoral (proximal, upper) surface centrodorsal containing the chambered organ and accessory structure.

cup or **calyx** (Fig. 4,*1*). The cup (in literature also called aboral cup) is the part of the animal between the origin of the free arms and the column. It includes the radial plates and all other plates beneath the radials and above the column, whereas the calyx includes all the plates above the column and beneath the point where the arms become free. In its simplest form, the cup is composed of two circlets of five plates each. The uppermost plates of the cup are radial plates. If the arms become free above the radials, as in most of the articulates, the cup is equivalent to the calyx. Alternatively, proximal arm plates (brachials) may be sutured directly into the body wall of the crinoid, rather than being part of the free, feeding arms. These brachials are called fixed brachials; fixed brachials are present in the uintacrinoids and apiocrinitids (*Guettardicrinus*), in which the cup is only the lower part of the calyx.

dorsal star (Fig. 3,*6b*). Stellate depression around aboral (distal, lower) pole of centrodorsal in some comatulids.

exterior pinnule. Designating the position of a pinnule on the arm of comasteroidean and mariametroidean comatulids; see also interior pinnule (MESSING, AMÉZIANE, & ELÉAUME, 2000; MESSING, 2001).

interior pinnule. Position of pinnule on the side closest to the extrapolated median axis of the preceding axillary in arms of comatulids (MESSING, AMÉZIANE, & ELÉAUME, 2000; MESSING, 2001).

proximal or **distal** (Fig. 4,*1–2*). For cup plates and brachials, the proximal side is directed downward, toward the column. Thus, the underside of the cup (with or without basals and infrabasals) is the proximal side. Starting from the underside of the cup, the distal side is directed upward, toward the tip of the crown. In columnals, the proximal side is directed toward the cup and the distal side is away from the cup. Fossil comatulids are commonly preserved as cups with the centrodorsal attached and, thus, have two distal sides, one for the centrodorsal (preferably called aboral side) and the other for the radial circlet. Centrodorsals are sometimes preserved with an attached basal circlet (Fig. 5,*4*), so that the upper side corresponds to the distal side of the basals, and the lower side is the aboral (distal) side of the centrodorsal. For radial circlets with attached basals, the underside is the proximal side. RASMUSSEN (1978) used the terms adoral and oral, adoral/aboral, ventral or oral/dorsal rather indiscriminately for the distal (upper) and proximal (lower or underside) sides of cups and their components. Brachial exteriors (=aboral) and interiors (=adoral) were terms used by RASMUSSEN (1978). JAGT (1999a) used the terms ventral and dorsal for cups and centrodorsals.

radial cavity (Fig. 5,*5*). Lumen inside radial circlet, may be separated into two cavities by the basal circlet in roveacrinids (Fig. 5,*6*).

radial pit (Fig. 3,*6c*). Radially disposed depression in adoral (proximal, upper) surface of centrodorsal in some comatulids.

rosette (Fig. 5,*2*). Delicate calcareous plate or structure formed of metamorphosed basals, typically located within the radial cavity and roofing the centrodorsal of comatulids. In many comatulids, five rodlike pieces known as basal rays extend from the rosette in interradial positions (Fig. 3,*4*).

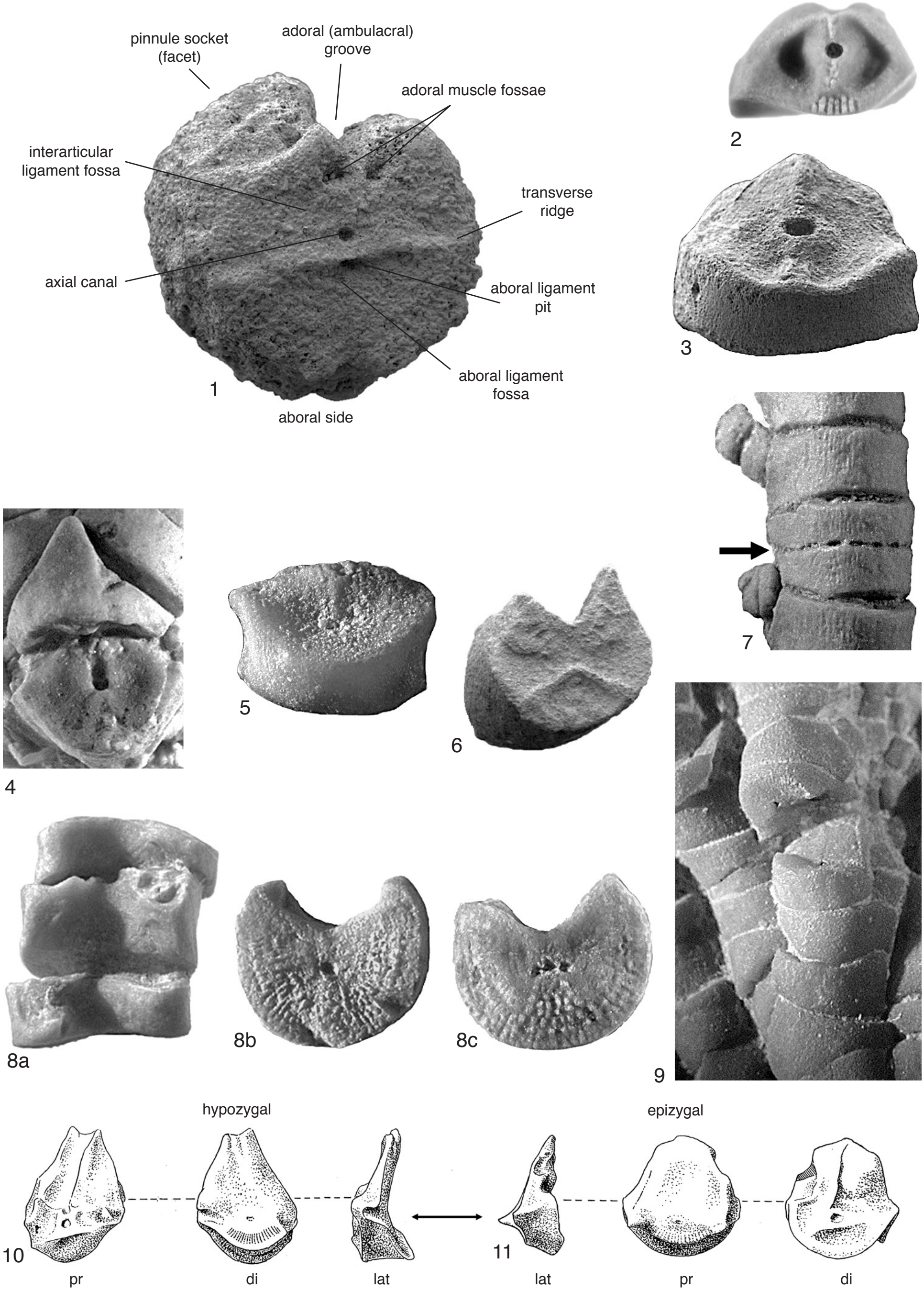

FIG. 6. *1, Bilecicrinus arenosus* HESS; oblique distal view of secundibrachial, Pliensbachian, Lower Jurassic, Switzerland, syntype, NMB M 10109, ×30 (Hess, 2006); *2, Apiocrinites roissyanus* D'ORBIGNY; synarthrial proximal facet of secundibrachial 2, Oxfordian, Upper Jurassic, France, NMB M10611, ×6 (Hess, new); *3, Balanocrinus subteroides* (QUENSTEDT); latus and distal synarthrial facet of primibrachial 1, Pliensbachian, Lower Jurassic, England, BMNH E70627, ×10 (Simms, 1989a); *4, Pentacrinites dargniesi* (TERQUEM & JOURDY); synarthry between primibrachials *(Continued on facing page.)*

subradial cleft. Deep, narrow furrow between aboral surface of radials and apposed surface of centrodorsal in comatulids (see Fig. 62,*3a*).

ARMS AND THEIR ARTICULATIONS

cryptosynarthry. Weakly sculptured ligamentary articulation of synarthrial type (ligamentary fossae shallow) (Fig. 6,*5*). In comasterids, ill-defined articulations with weak sculpturing occur in adult specimens (see Fig. 43,*1a*). Because an adoral-aboral ridge is at least partly developed and juvenile specimens have a distinct synarthry, the term cryptosynarthry has been used by Hoggett and Rowe (1986, p. 105) in such cases.

cryptosyzygy (Fig. 6,*8a–c*). Weakly sculptured ligamentary articulation of syzygial type, with fine marginal ridges that do not reach the axial canal; they occur in many Isocrinida and also in Comatulida, Holocrinida, Millericrinida, and Hyocrinida.

muscular articulations (Fig. 5,*3* and Fig. 6,*1*). Union of brachials effected by muscle fibers in addition to ligaments, characterized by presence of aboral ligament fossa (where a pit may be developed), transverse ridge perforated by axial canal, two interarticular ligament fossae (in many Mesozoic crinoids, rather flat areas or indistinct), and two adoral muscle fossae (also called muscle fossae in the literature).

pinnule comb. Modification of distal pinnulars of oral pinnules of comatulids. Ossicles bear one or a pair of blade-, spade-, or knob-shaped processes that together form a comb (a diagnostic feature of the Comasteridae) (Fig. 3,*7*).

pinnule socket. Pinnule articular facet (muscular).

symmorphy (Fig. 6,*9–11*, and see Fig. 24*d*; Fig. 31*i–l*). Ligamentary articulation with toothlike prominences on one facet interlocking with corresponding grooves on apposed facet; facet is mostly cryptosyzygial with fine, peripheral crenulae; occurring in isocrinids.

synarthry. Ligamentary articulation in which each apposed facet bears a transverse ridge separating two fossae for attachment of ligament bundles (Fig. 6,*2–4*).

synostosis. Ligamentary, mostly smooth and flat articulation; ligament areas may be more or less concave (loose synostosis, Fig. 2,*6*) or have calcareous deposits (tight synostoses or zygosynostoses, see Fig. 21*g* for an example), but such characteristics are grouped together in the text because intermediates are common.

syzygy. Ligamentary articulation in which ridges (culmina) of one articulum are opposed to corresponding ridges of adajcent articulum (Fig. 6,*7*). True syzygies with coarse ridges are widespread among Comatulida but occur in stalked crinoids only in Traumatocrinidae, Millericrinidae (e.g., *Ailsacrinus* Taylor, 1983), and Guillecrinidae (Roux, Messing, & Améziane, 2002). They are absent in Isocrinida. However, a type of syzygy has been reported by Hess (2006) from an Early Jurassic species of *Balanocrinus,* where two coarse ridges occur in the aboral part and a number of fine ridges are in the adoral part of the facet (Fig. 6,*6*). In an Oxfordian species of *Balanocrinus,* syzygies also occur, although rarely (H. Hess, personal observations, 2009). The term pseudosyzygy has been used for proximal syzygial articulations of *Marsupites* with very few, stout radiating ridges and lateral concave areas along the adoral margin, somewhat resembling a synarthrial articulation (see Fig. 47*d*) (Rasmussen, 1961, p. 399; Milsom, Simms, & Gale, 1994, p. 596).

COLUMNAL ARTICULATIONS

crenula (pl., crenulae) (Fig. 2,*3*). Ridge (culmen, pl., culmina) combined with adjacent groove or furrow (crenella, pl., crenellae) of columnal articulum.

cryptosymplexy (Fig. 2,*4a–b*).Weakly sculptured articulation of symplectial type, as developed between nodals and infranodals.

symplexy (Fig. 1,*4;* Fig. 2,*3–4*). Ligamentary articulation in which culmina on one joint face interlock with crenellar grooves on opposite joint face, marked externally by crenulate suture.

DISTRIBUTION AND BATHYMETRIC RANGE OF EXTANT FORMS

The following definitions are used (*Encyclopedia Britannica* online; www.britannica.com).

Distribution. Arctic Ocean, Atlantic Ocean (including Mediterranean), Indian Ocean, Pacific Ocean, Southern Ocean (Antarctic Ocean).

Fig. 6. *Continued from facing page.*

1 and 2, Bajocian, Middle Jurassic, Switzerland, NMB M10619, ×5 (Hess, new); *5–6, Balanocrinus ticinensis* Hess, Pliensbachian, Lower Jurassic, Switzerland, syntypes; *5,* distal synarthrial facet of primibrachial 1, NMB M10396, ×7; *6,* distal syzygial facet of hypozygal secundibrachial, NMB M10407, ×10 (Hess, 2006); *7, Paracomatula helvetica* Hess; arm fragment at approximately secundibrachial 20 and 21 with syzygy (*arrow*), Bajocian, Middle Jurassic, Switzerland, topotype, NMB M10618, ×6 (Hess, new; see also Fig. 37,*1f*); *8a–c, Apiocrinites roissyanus* d'Orbigny, arm fragment; *a,* adoral, *b,* proximal cryptosyzygial facet, *c,* distal cryptosyzygial facet with two nerve canals below axillary, Oxfordian, Upper Jurassic, France, NMB M10612, ×6 (Hess, new); *9, Chariocrinus andreae* (Desor); symmorphy between secundibrachials 3 and 4, Bajocian, Middle Jurassic, Switzerland, NMB M10614, ×7 (Hess, new); *10–11, Isocrinus cingulatus* (Münster), *pr*, proximal, *di*, distal, *lat*, lateral; *10*, secundibrachial 3 or tertibrachial 3; *11*, secundibrachial 4 or tertibrachial 4, *arrow* in lateral views indicates symmorphy, Oxfordian, Upper Jurassic, Switzerland, NMB M9890, ×5 (Hess, 1975).

Bathymetric range. Littoral to sublittoral (shallow water, between shoreline and 200 m), bathyal (between 200 and 3000 m, corresponding to the continental slope, or a depth of 100–1500 fathoms), abyssal (below 3000 m).

CLASSIFICATION

The following history of classification is taken from RASMUSSEN and SIEVERTS-DORECK (1978, p. 813), together with subsequent proposals.

AUSICH and LANE (2005) offered an account of the early history of crinoid classification, entirely based on parts of the column. Two of the names in the first publication on fossil crinoids by AGRICOLA (1564), *Encrinos* (for pentalobate columnals) and *Pentacrinus* (for pluricolumnals with a pentalobate shape), have survived in modified form with partly different meaning. During the 16th century, crinoid columnals were regarded as inanimate objects, and their naming may have been a result of their perceived medicinal use.

MILLER (1821, p. 13) introduced the concept of Crinoidea Articulata as a division of the family Crinoidea with the following definition: “The joints resting on the first or superior columnar joint, and forming the cup containing the viscera, articulate by liplike and transverse processes, having a minute perforation.” He proposed the name Articulata “in allusion to the articulating insertion of the joints forming the cup containing the viscera” (MILLER, 1821, p. 19), and he assigned three genera to the division: (1) *Apiocrinites* n. gen. (2 species); (2) *Pentacrinites vel Pentacrinus* (1 living and 4 fossil species); and (3) *Encrinites* (1 species). The new monotypic genus *Eugeniacrinites*, now included in the Articulata, comprised the small division Coadunata, with “joints of the pelvis anchylosed to the first columnar joint” (MILLER, 1821, p. 111). The genera *Comatula* and *Marsupites*, now included in the Articulata, were not assigned to any division by MILLER (1821), but he recognized *Comatula* LAMARCK as a true crinoid, “defined with sufficient precision as a *Pentacrinus* destitute of the column,” (MILLER, 1821, p. 127), and *Marsupites* was considered to be the “immediate link between the Crinoidea Inarticulata and the Euryale” (MILLER, 1821, p. 134).

MÜLLER (1843), in his anatomical study of “*Pentacrinus caput Medusae,*” first subdivided the Articulata, as now understood, into three families: Articulata (=MILLER’s Articulata + *Comatula*), Tessellata (=MILLER’s Semiarticulata + Inarticulata, as well as a few additional similar genera and *Marsupites*), and Costata (for *Saccocoma*). *Holopus* was given no special assignment. MÜLLER (1843) characterized the Articulata by the movable articulation between radials and primibrachials, the absence of plates between radials, and the leathery composition of the tegmen with or without calcareous plates. ROEMER (1855 in BRONN & ROEMER, 1851–1856) classified the Articulata, as now understood, in two suborders and nine families: Astylida, without an articulated column (families Holopocrinidae, Cyathidiocrinidae, Marsupitidae, Saccocomidae, and Comatulidae), and Stylida, with an articulated column (families Pentacrinidae, Apiocrinidae, Eugeniacrinidae, and Encrinidae, including *Dadocrinus*). BRONN (1860) adopted MÜLLER’s classification. Later, ZITTEL (1879 in 1876–1880), in *Handbuch der Paläontologie*, adopted MÜLLER’s classification and ROEMER’s families plus Plicatocrinidae. NEUMAYR (1889) followed ZITTEL’s classification but used the name Pentacrinacea for Articulata.

In 1880, WACHSMUTH and SPRINGER (p. 247) designated all Mesozoic and younger crinoids as Stomatocrinoidea but later (WACHSMUTH & SPRINGER, 1886, p. 226) adopted the name Neocrinoidea, introduced as a replacement by CARPENTER (in CARPENTER & ETHERIDGE, 1881, p. 296) for this group corresponding to the Articulata. In 1887, WACHSMUTH and SPRINGER (p. 64) transferred the name Articulata to a suborder of Paleozoic crinoids (including Ichthyocrinidae and Crotalocrinidae), but later they (WACHSMUTH & SPRINGER, 1897) used Articulata for two suborders: the Paleozoic

Articulata Impinnata for the Ichthyocrinidae [Icthyocrinidae], and the Articulata Pinnata for the Articulata, as now used. CHAPMAN (1883) introduced the name Canaliculata for the Articulata, emphasizing the important character of the axial nerve running in canals inside basals, radials, and brachials. ZITTEL (1895) adopted in principle the system outlined by WACHSMUTH and SPRINGER (1886) for Paleozoic crinoids containing the orders Larviformia, Camerata, and Fistulata; and he proposed the addition of a new order Flexibilia for the Paleozoic Articulata of WACHSMUTH and SPRINGER (1887) (*non* MILLER, 1821). Thus, the name Articulata of MILLER (1821) and MÜLLER (1843) was restricted to post-Paleozoic crinoids.

BATHER (1899, 1900) introduced an entirely new classification. He considered crinoids without infrabasals in the cup and crinoids with infrabasals in the cup as two completely separated lines of evolution, which he classified as subclasses under the names of Monocyclica (with basals only) and Dicyclica (with basals and infrabasals). All orders hitherto accepted were considered polyphyletic, including monocyclic as well as dicyclic forms. BATHER distributed the post-Paleozoic crinoids now classified as Articulata among several different groups as listed below.

CLASSIFICATION OF ARTICULATA (BATHER, 1899)

Subclass Monocyclica BATHER, 1899
  Order Monocyclica Inadunata BATHER, 1899 (Plicatocrinidae, Hyocrinidae, Saccocomidae)
Subclass Dicyclica BATHER, 1899
  Order Dicyclica Inadunata BATHER, 1899
    Suborder Dendrocrinoidea BATHER, 1899 (Pentacrinidae, Uintacrinidae, Marsupitidae, Bathycrinidae)
  Order Flexibilia ZITTEL, 1895
    Grade Pinnata WACHSMUTH & SPRINGER, 1897 (Apiocrinidae, Bourgueticrinidae, Antedonidae, Atelecrinidae, Actinometridae, Thaumatocrinidae, Eugeniacrinidae, Holopodidae, Eudesicrinidae)

BIESE (1935–1937) used BATHER's (1899) classification in all sections of the *Fossilium Catalogus* concerned with post-Paleozoic crinoids.

MATSUMOTO (1929) followed BATHER's (1899) arrangement of the Articulata with minor modifications, and he included taxa recognized by other paleontologists and zoologists. MATSUMOTO's (1929) classification is as follows.

CLASSIFICATION OF POST-PALEOZOIC CRINOIDS (MATSUMOTO, 1929)

Subclass Monocyclica BATHER, 1899
  Order Monocyclica Inadunata BATHER, 1899
    Suborder Costata MÜLLER, 1843
Subclass Dicyclica BATHER, 1899
  Order Articulata MILLER, 1821
    Suborder Uintacrinacea ZITTEL, 1879 in 1876–1880
    Suborder Encrinacea MATSUMOTO, 1929
    Suborder Pentacrinacea NEUMAYR, 1889 (Isocrinidae MATSUMOTO, 1929; Pentacrinitidae GRAY, 1842)
  Order Coadunata MILLER, 1821
  Order Comatulida A. H. CLARK, 1908h
  Order Holopoda MATSUMOTO, 1929

JAEKEL (1894) divided crinoids in two subclasses, Cladocrinoidea (=Camerata of WACHSMUTH & SPRINGER, 1886) and Pentacrinoidea (=Flexibilia + Inadunata + Articulata). He did not accept BATHER's use of the names Monocyclica and Dicyclica, and in 1918, JAEKEL published his *Phylogenie und System der Pelmatozoen,* with the following classification of post-Paleozoic crinoids.

CLASSIFICATION OF POST-PALEOZOIC CRINOIDS (JAEKEL, 1918)

Subclass Pentacrinoidea JAEKEL, 1894
  Order Articulata MILLER, 1821
    Suborder Typica JAEKEL, 1918 (Encrinidae, Holocrinidae, Pentacrinidae, Millericrinidae, Apiocrinidae, Thiolliericrinidae, Rhizocrinidae)
    Suborder Libera JAEKEL, 1918 (Comatulidae, Uintacrinidae, Marsupitidae)
    Suborder Compacta JAEKEL, 1918 (Sclerocrinidae, Eugeniacrinidae, Phyllocrinidae, Holopodidae)
  Order Costata MÜLLER, 1843
    Suborder Hyocrinites JAEKEL, 1918 (Eudesicrinidae, Plicatocrinidae, Hyocrinidae, Saccocomidae)

In the 1913 edition of ZITTEL's *Textbook of Paleontology*, SPRINGER, assisted by C. R. EASTMAN and A. H. CLARK, harmonized the classification of living and fossil crinoids. They classified all post-Paleozoic crinoids except the Encrinidae as Articulata, a concept adopted by RASMUSSEN and SIEVERTS-DORECK (1978).

CLASSIFICATION OF ARTICULATA (SPRINGER & CLARK IN ZITTEL, 1913)

Order Articulata MILLER, 1821
  Family Bourgueticrinidae DE LORIOL, 1882 in 1882–1889 (including Rhizocrinidae, Bathycrinidae)
  Family Phrynocrinidae A. H. CLARK, 1907a
  Family Apiocrinidae D'ORBIGNY, 1840 in 1840–1841
  Family Pentacrinidae GRAY, 1842
    Section Pentacrinids GRAY, 1842
    Section Thiolliericrinids A. H. CLARK, 1908b
    Section Comatulids A. H. CLARK, 1908h (*ex* FLEMING, 1828)
      Tribe Innatantes A. H. CLARK, 1909h
        Subtribe Marsupitids D'ORBIGNY, 1852 in 1850–1852
        Subtribe Uintacrinids ZITTEL, 1879 in 1876–1880
      Tribe Oligophreata A. H. CLARK, 1909h
      Tribe Macrophreata A. H. CLARK, 1909h
  Family Plicatocrinidae ZITTEL, 1879 in 1876–1880
  Family Saccocomidae D'ORBIGNY, 1852 in 1850–1852
  Family Eugeniacrinidae ROEMER, 1855 in BRONN & ROEMER, 1851–1856
  Family Holopidae ZITTEL, 1879 in 1876–1880 (=Holopodidae ZITTEL, 1879 in 1876–1880)

SPRINGER and CLARK (1913) characterized the Articulata by the complete muscular articulation of radials with the brachials, the exposed mouth and ambulacral furrows, the nerve canal perforating the calcareous substance of radials and brachials, the arms always being uniserial and pinnulate, the absence of anal plate or other interradial elements in the cup of adult specimens, the leathery tegmen with or without calcareous elements, and the dicyclic or cryptodicyclic cup, although commonly infrabasals and basals in some genera may be atrophied. CLARK further subdivided living comatulids into two suborders, Oligophreata and Macrophreata, with numerous superfamilies and families, a classification followed in his large *Monograph of the Existing Crinoids* (CLARK, 1915–1950; CLARK & CLARK, 1967).

GISLÉN (1924) slightly modified CLARK's (1915a in 1915–1950) proposed classification of comatulids and also considered fossil comatulids. He divided comatulids into four rather than two groups: Comasterida, Mariametrida, Thalassometrida, and Macrophreata.

RASMUSSEN (1961) in a monograph on Cretaceous crinoids, and A. H. MÜLLER (1963), in his *Lehrbuch der Paläozoologie,* followed SIEVERTS-DORECK's classification (in MOORE, LALICKER, & FISCHER, 1952). In preparing the Articulata for MOORE and TEICHERT (1978), SIEVERTS-DORECK proposed a classification including six orders she had used earlier. This classification, including very short diagnoses, was reproduced in MOORE, LALICKER, and FISCHER (1952, p. 614) and was used with more extended diagnoses in UBAGHS (1953, p. 757–765). Further investigations of fossil articulates led RASMUSSEN to consider the affinity of the Bourgueticrinina to the Millericrinida as dubious, and he raised the suborder to ordinal level. Also, the sequence of orders has been changed, leading to the outline of the Articulata adopted by RASMUSSEN and SIEVERTS-DORECK (1978).

CLASSIFICATION OF ARTICULATA (RASMUSSEN & SIEVERTS-DORECK IN MOORE & TEICHERT, 1978)

Subclass Articulata MILLER, 1821
  Order Millericrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952; SIEVERTS-DORECK in UBAGHS, 1953
    Suborder Millericrinina SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952; SIEVERTS-DORECK in UBAGHS, 1953 (Dadocrinidae, Millericrinidae, Apiocrinitidae, Cyclocrinidae)
    Suborder Hyocrinina RASMUSSEN *nov.* (Hyocrinidae)
  Order Cyrtocrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952; SIEVERTS-DORECK in UBAGHS, 1953
    Suborder Cyrtocrinina SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952 (Plicatocrinidae, Sclerocrinidae, Hemicrinidae, Eugeniacrinitidae, Phyllocrinidae)
    Suborder Holopodina ARENDT, 1974 (Eudesicrinidae, Hemibrachiocrinidae, Holopodidae)
  Order Bourgueticrinida SIEVERTS-DORECK in UBAGHS, 1953 (Bourgueticrinidae, Bathycrinidae, Phrynocrinidae, Porphyrocrinidae)
  Order Isocrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952 (Holocrinidae, Isocrinidae, Pentacrinitidae, Proisocrinidae)

Order Comatulida A. H. Clark, 1908h
  Superfamily Paracomatulacea Hess, 1951 (Paracomatulidae, Atelecrinidae)
  Superfamily Solanocrinitacea Jaekel, 1918 (Solanocrinitidae, Decameridae, Thiollericrinidae)
  Superfamily Comasteracea A. H. Clark, 1908h (Comasteridae)
  Superfamily Mariametracea Gislén, 1924 (Mariametridae, Zygometridae, Eudiocrinidae, Himerometridae, Colobometridae)
  Superfamily Tropiometracea A. H. Clark, 1908h (Tropiometridae, Conometridae, Calometridae, Ptilometridae, Asterometridae, Thalassometridae, Charitometridae)
  Superfamily Notocrinacea Mortensen, 1918 (Notocrinidae, Aporometridae)
  Superfamily Antedonacea Norman, 1865 (Antedonidae, Pentametrocrinidae)
Order Uintacrinida Broili (=Zittel, 1921) (Uintacrinidae, Marsupitidae)
Order Roveacrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952; Sieverts-Doreck in Ubaghs, 1953 (Roveacrinidae, Saccocomidae)

Arendt's (1974) monograph on the cyrtocrinids (in Russian) included superfamilies not considered by Rasmussen (1978).

CLASSIFICATION OF CYRTOCRINIDA (ARENDT, 1974)

Order Cyrtocrinida Sieverts-Doreck in Ubaghs, 1953
  Suborder Cyrtocrinina *nov.*
    Superfamily Plicatocrinacea Zittel, 1879, in 1876–1880
      Family Plicatocrinidae Zittel, 1879, in 1876–1880
    Superfamily Eugeniacrinitacea Zittel, 1879, in 1876–1880
      Family Eugeniacrinitidae Zittel, 1879, in 1876–1880
      Family Sclerocrinidae Jaekel, 1918
      Family Phyllocrinidae Jaekel, 1907
      Family Hemicrinidae Rasmussen, 1961
  Suborder Holopodina *nov.*
    Superfamily Holopodacea Roemer, 1856, in Bronn & Roemer, 1851–1856
      Family Eudesicrinidae Bather, 1899
      Family Hemibrachiocrinidae Arendt, 1968
      Family Holopodidae Roemer, 1856, in Bronn & Roemer, 1851–1856

Roux (1981) discussed extant genera of the Isocrinidae and proposed several subfamilies (Isocrininae, Balanocrininae, Diplocrininae, and Metacrininae). Simms (1988a) discussed the relationships and phylogeny of post-Paleozoic crinoids based on a cladistic analysis. He included the encrinids that had been excluded from the Articulata by Rasmussen and Sieverts-Doreck (1978). He placed dadocrinids within the Millericrinida and treated the Marsupitidae (with *Uintacrinus*) as a highly specialized offshoot of the Isselicrinidae, although he did not exclude some relationship with the comatulid families Zygometridae and Comasteridae.

REVISED CLASSIFICATION OF ARTICULATA (SIMMS, 1988a)

Subclass Articulata Zittel, 1879 in 1876–1880
    Plesion (Family) Encrinidae Dujardin & Hupé, 1862
  Order Isocrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952
    Plesion (Family) Holocrinidae Jaekel, 1918
    Plesion (Family) Pentacrinitidae Gray, 1842
   Suborder Comatulidina A. H. Clark, 1908h (*nom. transl.*)
    Plesion (Superfamily) Paracomatulacea Hess, 1951, *emend.*, Simms, to exclude Atelecrinidae
    Plesion (Family) Eocomatulidae *nov.*
    Plesion (Family) Paracomatulidae Hess, 1951
  Infraorder Comatulidia A. H. Clark, 1908h (*nom. transl.*), *emend.*, Simms, to exclude Paracomatulidae
   Suborder Isocrinina Gislén, 1924 (*nom. transl.*) (=Isocrinidae Gislén, 1924)
    Family Isocrinidae Gislén, 1924
    Family Cainocrinidae (*nov.*)
    Family Isselicrinidae Klikushin, 1977
    Family Marsupitidae d'Orbigny, 1852 in 1850–1852, *emend.*, Simms, to include Uintacrinidae
   Suborder Bourgueticrinina Sieverts-Doreck in Ubaghs, 1953 (*nom. transl.*)
  Order Millericrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952, *emend.*, Simms, to include Cyrtocrinida
    Plesion (Family) Dadocrinidae *s.l.* Lowenstam, 1942
   Suborder Millericrinina Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952, *nov.*, Simms, to exclude Dadocrinidae *s.l.* with dicyclic cup
  Infraorder Millericrinidia Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952 (*nom. transl.*) (=Millericrinina Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952)
  Infraorder Hyocrinidia Rasmussen, 1978 (*nom. transl.*) (=Hyocrinina Rasmussen, 1978)
   Suborder Cyrtocrinina Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952 (=Cyrtocrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952)
  Infraorder Cyrtocrinidia Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952 (*nom. transl.*) (=Cyrtocrinina Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952)
  Infraorder Holopodinidia Arendt, 1974 (*nom. transl.*) (=Holopodina Arendt, 1974)
  Incertae sedis (Order) Roveacrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952

Hagdorn (1988) raised the encrinids to ordinal status and included the Traumatocrinidae and the newly created family Ainigmacrinidae.

In the *Fossil Record 2*, Simms and others (1993) proposed the following somewhat altered scheme. The most important deviations from Rasmussen and Sieverts-Doreck (1978) and Simms's classification of 1988a were the assignment of Pentacrinitidae to Comatulidina and of Marsupitidae (including *Uintacrinus*) to comasteroidean comatulids. The Triassic forms were not assigned to one of the orders, and the Isocrinina was not further subdivided.

CLASSIFICATION OF ARTICULATA (SIMMS & OTHERS, 1993)

Subclass Articulata Miller, 1821
Family Holocrinidae Jaekel, 1918
Family Encrinidae Dujardin & Hupé, 1862
Family Dadocrinidae Loewenstam, 1942
Order Isocrinina Simms, 1988a (no further subdivision given)
Order Comatulidina Clark, 1908h (*pro* Comatulida A. H. Clark, 1908h)
Family Pentacrinitidae Gray, 1842
Superfamily Paracomatulacea Hess, 1951
Family Eocomatulidae Simms, 1988a
Family Paracomatulidae Hess, 1951
Infraorder Comatulidia Clark, 1908h
Family Atelecrinidae Bather, 1899
Superfamily Solanocrinitacea Jaekel, 1918
Family Solanocrinitidae Jaekel, 1918
Family Decameridae Rasmussen, 1978
Family Thiollierierinidae A. H. Clark, 1908b
Family Bourgueticrinidae de Loriol, 1882 in 1882–1889 (including Bathycrinidae, Phrynocrinidae, Porphyrocrinidae)
Superfamily Comasteracea A. H. Clark, 1908h
Family Comasteridae A. H. Clark, 1908h
Family Marsupitidae d'Orbigny, 1852 in 1850–1852 (including *Uintacrinus socialis* Grinnell, 1876)
Superfamily Mariametracea A. H. Clark, 1909h
Family Mariametridae A. H. Clark, 1909h
Family Zygometridae A. H. Clark, 1908h
Family Eudiocrinidae A. H. Clark, 1907f
Family Himerometridae A. H. Clark, 1908h
Family Colobometridae A. H. Clark, 1909h
Superfamily Tropiometracea A. H. Clark, 1908h
Family Tropiometridae A. H. Clark, 1908h
Family Pterocomidae Rasmussen, 1978
Family Conometridae Gislén, 1924
Family Calometridae A. H. Clark, 1911e
Family Ptilometridae A. H. Clark, 1914b
Family Asterometridae Gislén, 1924
Family Thalassometridae A. H. Clark, 1908h
Family Charitometridae A. H. Clark, 1909a
Superfamily Notocrinacea Mortensen, 1918
Family Notocrinidae Mortensen, 1918
Family Aporometridae H. L. Clark, 1938
Superfamily Antedonacea Norman, 1865
Family Antedonidae Norman, 1865
Family Pentametrocrinidae A. H. Clark, 1908h
Order Roveacrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952
Family Somphocrinidae Rasmussen, 1978
Family Saccocomidae d'Orbigny, 1852 in 1850–1852
Family Roveacrinidae Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952
Order Millericrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952
Suborder Millericrinina Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952
Infraorder Millericrinidia Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952
Family Millericrinidae Jaekel, 1918
Family Apiocrinitidae d'Orbigny, 1840 in 1840–1841
Infraorder Hyocrinidia Rasmussen, 1978
Family Hyocrinidae Carpenter, 1884a
Suborder Cyrtocrinina Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952
Infraorder Cyrtocrinidia Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952
Family Plicatocrinidae Zittel, 1879 in 1876–1880
Family Sclerocrinidae Jaekel, 1918
Family Hemicrinidae Rasmussen, 1961
Family Eugeniacrinitidae Roemer, 1855 in Bronn & Roemer, 1851–1856 (includes *Capsicocrinus souti* Delogu & Nicosia, 1987)
Family Phyllocrinidae Jaekel, 1907
Infraorder Holopodinidia Arendt, 1974
Family Eudesicrinidae Bather, 1899
Family Hemibrachiocrinidae Arendt, 1968
Family Holopodidae Zittel, 1879 in 1876–1880

In a taxonomic survey of fossil isocrinids, Klikushin (1982a) classified the Isocrinida following Rasmussen and Sieverts-Doreck (1978) but added a number of new taxa. However, his monograph on the fossil Pentacrinid crinoids and their occurrence in the USSR (Klikushin, 1992 [in Russian]) offered a radically altered classification.

CLASSIFICATION (KLIKUSHIN, 1992)

Subclass Dadocrinoidea *nov.*
Order Millericrinida Sieverts-Doreck in Ubaghs, 1953
Order Cyrtocrinida Sieverts-Doreck in Ubaghs, 1953

Order Bourgueticrinida Sieverts-Doreck in Ubaghs, 1953
Subclass Holocrinoidea *nov.*
  Order Encrinida Matsumoto, 1929
  Order Pentacrinida Tortonese, 1938
  Order Comatulida A. H. Clark, 1908h
  Order Roveacrinida Sieverts-Doreck in Ubaghs, 1953
  Order Tulipacrinida *nov.*

The order Pentacrinida Tortonese, 1938 (=Isocrinida of Rasmussen & Sieverts-Doreck, 1978) was subdivided as follows:

Family Holocrinidae Jaekel, 1918
Family Pentacrinidae Gray, 1842
Family Isocrinidae Gislén, 1924
  Subfamily Balanocrininae Roux, 1981
  Subfamily Diplocrininae Roux, 1981
  Subfamily Isocrininae Gislén, 1924
  Subfamily Isselicrininae Klikushin, 1977
  Subfamily Metacrininae Klikushin, 1977

In reassessing articulates and their Paleozoic sister taxa, Simms and Sevastopulo (1993) raised the Disparida and Cladida to subclass level alongside the Camerata and included the Articulata Miller (1821) and Flexibilia as infraclasses within the Cladida Moore & Laudon (1943). Their cladistic analysis indicated that the post-Paleozoic crinoids, grouped as Articulata, constitute a monophyletic clade and were derived from late Paleozoic Ampelocrinidae (Cladida). The most important diagnostic characters of Articulata are the lack of anal plates in the adult cup and a entoneural system enclosed in brachials and radial plates. Webster and Jell (1999) did not regard the absence of anal plates in the cup as a synapomorphy of the Articulata. They asserted (p. 283) that the defining synapomorphy of Articulata was the development in the arms of syzygial brachial pairs in which muscular articulations alternate with cryptosyzygial ligamentary articulation. They proposed that the Articulata possessed the following morphological features: (1) dicyclic or cryptodicyclic cup; (2) cirri with multiradiate articula distally and transverse ridge articula proximally or cirri with transverse ridge articula throughout; (3) pinnulate arms; (4) brachial articula with ligamentary and clearly defined muscle fossae; (5) first arm division on primibrachials 2 to 4; (6) entoneural system enclosed in paired canal; (7) syzygial brachial pairs in arms; (8) anals in cup, 1 to 3; and (9) uniserial arms with cuneate brachials. These morphologic features occur in *Chlidonocrinus*, *Ampelocrinus*, and *Nowracrinus*, taxa included by Simms and Sevastopulo (1993) in their stem-group articulates. Thus, Webster and Jell (1999) extended the range of articulates well into the Paleozoic and considered *Corythocrinus* from the late Osagean (Tournaisian) of Indiana to be the oldest Articulata. By treating the Devonian (Givetian) *Logocrinus*, which they assigned to the Corythocrinidae, as the oldest articulate crinoid, Webster and Hafley (in Webster & others, 2004) and Webster and Lane (2007) extended the range even further.

A classification that recognizes Paleozoic articulates from among the cladids is not followed herein; and Articulata are considered a monophyletic, post-Paleozoic clade, the crown-group articulates of Simms and Sevastopulo (1993). The position of *Archaeoisocrinus* from the Permian (Artinskian) is open to question, and its assignment to the Isocrinidae is rejected.

Nicosia (1991) and Manni and Nicosia (1996) revised the systematics of cyrtocrinids and established several new genera in this group. They retained the order Millericrinida following Rasmussen and Sieverts-Doreck (1978), but doubted the position of the Cyclocrinidae. They also assigned the Dadocrinidae to a new order, which replaced the Cyrtocrinida of Rasmussen and Sieverts-Doreck (1978) and included the suborders Dadocrinina (with families Dadocrinidae, Plicatocrinidae, and Proholopidae), Holopodina (with families Cotyledermatidae and Holopodidae), Eudesicrinina (with families Eudesicrinidae, Tetracrinidae, and Sclerocrinidae), and Cyrtocrinina (superfamilies Eugeniacrinitoidea [with families Eugeniacrinitidae, Psalidocrinidae, Phyllocrinidae, Hoyacrinitidae, and Nerocrinidae] and Hemicrinoidea [with families Hemicrinidae and Hemibrachiocrinidae]).

Mironov and Sorokina (1998a, 1998b) proposed new taxa and extensive revision of the Hyocrinida. Roux (2004) essentially followed this classification but did not recognize Mironov and Sorokina's intermediate taxonomic levels (subfamily, subgenus). Mironov (2000) also revised the Bourgueticrinina, adding a few taxa. Roux, Messing, and Améziane (2002) published useful artificial keys to the genera of living stalked crinoids. Messing (1997) presented an artificial key to the families of living comatulids and also revised several groups of these "infernal organisms" (Messing, 2003b, p. 161) (Messing, 1998, 2001, 2003a; Messing & White, 2001). Taxonomic relationships of living comatulids remain poorly understood (Messing, Améziane, & Eléaume, 2000).

Many species of articulates, especially isocrinids and millericrinids, but also encrinids and holocrinids, are based on columnals and pluricolumnals only. Whereas the specific value of columnals and pluricolumnals is doubtful in many cases, their assignment at the generic level normally presents no problems. Hess (2006) proposed a number of new taxa based on brachials, using the explanatory suffix (br.), similar to the suffix (col.) for columnals, as done by previous authors for Paleozoic forms. In contrast to the Paleozoic forms, the distinctive brachials, thus named, were assigned to higher (suprafamilial) taxa by their articulation types, thus avoiding the difficulties of parataxonomy. These suffixes are not used in the current text.

Attempts at a phylogenetic classification of fossil genera and families of Articulata using cladistics are few or have been unsuccessful (unpublished data by Hagdorn, 2000; Hess, 2001). This is mostly due to difficulties with recognition of heterochronies that appear to dominate the taxa examined and also to the lack of characters in various fossil groups for reasons of preservation. Many articulate crinoids have been described on the basis only of dissociated remains, particularly columnals, and thus are largely excluded from cladistic analysis. For this reason, Simms (2011) suggested that stereom microstructure of columnal latera may be of potential value to resolve phylogenetic relationships within the Isocrinina. Several clades, such as holocrinids and encrinids, but especially cyrtocrinids, exhibit great ecophenotypic variation that has led to a proliferation of species and genus names. Most taxa of living comatulids and stalked crinoids have not yet been subjected to phylogenetic analysis (Messing, 1997; Roux, Messing, & Améziane, 2002). Molecular methods may elucidate the relationships of extant forms difficult to classify, such as *Caledonicrinus*, *Guillecrinus*, and *Proisocrinus*. For example, preliminary molecular and cladistic morphological analysis of some extant forms suggests that bathycrinids, comatulids, and *Guillecrinus* belong to one clade (Cohen & others, 2004). Another study confirms placement of *Proisocrinus* as part of the Isocrinida (Rouse, Jermin, & Messing, 2006); these authors also conclude that Isocrinida, Cyrtocrinida, and Hyocrinida are monophyletic.

CLASSIFICATION ADOPTED HEREIN

It is generally accepted that cirri-bearing articulates are closely related (holocrinids, isocrinids, comatulids, and the forms derived from them, such as thiolliericrinids and bourgueticrinids); indeed, Heinzeller (1998), from a neuroanatomical point of view, combined short-stalked (avoiding the term stalkless) comatulids and long-stalked (stalked) isocrinids in a taxon Cirrata. Therefore, in a truly phylogenetic classification, they should be grouped in the same taxon. For practical reasons, however, the orders Isocrinida and Comatulida of Rasmussen and Sieverts-Doreck (1978) are retained herein. The name Isocrinida, for the order that includes pentacrinitids and isocrinids, is maintained, because pentacrinitids are a derived group with characteristics for a specific lifestyle. One could use Pentacrinitida, derived from the older name *Pentacrinites;* however, ICZN (International Code of Zoological Nomenclature, 2010) rules of priority lack any force as applied to suprafamilial taxa, and the established name Isocrinida is used. The Triassic Holocrinidae at the base of crown-group of articulates is raised to ordinal status, following a proposal by HAGDORN (1996a). The exclusively Triassic encrinids are also treated as a distinct order with four families (Encrinidae, Dadocrinidae, Traumatocrinidae, Ainigmacrinidae); however, assignment of the Triassic Lanternocrinidae and Leocrinidae to this order is doubtful. The uintacrinoids (order Uintacrinida of RASMUSSEN & SIEVERTS-DORECK, 1978) were classified by SIMMS and others (1993) in the family Marsupitidae, superfamily Comasteracea A. H. CLARK, 1908h, and thus in the Comatulida. Placement in the Comatulida is supported by the findings of MESSING and others (2004), who compared *Uintacrinus socialis* with extant comatulids. The bourgueticrinids are classified with the Comatulida as a suborder (Bourgueticrinina); other authors (A. M. CLARK, 1977; ROUX, 1977b, 1978b; KLIKUSHIN, 1982b; MIRONOV, 2000) have assigned them to the Millericrinida or treated them as an order of their own (RASMUSSEN, 1978). Also classified with the Comatulida are the Guillecrinina, previously thought to be related to the hyocrinids. The hyocrinids are treated as a separate order, Hyocrinida, not as a suborder of Millericrinida, as in RASMUSSEN and SIEVERTS-DORECK (1978). Therefore, the corresponding suborder Millericrinina is abolished. The cyrtocrinids, although possibly related to the millericrinids, are retained as a separate order, because the early, Triassic history of the two groups is still largely unknown.

Use of suprageneric taxa has been inconsistent in the literature on post-Paleozoic crinoids. Consistent with current literature, this volume uses suborders and superfamilies (but no infraorders). In the suborder Isocrinina, no superfamilies are proposed, but a number of subfamilies are recognized in the Isocrinidae. In contrast, the classification of the suborder Comatulidina (the comatulids proper) relies on superfamilies, and these have been adopted herein. In summary, despite a number of contrasting opinions, the classification of RASMUSSEN and SIEVERTS-DORECK (1978) is not drastically modified. Pending further investigation on the classification of the Cladida, the Articulata is thus retained as a subclass, not as an infraclass of the Cladida (SIMMS & SEVASTOPULO, 1993); and the Articulata is divided into eight orders: Holocrinida, Encrinida, Isocrinida, Comatulida, Millericrinida, Hyocrinida, Cyrtocrinida, and Roveacrinida.

TREATISE CLASSIFICATION, 2011
(HESS & MESSING, herein)

Subclass ARTICULATA Zittel, 1879
  Order HOLOCRINIDA Jaekel, 1918
      Family HOLOCRINIDAE Jaekel, 1918
  Order ENCRINIDA Matsumoto, 1929
      Family ENCRINIDAE Dujardin & Hupé, 1862
      Family AINIGMACRINIDAE Hagdorn, 1988
      Family DADOCRINIDAE Lowenstam, 1942
      Family TRAUMATOCRINIDAE Mu, 1949
  Order ISOCRINIDA Sieverts-Doreck, 1952
    Suborder PENTACRINITINA Gray, 1842
      Family PENTACRINITIDAE Gray, 1842
      Family EOCOMATULIDAE Simms, 1988
    Suborder ISOCRININA Sieverts-Doreck, 1953
      Family ISOCRINIDAE Gislén, 1924
      Family CAINOCRINIDAE Simms, 1988
      Family ISSELICRINIDAE Klikushin, 1977
      Family PROISOCRINIDAE Rasmussen, 1978
  Order COMATULIDA A. H. Clark, 1908
    Suborder COMATULIDINA A. H. Clark, 1908
      Superfamily PARACOMATULOIDEA Hess, 1951
        Family PARACOMATULIDAE Hess, 1951
      Superfamily ATELECRINOIDEA Bather, 1899
        Family ATELECRINIDAE Bather, 1899
      Superfamily SOLANOCRINITOIDEA Jaekel, 1918
        Family SOLANOCRINITIDAE Jaekel, 1918
        Family DECAMERIDAE Rasmussen, 1978
        Family THIOLLIERICRINIDAE A. H. Clark, 1908
      Superfamily COMASTEROIDEA A. H. Clark, 1908
        Family COMASTERIDAE A. H. Clark, 1908
      Superfamily UINTACRINOIDEA Zittel, 1879
        Family UINTACRINIDAE Zittel, 1879
        Family MARSUPITIDAE d'Orbigny, 1852
      Superfamily MARIAMETROIDEA A. H. Clark, 1909
        Family MARIAMETRIDAE A. H. Clark, 1909

- Family COLOBOMETRIDAE A. H. Clark, 1909
- Family EUDIOCRINIDAE A. H. Clark, 1907
- Family HIMEROMETRIDAE A. H. Clark, 1908
- Family ZYGOMETRIDAE A. H. Clark, 1908
- Superfamily TROPIOMETROIDEA A. H. Clark, 1908
- Family TROPIOMETRIDAE A. H. Clark, 1908
- Family ASTEROMETRIDAE Gislén, 1924
- Family CALOMETRIDAE A. H. Clark, 1911
- Family CHARITOMETRIDAE A. H. Clark, 1909
- Family CONOMETRIDAE Gislén, 1924
- Family PSEUDOCONOMETRIDAE Eagle, 2001
- Family PTEROCOMIDAE Rasmussen, 1978
- Family PTILOMETRIDAE A. H. Clark, 1914
- Family THALASSOMETRIDAE A. H. Clark, 1908
- Superfamily NOTOCRINOIDEA Mortensen, 1918
- Family NOTOCRINIDAE Mortensen, 1918
- Family APOROMETRIDAE H. L. Clark, 1938
- Superfamily ANTEDONOIDEA Norman, 1865
- Family ANTEDONIDAE Norman, 1865
- Family PENTAMETROCRINIDAE A. H. Clark, 1908
- Family ZENOMETRIDAE A. H. Clark, 1909
- Superfamily UNCERTAIN
- Family JAEKELOMETRIDAE Hess, new family
- Family ATOPOCRINIDAE Messing, new family
- Superfamily and Family UNCERTAIN
- Suborder BOURGUETICRININA Sieverts-Doreck, 1953
- Family BOURGUETICRINIDAE de Loriol, 1882
- Family BATHYCRINIDAE Bather, 1899
- Family PHRYNOCRINIDAE A. H. Clark, 1907
- Family SEPTOCRINIDAE Mironov, 2000
- Suborder GUILLECRININA Mironov & Sorokina, 1998
- Family GUILLECRINIDAE Mironov & Sorokina, 1998
- Order MILLERICRINIDA Sieverts-Doreck, 1952
- Family MILLERICRINIDAE Jaekel, 1918
- Family APIOCRINITIDAE d'Orbigny, 1840
- Family NEODADOCRINIDAE Hess, 2006
- Family BANGTOUPOCRINIDAE Stiller, 2000
- Family UNCERTAIN
- Order HYOCRINIDA Rasmussen, 1978
- Family HYOCRINIDAE Carpenter, 1884
- Order CYRTOCRINIDA Sieverts-Doreck, 1952
- Suborder CYRTOCRININA Sieverts-Doreck, 1952
- Superfamily EUGENIACRINITOIDEA Roemer, 1855
- Family EUGENIACRINITIDAE Roemer, 1855
- Family GUTTICRINIDAE Klikushin, 1987
- Family HOYACRINIDAE Delogu & Nicosia, 1986
- Family PHYLLOCRINIDAE Jaekel, 1907
- Family PROHOLOPODIDAE Žitt, 1974
- Family PSALIDOCRINIDAE Žitt, 1978
- Family SCLEROCRINIDAE Jaekel, 1918
- Family UNCERTAIN
- Superfamily PLICATOCRINOIDEA Zittel, 1879
- Family PLICATOCRINIDAE Zittel, 1879
- Family TETRACRINIDAE Nicosia, 1991
- Family QUENSTEDTICRINIDAE Klikushin, 1987
- Suborder HOLOPODINA Arendt, 1974
- Family HOLOPODIDAE Zittel, 1879
- Family COTYLEDERMATIDAE Wright, 1876
- Family EUDESICRINIDAE Bather, 1899
- Family HEMIBRACHIOCRINIDAE Arendt, 1968
- Family PSEUDOSACCOCOMIDAE Patrulius, 1956
- Order ROVEACRINIDA Sieverts-Doreck, 1953
- Family ROVEACRINIDAE Peck, 1943
- Family AXICRINIDAE Hess, new family
- Family SACCOCOMIDAE d'Orbigny, 1852
- Family SOMPHOCRINIDAE Peck in Rasmussen, 1978
- Articulata Order UNCERTAIN
- Family CYCLOCRINIDAE Sieverts-Doreck, 1953
- Family LANTERNOCRINIDAE Kristan-Tollmann, 1990
- Family LEOCRINIDAE Kristan-Tollmann, 1990
- Family QINGYANOCRINIDAE Stiller, 2000
- Family TULIPACRINIDAE Kristan-Tollmann, 1980
- Articulata Order and Family UNCERTAIN
- NOMINA DUBIA
- Crinoidea Subclass UNCERTAIN

ARTICULATA

HANS HESS

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Subclass ARTICULATA Zittel, 1879

[*nom. transl.* MOORE, 1950, p. 50, *ex* suborder Articulata ZITTEL, 1879 in 1876–1880, p. 380] [=division Articulata MILLER, 1821, p. 13; incl. Stomatocrinoidea WACHSMUTH & SPRINGER, 1880, p. 253; Neocrinoidea CARPENTER & ETHERIDGE, JR., 1881, p. 296; Canaliculata E. J. CHAPMAN, 1883, p. 115; *non* Articulata WACHSMUTH & SPRINGER, 1887, p. 140 (=Flexibilia and some Inadunata)]

Cup dicyclic or cryptodicyclic without anal plates in the adult. Mouth exposed on the tegmen surface. Axial nerves enclosed in a canal penetrating the basals, radials, and brachials. Brachials generally connected by muscular articulation but nonmuscular articulations in almost all species. Arms pinnulate except in some microcrinoids. *Lower Triassic–Holocene.*

SIMMS (1988a) and SIMMS and SEVASTOPULO (1993) discussed the problems in defining the Articulata in detail. Articulates have typically been recognized by a suite of characters, but no single character is both unique to the group and readily recognizable in fossil material. Characters used in previous diagnoses have included the following: (1) cup simple dicyclic or cryptodicyclic; (2) anal plate absent in adult; (3) flexible tegmen with central peristome and exposed food grooves; (4) axial nerves enclosed in canals that penetrate the basals, radials, and brachials; (5) muscular articulation between radial and arm and between some or all brachials; (6) arms uniserial; (7) arms pinnulate. Clearly, not all of these characters are restricted to the articulates. Some camerates, flexibles, and cladids have dicyclic cups and/or uniserial arms. Inclusion of the Encrinida in the Articulata eliminates uniserial arms as being diagnostic. Not all encrinids have truly biserial arms, and some comatulids have nearly biserial arms with wedge-shaped brachials (see Fig. 39). Most camerates and advanced cladids (KAMMER & AUSICH, 2006), as well as articulates, have pinnulate arms, although muscular arm articulations in the arms are confined to the articulates and certain derived late Paleozoic cladids. Adult articulates lack an anal plate in the cup, but some juvenile comatulids and presumably other post-Paleozoic crinoids may possess one (SIMMS & SEVASTOPULO, 1993). Enclosure of the axial nerves within canals penetrating the basals, radials, and brachials is also not unique to articulates. A flexible tegmen with a centrally positioned peristome and exposed food grooves appears to be unique to the articulates, although these structures are rarely preserved in fossil material. The conclusion from this is that no single character can be used to define the articulates relative to other crinoids, with the possible exception of the tegminal structure. For fossil material, the most diagnostic characters are the absence of an anal plate in the adult cup; the enclosure of the axial nerves in a canal penetrating the basals, radials, and brachials; and pinnulate arms with well-developed muscular articulations. Articulates share with most advanced cladids muscular articulations along the arms and at the radial plate-first primibrachial articulation.

The name Articulata ZITTEL, 1879 in 1876–1880, is a homonym of Articulata HUXLEY (1869, p. 116), established for a class of the phylum Brachiopoda. Although the Law of Priority lacks any force under the *International Code of Zoological Nomenclature* (ICZN, 1999) as applied to suprafamilial taxa, it has been the policy of the *Treatise* editors to avoid, as far as possible, use of such homonyms for suprafamilial taxa. However, we can see no justification for suppressing ZITTEL's name, because the name Articulata has been used for both brachiopods and crinoids for more than a century, and suppression of the name for a group of crinoids would certainly deviate from long-established usage and lead to confusion.

HOLOCRINIDA

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Order HOLOCRINIDA Jaekel, 1918

[*nom. transl.* Hagdorn in Hagdorn, Głuchowski, & Boczarowski, 1996, p. 57, *ex* Holocrinidae Jaekel, 1918, p. 67]

Cup dicyclic, high and thick walled, barrel shaped or cylindrical, body cavity very narrow; cup strongly variable even at species level; infrabasals low, forming closed circlet; basals typically higher than radials. Radial articular facet directed upward, constricted, muscle fossae small. Synostosis between primibrachials 1 and 2 and secundibrachials 1 and 2; aboral-adoral median ridge may divide proximal facet of primaxil facet in 2 parts, resembling synarthry. Arms uniserial, highly flexible, with muscular and ligamentary (cryptosyzygial or synostosial) articulations, synostosial facets may have deep ligamentary pits separated by median ridge with a nerve canal; nerve canals mostly uniaxial, sometimes fused uniaxial, rarely paired; arms branch normally once at axillary second primibrachial, but larger specimens may have secondary or even tertiary branching on one or more rays. Tegmen high. Column pentagonal to subpentagonal or subcircular; articular facets symplectial with petaloid pattern, distal columnals with long, radial crenulae. Attachment by cirri; cirrinodals with 2 to 5 elliptical cirrus sockets, lower facets symplectial to cryptosymplectial. *Lower Triassic (Induan)–Upper Triassic (Carnian).*

Holocrinids are the earliest articulates and first appeared in small numbers in sediments of Lower Triassic (Scythian) age. Kashiyama and Oji (2004) described some very small columnals from the Smithian of Japan (see Fig. 7,*1p*), while Schubert, Bottjer, and Simms (1992) described similarly small columnals as well as cup and arm plates from the Spathian of North America. From these modest beginnings, the articulates radiated to form the taxa described below. Basal morphology of holocrinids with their column of cirrinodals and internodals united by symplexy or cryptosymplexy has thus proved to be particularly successful, as demonstrated by the living isocrinines and comatulids.

Family HOLOCRINIDAE Jaekel, 1918

[Holocrinidae Jaekel, 1918, p. 67]

Characters as for order. *Lower Triassic (Induan)–Upper Triassic (Carnian).*

Holocrinus Wachsmuth & Springer, 1887, p. 139 [**Encrinus beyrichi* Picard, 1883, p. 199; M]. Arms 5 to 15, long, branching irregularly. Column subcircular to pentalobate; 2 to 5 long cirri; proximal cirrals with elliptical, synarthrial articulation. Internodes short, of 5 to 9 columnals. Articular facet of columnals from proxistele and mesistele with short, marginal crenulae in a petaloid pattern similar to small columnals of isocrinids. [Distal facet of nodals is a symplexy in most cases, but cryptosymplexy has been mentioned from the earliest occurrence of *Holocrinus* in the Lower Triassic Hiraiso Formation (Smithian) of Japan (Kashiyama & Oji, 2004). A high tegmen with numerous plates, including smaller marginal and larger central plates reaching approximately the third secundibrachial, is in *H. beyrichi* and in a specimen with a partial crown referred to *H. wagneri* (Benecke, 1887).] *Lower Triassic (Induan)–Upper Triassic (Carnian):* Japan (Kashiyama & Oji, 2004), *Scythian (Smithian);* North America (Schubert, Bottjer, & Simms, 1992, described as *Holocrinus? smithi* (W. B. Clark in Clark & Twitchell, 1915), Alps, Slovenia, Hungary, *Scythian (Spathian);* Germany, Poland, Spain, *Anisian;* Poland, *Ladinian;* Turkey, China, New Zealand, *Carnian.*——Fig. 7,*1a.* **H. beyrichi* (Picard); crown, Anisian, Germany, lectotype, MNHB MB.E 508, ×3 (Neumann, new).——Fig. 7,*1b–n. H. meyeri* Hagdorn & Głuchowski, 1993, Anisian, Poland; *b–d,* nodal from mesistele, lateral, distal, proximal facets, GIUS-7-59/8f, ×5; *e,* facet of distal cylindrical internodal, MHI 1166/1/2, ×8; *f,* facet of distal internodal with long crenulae, GIUS-7-59/6i, ×8; *g,* facet of proximal cirral, GIUS-7-59/56, ×10; *h–i,* basal, *h,* adoral, *i,* distal, GIUS-7-59/57, ×10; *j–k,* radial, *j,* adoral, *k,* distal, GIUS-7-59/58, ×10; *l–m,* primibrachial 2, *l,* aboral, *m,* proximal, GIUS-7-59/60, ×10; *n,* cryptosyzygial facet of secundibrachial, GIUS-7-59/65, ×10 (Hagdorn, Głuchowski, & Boczarowski, 1996).——Fig. 7,*1o–p. Holocrinus* sp.; *o,* schematic view of proximal column and cup with attached arms, lateral view and section; *B,*

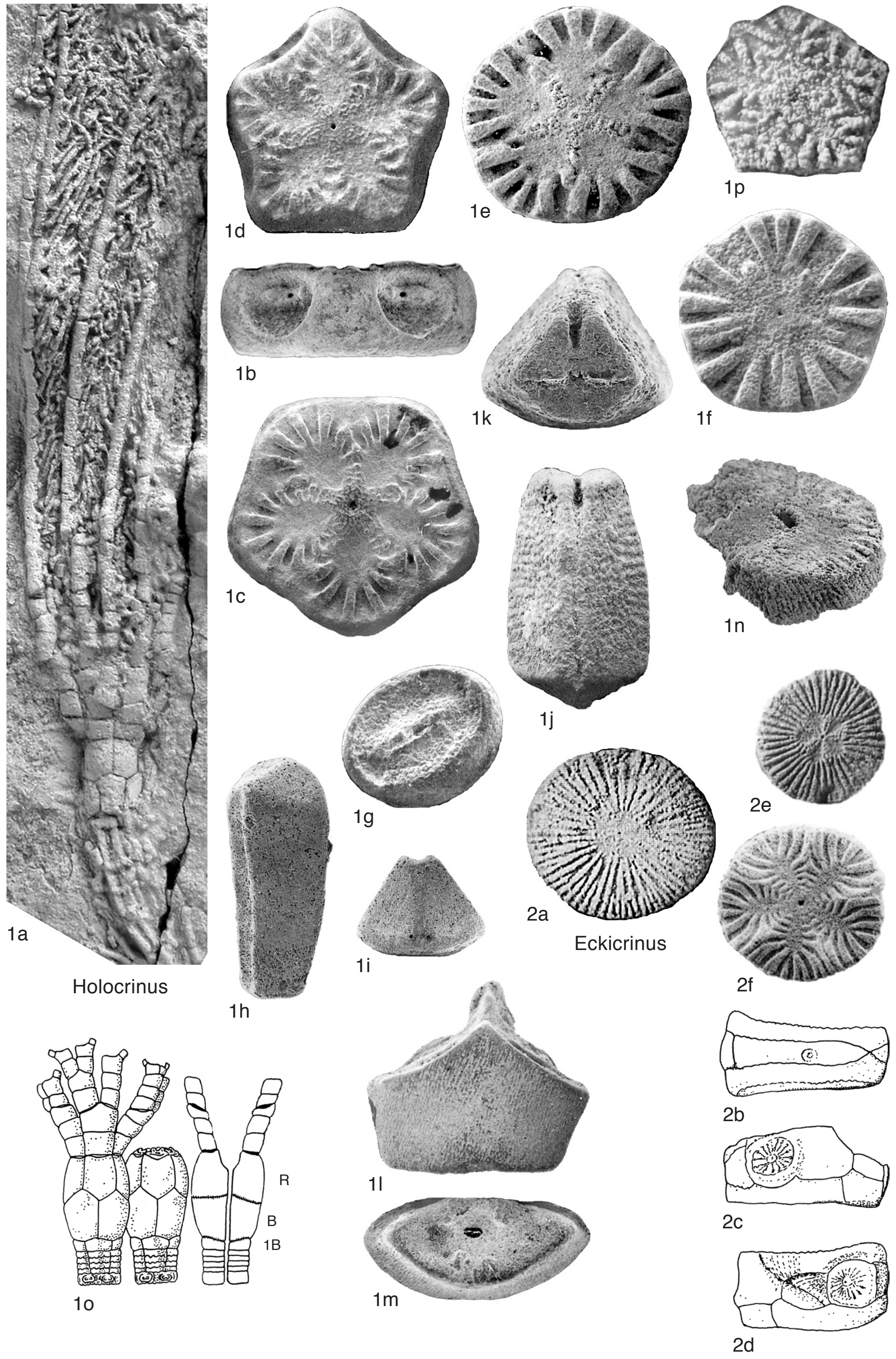

FIG. 7. Holocrinidae (p. 24–26).

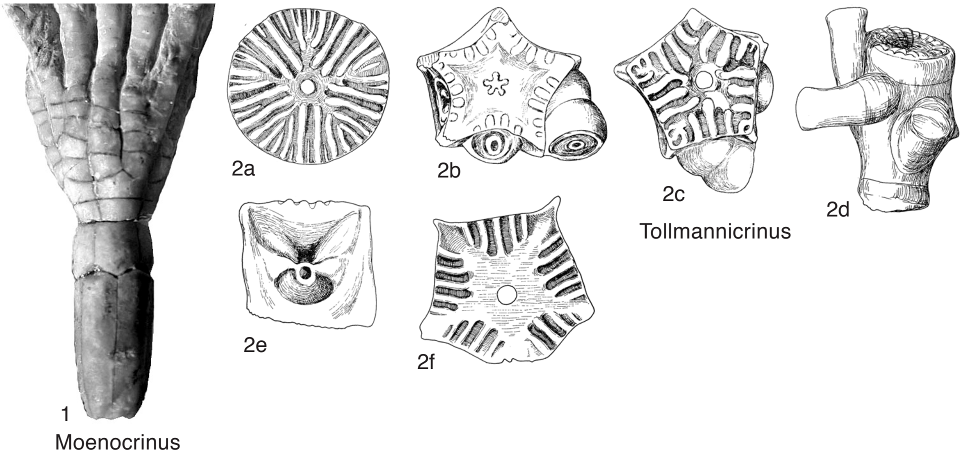

FIG. 8. Holocrinidae (p. 26–27).

basal; *R,* radial; *1B,* primibrachial; approximately ×3 (Hagdorn & Baumiller, 1998); *p,* facet of internodal, Scythian (Smithian), Japan, ×10 (Oji, new).

Eckicrinus HAGDORN & GŁUCHOWSKI, 1993, p. 174 [**Encrinus*? *radiatus* SCHAUROTH, 1859, p. 288; OD]. Crown unknown. Columnals mostly very low, circular to subcircular, cylindrical; proximal columnals with marginal crenulae and granulated radial bands, petal floors pyriform; distal columnals with long, marginal crenulae, petal floors very small; bifurcation and intercalation of extra culmina toward periphery. Nodals not wider than internodals, only slightly higher; 2 to 5 circular cirrus sockets, fulcral ridge indistinct or lacking; enlarged cirri with multiradiate articulation; cirrus sockets small or large, large sockets may extend over several columnals. Internodes very short, of 2 to 6 columnals. [The petaloid articular facet pattern with symplectial lower nodal facets suggests that *Eckicrinus* is a holocrinid. It differs from all other holocrinid genera, except *Tollmannicrinus*, by having very low columnals and circular cirrus sockets. These are typically very small but may include both infranodal and supranodal and have a multiradiate articulation pattern. Because the cup of *Eckicrinus* is unknown, assignment to the Holocrinidae is uncertain. Striking similarity with the isocrinids *Laevigatocrinus insignis* (TOULA, 1877) (Carnian, Tethys) and *Austinocrinus* (Upper Cretaceous), both in articulation facet pattern and in size and morphology of cirrus sockets, is regarded as a convergence of low, cylindrical columnals. These isocrinid taxa have nodals with cryptosymplectial or synostosial lower facets. The circular cirrus sockets of *Austinocrinus* may also include several columnals and may have multiradiate crenulae in addition to a synarthrial type transverse ridge (RASMUSSEN, 1961, pl. 2,*8;* KLIKUSHIN, 1992, pl. 14,*13*). Because of its articulation facet pattern, KLIKUSHIN (1979b) included *E. radiatus* in his isocrinid genus *Laevigatocrinus*. It differs from this genus by the small, circular cirrus sockets, the principally very low columnals, and the symplectial lower nodal facet.] *Middle Triassic (Anisian):* Alps, Poland, Amur Basin.——FIG. 7,*2a–f.* **E. radiatus* (SCHAUROTH); *a,* facet of internodal, Anisian, Italy, lectotype, NMC 2682-L, ×5 (Hagdorn, Głuchowski, & Boczarowski, 1996); *b–d,* pluricolumnal with 2 cirrus sockets, lateral views, Anisian, Italy, ×3.5 (Hagdorn, Głuchowski, & Boczarowski, 1996; original in Quenstedt, 1876, pl. 107,*87*); *e,* facet of internodal, Anisian, Italy, ×3.5 (Hagdorn, Głuchowski, & Boczarowski, 1996; original in Quenstedt, 1876, pl. 107,*83*); *f,* facet of proximal columnal, Anisian, Hungary, MHI 1563/7, ×7 (Hagdorn, Konrád, & Török, 1997).

Moenocrinus HILDEBRAND, 1926, p. 259 [**M. deeckei;* M]. Arms divided at primibrachial 2 and at some secundibrachials 2. Nonmuscular articulations apparently at every second brachial articulation. Column rounded subpentagonal to slightly pentalobate in its entire length; proximal columnals low but uniform, not alternating. Nodals few; internodes long, of approximately 17 internodals or more. Articular facet of columnals with more or less distinct marginal crenulae, which may be short and uniform or may be longer in radial marginal area, thus delimiting a more or less petaloid or stellate, smooth central area. Nodals with 5 rounded cirrus sockets facing outward or, especially in proximal part of column, slightly upward. Cirri short, circular in section. *Middle Triassic (Anisian):* Germany.——FIG. 8,*1.* **M. deeckei;* base of crown, holotype, BSP 1926 I 33, ×3 (Hagdorn, new).

Tollmannicrinus KLIKUSHIN, 1992, p. 73 [**Entrochus saklibelensis* KRISTAN-TOLLMANN, 1975, p. 292; OD]. Crown unknown. Proximal column pentagonal, more distally circular, smooth; columnals high, nodals larger than internodals; proximal articular facets with crenulae grouped in radial areas and star-shaped areola, more distal columnar facets with radiating, commonly branching crenulae and very small areola. Number of nodals few in relation to internodals. Cirrus sockets 5, in proximal columnals small and widely separated, in distal columnals prominent and commonly different in size. Enlarged cirri in distal part of column with multiradiate articulation. Distalmost part of column may be swollen without a scar or axial canal. [KRISTAN-TOLLMANN (1975) and KLIKUSHIN (1992) combined the genus from isolated columnal material. KRISTAN-TOLLMANN (1975, fig. 16/1 and 4) figured juvenile nodals with a symplectial proximal facet and a cryptosymplectial distal facet, an arrangement that is different from most other holocrinids. Because the cup is unknown, assignment to the Holocrinidae is provisional.] *Middle Triassic (Anisian)–Upper Triassic (Carnian):* Italy, Hungary, Turkey, China, New Zealand.——FIG. 8,*2a–f*. **T. saklibelensis* (KRISTAN-TOLLMANN), Turkey; *a,* facet of columnal from mesistele, Ladinian, holotype, Kr-To V 70, ×15; *b–c*, nodal with cirrals, *b*, distal facet, *c*, proximal facet, Ladinian, Kr-To 73/63/32, ×25; *d,* distal columnal with cirrus sockets and cirrals, Ladinian, Kr-To 73/63/4, ×15; *e–f,* nodal, *e,* lateral, *f,* proximal facet, Carnian, Kr-To 73/63/32, ×15 (Kristan-Tollmann, 1975).

ENCRINIDA

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Order ENCRINIDA Matsumoto, 1929

[*nom. transl. et correct.* Hagdorn, 1988, p. 73, *ex* suborder Encrinacea Matsumoto, 1929, p. 30] [=suborder Encrinina Sieverts-Doreck in Ubaghs, 1953, p. 757; *emend.*, Hagdorn, 1988, p. 73, to include Traumatocrinidae and Ainigmacrinidae; *emend.*, Hess, herein, to include Dadocrinidae]

Cup symmetrical, dicyclic, or cryptodicyclic with small infrabasals; infrabasals may be absent; basals partly or completely hidden by column. Basals, radials, and brachials with paired axial canals. Cryptosyzygy or synostosis between primibrachials 1 and 2. Primibrachial 2 axillary. Arm uniserial in juveniles; in adults, uniserial proximally and commonly biserial distally; in dadocrinids uniserial throughout arms. Brachial articulations muscular and ligamentary (cryptosyzygial and synostosial). Tegmen comparatively low to high, anal cone short. Column cylindrical to pentalobate proximally with nodals that may bear rudimentary cirri; distal column cylindrical with multiradiate crenulation, nodals like internodals. Attachment by discoid or irregularly encrusting terminal holdfast, or by articulated radicular cirri of terminal columnals. *Middle Triassic (Anisian)–Upper Triassic (lower Carnian).*

Family ENCRINIDAE Dujardin & Hupé, 1862

[*nom. correct.* ICZN, 1962, p. 263, *pro* Encriniens Dujardin & Hupé, 1862, p. 161]

Cup low cone- to low bowl-shaped, base flat or depressed. Infrabasals completely and basals partly hidden in columnar pit. Interradial facets synostosial, smooth or with marginal crenulae. Arm branching isotomous at primibrachial 2 in 10-armed forms, additionally at secundibrachial 2 in 20-armed forms, and further distally endotomous branching in forms with more than 20 arms. Arms biserial after secundibrachial 2 to 10. No interradials. No radicular cirri in terminal disk. *Middle Triassic (Anisian)–Upper Triassic (lower Carnian).*

Encrinus Lamarck, 1801, p. 379 [**E. liliiformis;* SD ICZN, 1962, p. 262] [=*Encrina* Bronn, 1848 in 1848–1849, p. 459, *nom. null.; =Jenaicrinus* Jaekel, 1918, p. 67 (type, *Encrinus* cf. *aculeatus* von Meyer, 1847, in Wagner, 1886, p. 28, pl. 2,*15,* OD)]. Cup low, bowl shaped, pentagonal to subcircular, flat base. Arms 10, proximally uniserial, biserial after secundibrachials 1 to 10. Column moderately long to very long, proximally subpentagonal to cylindrical, distally cylindrical; proximal nodals thickened, with or without cirri; distal columnar facets multiradiate. [For a discussion of authorship, see ICZN Opinion 636, 1962, where the validation for *Encrinus* Schulze (1760, p. 21) was rejected, because the author did not apply the principles of binomial nomenclature (Case 434). Previously, Schulze was considered by Bather (1909c) and Biese (1934) to be the author of the genus.] *Middle Triassic (Anisian)–Upper Triassic (lower Carnian):* Austria, France, Germany, Italy, Poland, Switzerland, ?New Zealand.——Fig. 9*a–f.* **E. liliiformis,* Anisian, Germany*; a,* crown with proximal column, MHI 1043/3, ×1 (Hagdorn, 2004b); *b,* partly opened crown with tegmen, ×1 (Ausich & others, 1999); *c,* proximal view of cup with infrabasal, basal, and radial circlets, MHI 1214/1, ×2 (Hagdorn, 2004b); *d,* oblique proximal-adoral view of radial, MHI 1877/1, ×2.5 (Hagdorn, new); *e,* facet of proximal columnal, NMB M10606, ×3; *f,* facet of columnal, NMB M10607, ×3 (Hess, new).——Fig. 10*a.* **E. liliiformis; a,* reconstruction of an encrinid bioherm from the Crailsheim Trochitenkalk, Anisian, Germany. Crinoids of different ages are attached with holdfasts (*c*) to the oysterlike terquemiids *Newaagia noetlingi* (*a*) and *Enantiostreon difforme* (*b*); also shown are brachiopod *Coenothyrus vulgaris* (*d*), mussels *"Mytilus" eduliformis* (*e*) and *Myalina blezingeri* (*f*), *Pleuronectites laevigatus* (*g*), *Placunopsis ostracina* (*h*), serpulid *Spirorbis valvata* (*i*), and juvenile *E. liliiformis* (*j*); on the seafloor are *Plagiostoma striatum* (*k*), snail *Naticella triadica* (*l*), and echinoid *Serpianotiaris coeva* (*m*); infaunal elements include *Palaeoneilo elliptica* (*n*) and *Palaeonucula goldfussi* (*o*) (Hagdorn, 2004b).——Fig. 10*b–c. Encrinus* sp. cf. *brahli* Overweg, 1850; growth stages, upper row enlarged to same scale as lower, Anisian, Germany, MHI1152/16 (*1*); MHI1152/3 (*2*); MHI1152/15 (*3*); MHI1152/14 (*4*); CSG E-69 (*5*); CKB E-11 (*6*); *B,* basal; *R,* radial; *IBr,* primibrachial (Hagdorn & Schulz, 1996).

Cassianocrinus Laube, 1865, p. 274, *emend.,* Hagdorn 2004a, p. 246 [**Encrinus (Cassianocrinus) tetarakontadactylus* Laube, 1865, p. 274;

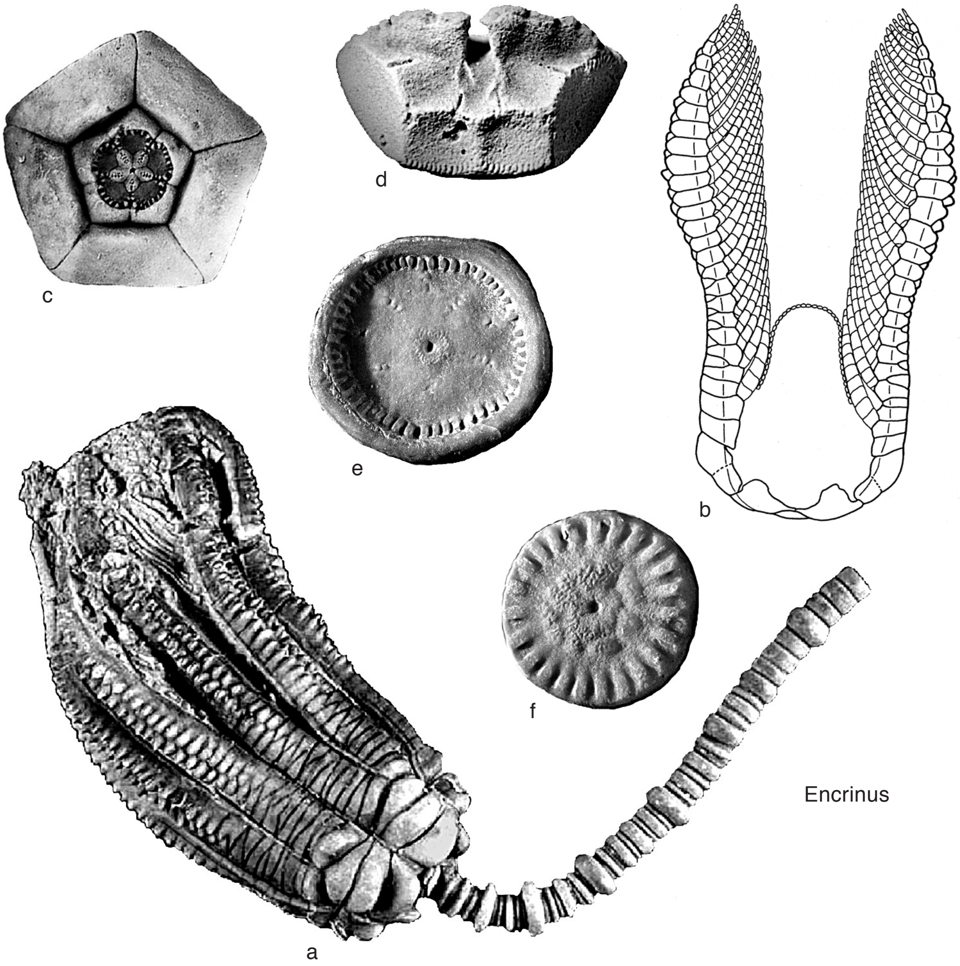


Fig. 9. Encrinidae (p. 28).

M; =*Encrinus varians* Münster, 1841, p. 52]. Cup flat, base depressed, rounded pentagonal to almost circular; basal circlet almost completely hidden by column, aboral pit flat; diameter of columnal articular facet less than half of cup diameter. Radial articular facet directed upward; ridge of aboral ligament pit with distinct marginal crenulae. Primibrachial 2 and secundibrachial 2 axillary, subsequent branching endotomous, more than 20 arms. Arms biserial from secundibrachial 2 to 5. Aboral side of axillaries convex. Pinnulars with distal hook. Column cylindrical; proximal part of column with nodals that rarely carry cirri; cirrus sockets circular, with multiradiate facets. Facets of proximal columnals with short marginal crenulae and petaloid pattern of short granules originating radially from perilumen. Distal columnals with short, multiradiate ridges and a string of granules around perilumen. *Middle Triassic (upper Ladinian)–Upper Triassic (lower Carnian):* Italy, Austria, Germany, Romania.——Fig. 11,*1a–h*. **C. varians* (Münster), type of *E. (C.) tetarakontadactylus* Laube, Italy; *a,* juvenile crown, NHMW 1865/IX/130, ×3.6 (Hagdorn, 2004a); *b–d,* cup, *b*, lateral, *c*, proximal, *d*, distal, lectotype, BSP 1877 X 1013, ×2 (Hagdorn, 2004a); *e,* part of biserial crown, NHMW 1865/0050/0259, ×3; *f,* nodal, NHMW 2006z0264/0008, ×3; *g,* columnal facet, NHMW 2006z0264/0007, ×3; *h,* aboral view of cup, NHMW 2006z0261/0002, ×2 (Hagdorn, new).

Chelocrinus von Meyer, 1837, p. 260, *emend.*, Hagdorn 2004a, p. 247 [**Encrinites schlottheimii* Quenstedt, 1835, p. 223; M] [=*Chelocrinites* Geinitz, 1846, p. 540, *nom. van.*]. Cup low, bowl shaped, pentagonal, flat base; basal pit

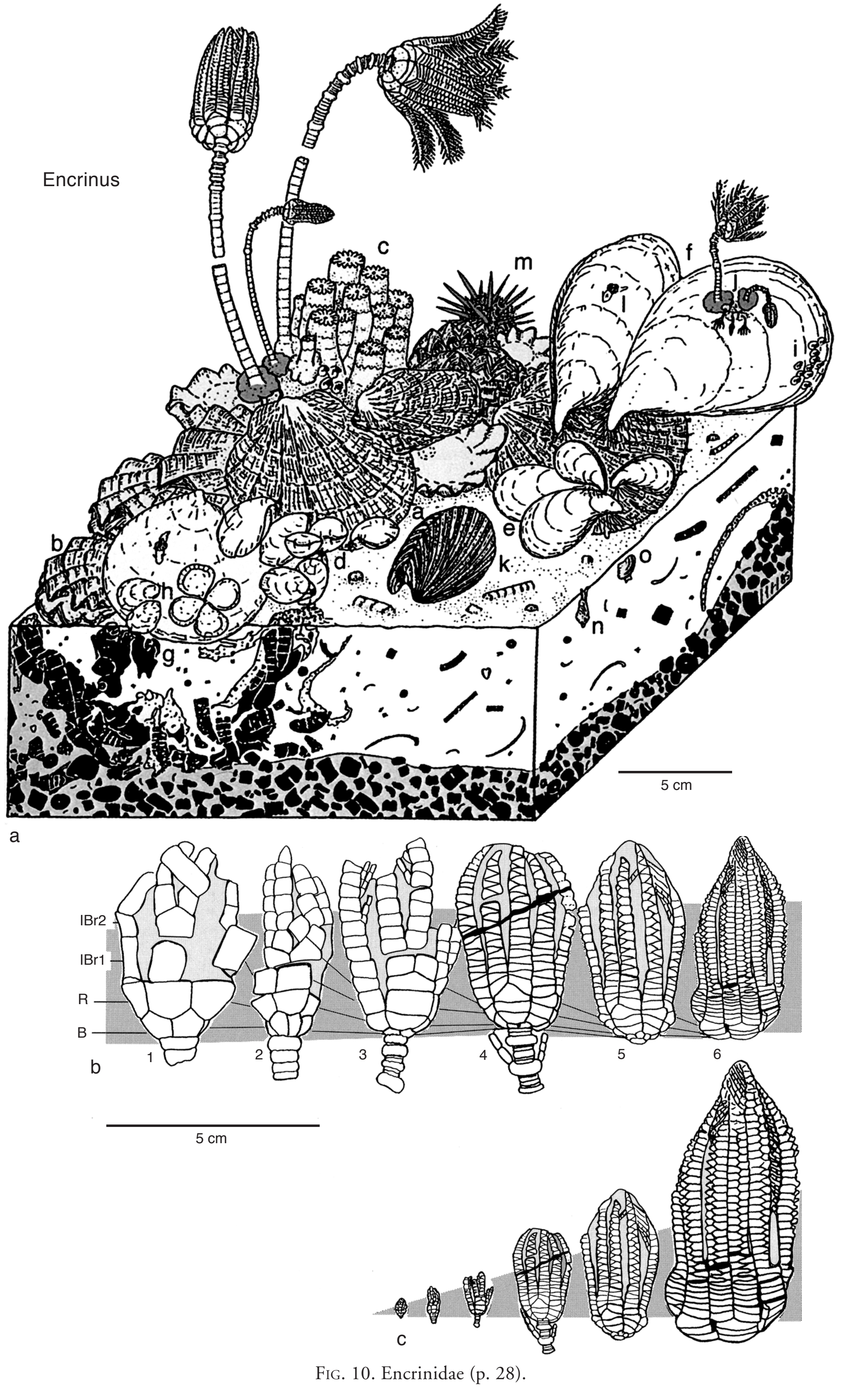


FIG. 10. Encrinidae (p. 28).

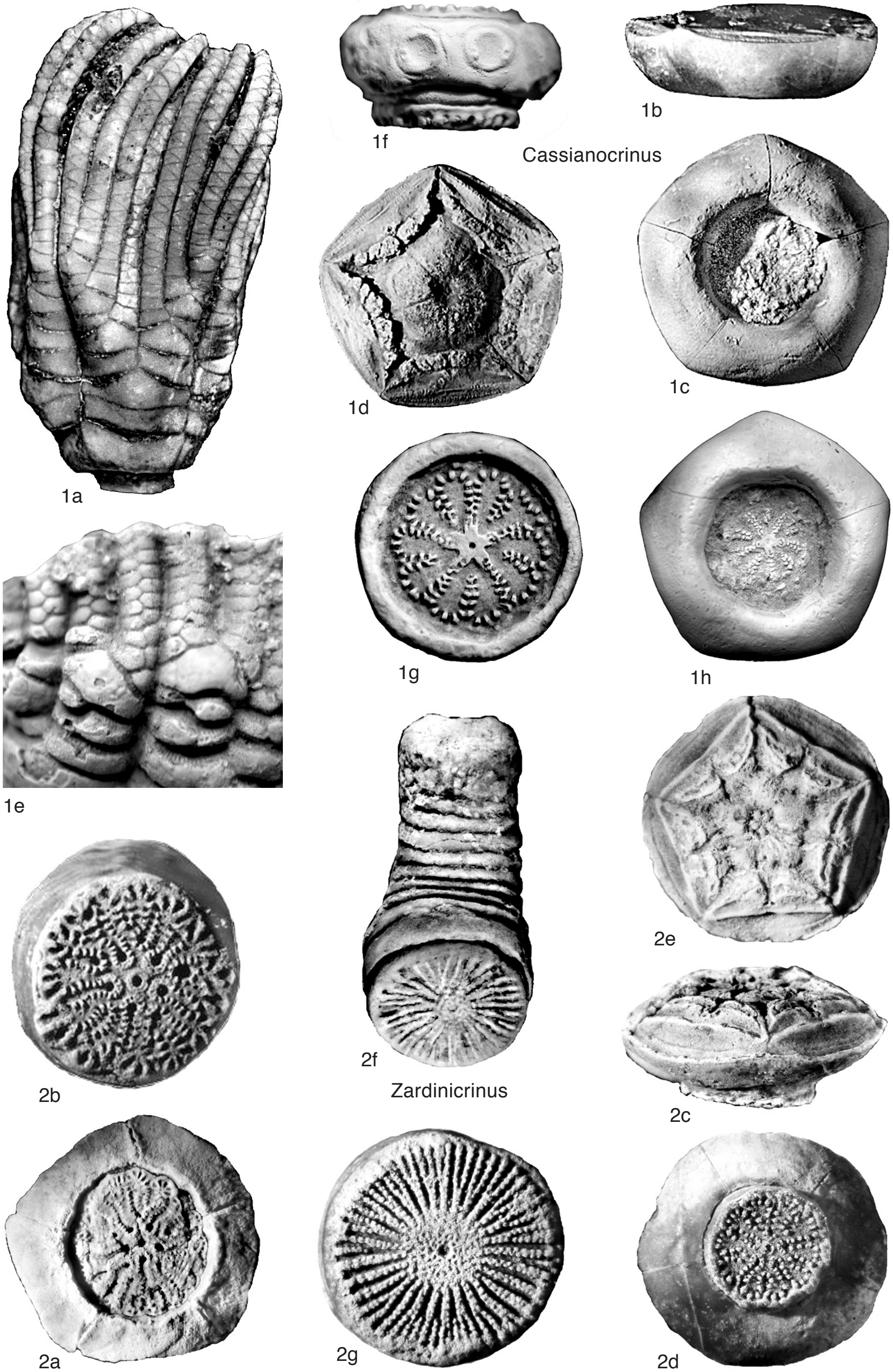


FIG. 11. Encrinidae (p. 28–33).

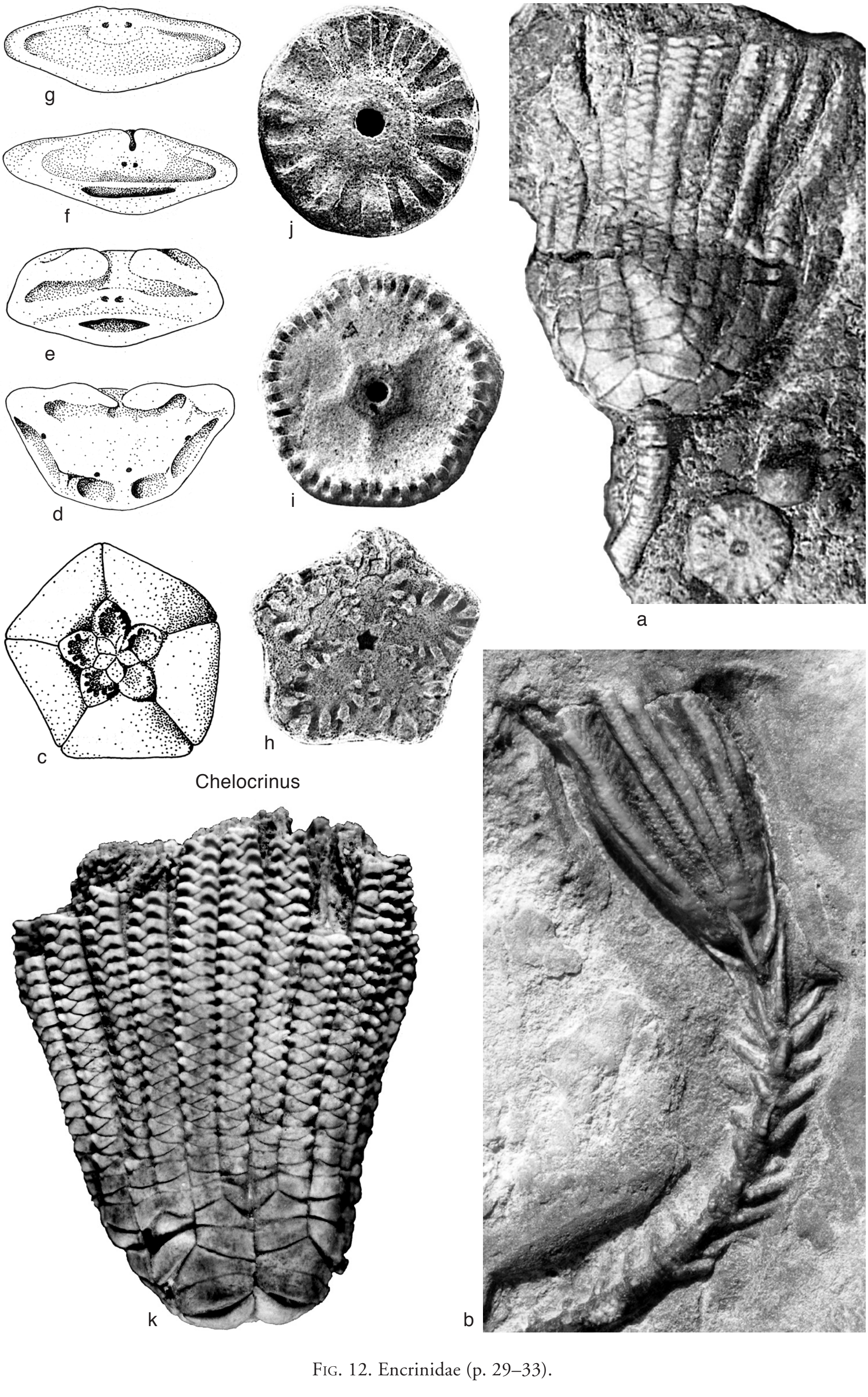


FIG. 12. Encrinidae (p. 29–33).

moderately deep to shallow, subpentagonal to subcircular; basals partly hidden in columnar pit. Primibrachial 2 and secundibrachial 2 axillary. Arms 20, biserial after secundbrachial 4 to 10. Pinnulars with distal hook. Column moderately long, proximally subpentagonal to circular, nodals with or without cirri; distal columnals circular with multiradiate facets. [The original species name, *schlottheimii*, is a printing error. On QUENSTEDT's original label of the holotype E85 is the name *Encrinites Schlotheimii* (reproduced by HAGDORN, 1991, p. 13). The same name was used by VON MEYER (1837, p. 262) and again by QUENSTEDT (1876, p. 470). Subsequent authors (BIESE, 1934, p. 83; HAGDORN, 2004a) used *Chelocrinus schlotheimi.*] *Middle Triassic (upper Anisian)–Upper Triassic (lower Carnian):* Germany, Italy, USA (?Nevada).——FIG. 12*a–k*. **C. schlotheimii* (QUENSTEDT), upper Muschelkalk, Germany; *a,* crown with tertibrachials, holotype, MNHB Quenstedt Kat. P. 1340, E 85, ×2 (Hagdorn, 1982); *b,* crown of subadult specimen with strong cirri on proximal column, Coll. Weissmüller, Kassel, ×1 (Weissmüller, new); *c,* proximal view of cup with infrabasals and basals, NMBi ES/mo1-2/3, ×3 (Hagdorn, 1982); *d–e,* radial, *d,* adoral, interradial facets and facets to basals synostosial with deep ligamentary pits, *e,* distal, MHI 1124/3, ×5 (Hagdorn, 1982); *f–g,* primibrachial 1, *f,* proximal, *g,* distal, MHI 1124/7, ×5 (Hagdorn, 1982); *h,* facet of isocrinid-like proximal internodal, MHI 1093/11, ×10 (Hagdorn, 1982); *i,* facet of proximal internodal, MHI 1124/20, ×10 (Hagdorn, 1982); *j,* facet of columnal from mesistele, MHI 1124/22, ×10 (Hagdorn, 1982); *k,* crown, MHI 1093/14, ×3 (Hagdorn, 2004b).

Zardinicrinus HAGDORN, 2004a, p. 247 [**Apiocrinites*? *granulosus* MÜNSTER, 1834, p. 8; M]. Cup flat, rounded pentagonal, base depressed; basal pit circular, very deep, with steep sides completely filled by column; diameter of pit wider than half of cup diameter. Basal circlet completely hidden. Radial articular facet wide, inclined. Primibrachial 2 and secundibrachial 2 axillary, tertibrachial 2 may also be axillary. More than 20 arms. Columnals cylindrical or elliptical, very low, no cirri. Facets of proximal columnals with short ridges arranged in loops, within the loops 5 longitudinal tubuli; facets of distal columnals with long, granulated ridges that may bifurcate, additional ridges intercalated; perilumen smooth or finely granulated. *Middle Triassic (Ladinian)–Upper Triassic (lower Carnian):* Italy.——FIG. 11,*2a–g*. **Z. granulosus* (MÜNSTER); *a,* proximal view of cup, lectotype, BSP 1877 X 1015, ×3 (Hagdorn, new; also figured by Münster, 1841); *b,* facet of proximal columnal, syntype, BSP 1877 X 1023, ×5 (Hagdorn, new); *c–e,* cup with proximal column, *c,* lateral, *d,* proximal, *e,* distal, syntype, BSP 1877 X 1014, ×2 (Hagdorn, new; also figured by Münster, 1841); *f–g,* column, *f,* lateral, ×2.5, *g,* distal facet, syntype, BSP 1877 X 1022, ×5 (Hagdorn, new; also figured by Münster, 1841).

Family AINIGMACRINIDAE Hagdorn, 1988

[Ainigmacrinidae HAGDORN, 1988, p. 74]

Small crinoids with extremely enlarged first columnal (calyconodal), enclosing aboral side of cup; calyconodal with 5 large cirrus sockets with fulcrum; cirrals flat, very large. Cup dicyclic, enclosed by calyconodal proximally to just below radial articular facet. Infrabasals very small, basals large. Primibrachials very low; primibrachial 2 axillary, prolonged into long aboral spine. Other columnals circular, facets with short radial crenulae. *Middle Triassic (Ladinian)–Upper Triassic (Carnian).*

Ainigmacrinus HAGDORN, 1988, p. 74 [**A. calyconodalis;* M]. Characters as for family. *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* Italy.——FIG. 13,*1a–f*. **A. calyconodalis*, Carnian; *a,* reconstruction of juvenile individual in feeding position with opened cirrus cover, ×5; *b,* reconstruction of juvenile individual protected by closed cirrus cover, ×5; *c,* proximal (upper) side of calyconodal, holotype, BSP AS VII 563, ×20; *d,* proximal side of calyconodal with infrabasal and basal circlets, SMNS 24846, ×20; *e,* lateral view of calyconodal with cup and proximal columnal, BMNH E5299/1, ×13; *f,* oblique distal view of calyconodal with cup, MCA 1001, ×10 (Hagdorn, 1988).

Family DADOCRINIDAE Lowenstam, 1942

[Dadocrinidae LOWENSTAM, 1942, p. 1832]

Cup conical, dicyclic to cryptodicyclic. Basals contiguous, connected by synostoses with deep ligament pits; these may also be flat with crenulate edge in *Carnallicrinus.* Radial articular facet sloping outward, radial cavity wide; interradial facets and facets to basals with deep ligament pits. Arms 5, 10, or 20, uniserial in *Dadocrinus,* tending to biserial in *Carnallicrinus,* synostosis between primibrachials 1 and 2 and secundibrachials 1 and 2. Tegmen high, composed of polygonal platelets. Column cylindrical or proximally pentalobate, no cirri. Attachment by terminal disk. [The dadocrinids have commonly been regarded to belong to Millericrinida, e.g., by RASMUSSEN (1978), KLIKUSHIN (1987c), and SIMMS (1988a). However, *Dadocrinus* has basals and radials

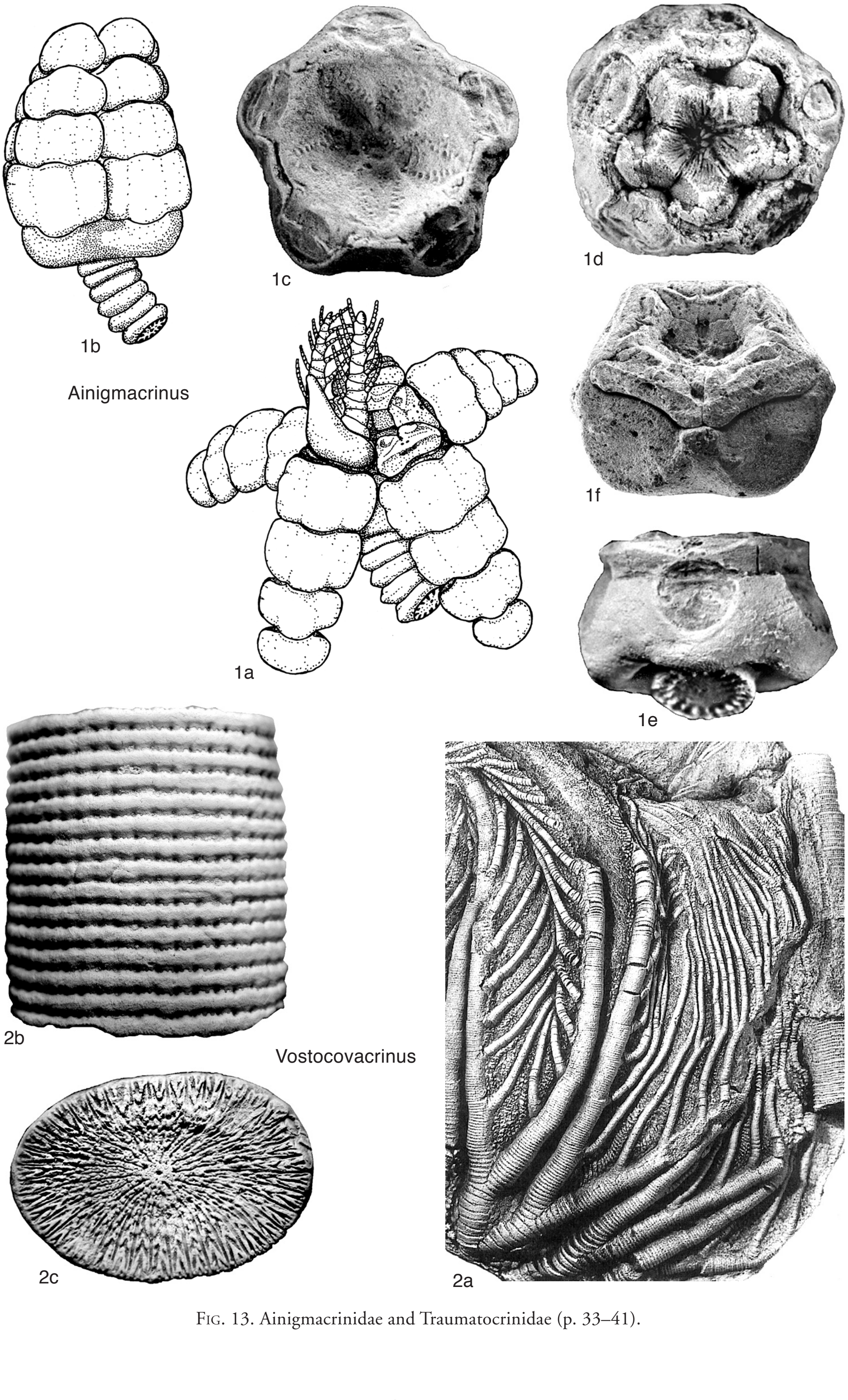


FIG. 13. Ainigmacrinidae and Traumatocrinidae (p. 33–41).

connected by synostoses with deep ligament pits (Hagdorn, 1996b, pl. 1,*i,k,l*), quite unlike millericrinids. Hagdorn (1996b, 1999a, 1999b) considered Dadocrinidae to be encrinids in which juveniles and less specialized forms also have uniserial arms, similar cup structure, and comparable attachment disks with strongly crenulate columnal facets. Hagdorn (2011) transferred *Carnallicrinus* from Encrinidae to this family.] *Middle Triassic.*

Dadocrinus von Meyer, 1847, p. 575 [**Encrinus gracilis* von Buch, 1845, p. 27; M] [=*Calathocrinus* von Meyer, 1847, p. 576 (type, *C. digitatus,* M; according to Beyrich, 1858, p. 45, a synonym of *Dadocrinus gracilis*); =*Cremacrinus* Jaekel, 1918, p. 70 (type, *Apiocrinus recubariensis* Crema, 1896, p. 858, OD; =*Millericrinus recubariensis* Bather, 1897, p. 123), *non* Ulrich, 1886; =*Recoarocrinus* Gislén, 1924, p. 201, obj., *nom. nov. pro Cremacrinus* Jaekel, 1918, p. 70 (type, *Apiocrinus recubariensis* Crema, 1896, p. 858, OD)]. Cup conical, dicyclic to cryptodicyclic, base convex. Basals and radials high and thin. Arms 5 or 10, brachials relatively high, rectangular. Pinnulars smooth or distally with small hooks. [The species *D. kunischi* Wachsmuth & Springer, 1887, and *D. grundeyi* Langenhan, 1903, may be ecophenotypes (Hagdorn, 1996b).] *Middle Triassic:* Austria, Germany, Italy, Poland, Hungary.——Fig. 14*a–c.* **D. gracilis* (von Buch), Anisian, Italy; *a,* adoral view of radial and primibrachial 1, interradial facets and facets to basals synostosial with deep ligamentary pits, MHI 1283/13, ×25 (Hagdorn, 1996b); *b*, adoral view of basal, interbasal facets, and facets to radials synostosial with deep ligamentary pits, MHI 1283/15, ×25 (Hagdorn, 1996b); *c*, facet of proximal columnal, MHI 1283/22, ×17 (Hagdorn, 1996b).——Fig. 14*d–g. D. kunischi* Wachsmuth & Springer, Anisian; *d,* slab with 2 crowns, Germany, MHI 1284/1, ×1.6 (Hagdorn, 1999a); *e*, attachment disk with distal column, Poland, MHI 1290, ×1.5 (Hagdorn, 1996b); *f,* facet of columnal from proxistele, Poland, NMB M10604, ×5; *g*, columnal facet, Poland, NMB M10605, ×5 (Hess, new).——Fig. 14*h–i. D. grundeyi* Langenhan, Anisian, Poland; *h,* cup with proximal column, MHI 1287/1, ×6; *i*, base of crown, MHI 1287/10, ×4 (Hagdorn, new).

Carnallicrinus Hagdorn, 2004a, p. 246 [**Encrinus (Chelocrinus) carnalli* Beyrich, 1856, p. 10; M] [=*Beyrichocrinus* Jaekel, 1918, p. 67 (type, *B. humilis*, M), *non* Waagen & Jahn, 1899, p. 12]. Cup low cone shaped, rounded pentagonal, cryptodicyclic. Radials wide and rather low; basals radially elongate, visible in side view. Primibrachial 2 and secundibrachial 2 axillary. Arms 20, brachials low, wedge shaped, with oblique articular facets tending to biserial condition. Proximal brachials with flat aboral side and sharp edges, distal brachials increasingly rounded. Pinnulars pectinate. Column long, nodals without cirri. *Middle Triassic (Anisian):* Germany, Poland.——Fig. 15*a–e.* **C. carnalli* (Beyrich); *a,* crown and proximal column, Germany, ×0.5 (Hellmund & others, 2006); *b,* oblique proximal view of primibrachial 1, Poland, GIUS-7-59/47, ×7; *c,* proximal view of primibrachial 2, Poland, GIUS-7-59/51, ×6 (Hagdorn, Głuchowski, & Boczarowski, 1996); *d–e,* cup, *d,* aboral with columnal, *e,* lateral, Germany, HGD 1, ×3 (Hagdorn, 1982).——Fig. 16. **C. carnalli* (Beyrich); aboral view of splayed crown, Germany, HGD, ×1.2 (Hagdorn, 1999b).

Family TRAUMATOCRINIDAE Mu, 1949

[Traumatocrinidae Mu, 1949, p. 86]

Cup very small. Rays 5, branching twice isotomously into 4 major arms per ray, further distal, multiple, endotomous branchings into many smaller armlets. Brachial articulations ligamentary. Brachials pinnulate. Tegmen includes irregular plating of polygonal interradials between proximal part of each major arm. Column long, proximally with distinct nodals and internodals; nodals without cirri. Columnals very low, circular to elliptical; articular facets with very short crenulae, arranged in multiradiate ridges of chevron-like pattern; between the ridges, fossulae appearing as intercolumnar pores at the column surface; in proximal column, fossulae leading to longitudinal tubuli running parallel to narrow axial canal. [Colonies of *Traumatocrinus*, attached to driftwood in black shale sediments, document a pseudoplanktonic lifestyle for this specialized offshoot of otherwise benthic encrinids; see discussion in *Treatise Online,* Part T, Revised, vol. 1, Chapter 19.] *Middle Triassic (Ladinian)–Upper Triassic (lower Carnian).*

Traumatocrinus Wöhrmann, 1889, p. 190 [**Porocrinus caudex* Dittmar, 1866, p. 394; SD Hagdorn, Wang, & Wang, 2007, p. 183]. Cup cryptodicyclic, infrabasals reduced or lacking, basals small, completely concealed by column. Radials low, with low exposed surface; aboral ligament area large, flat, inclined outward with numerous radial ridges composed of strings of nodules, tending to be chevron-like near interradial margins. First interradial large, intercalating between radials. Primibrachial 2 axillary,

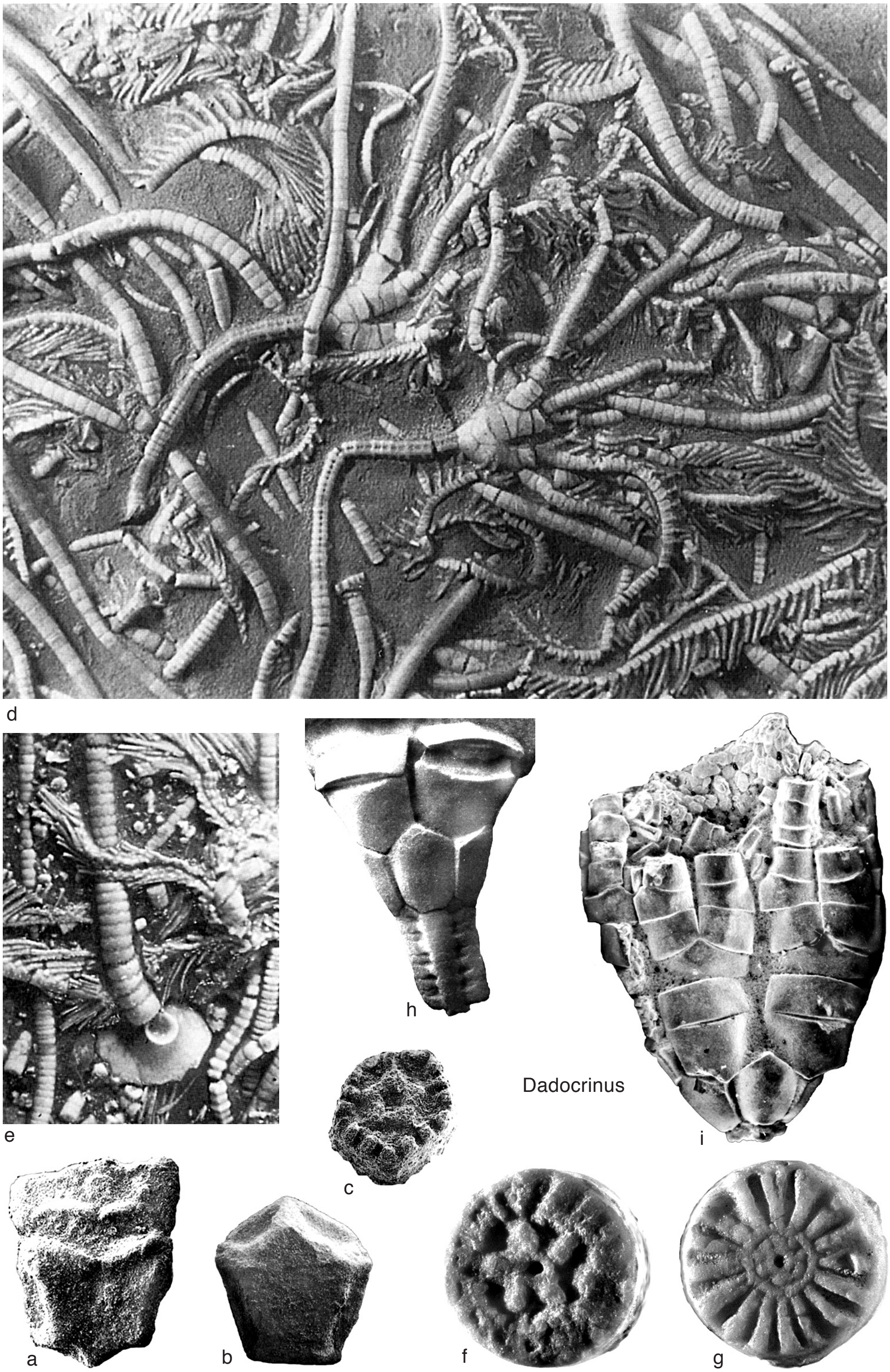


FIG. 14. Dadocrinidae (p. 35).

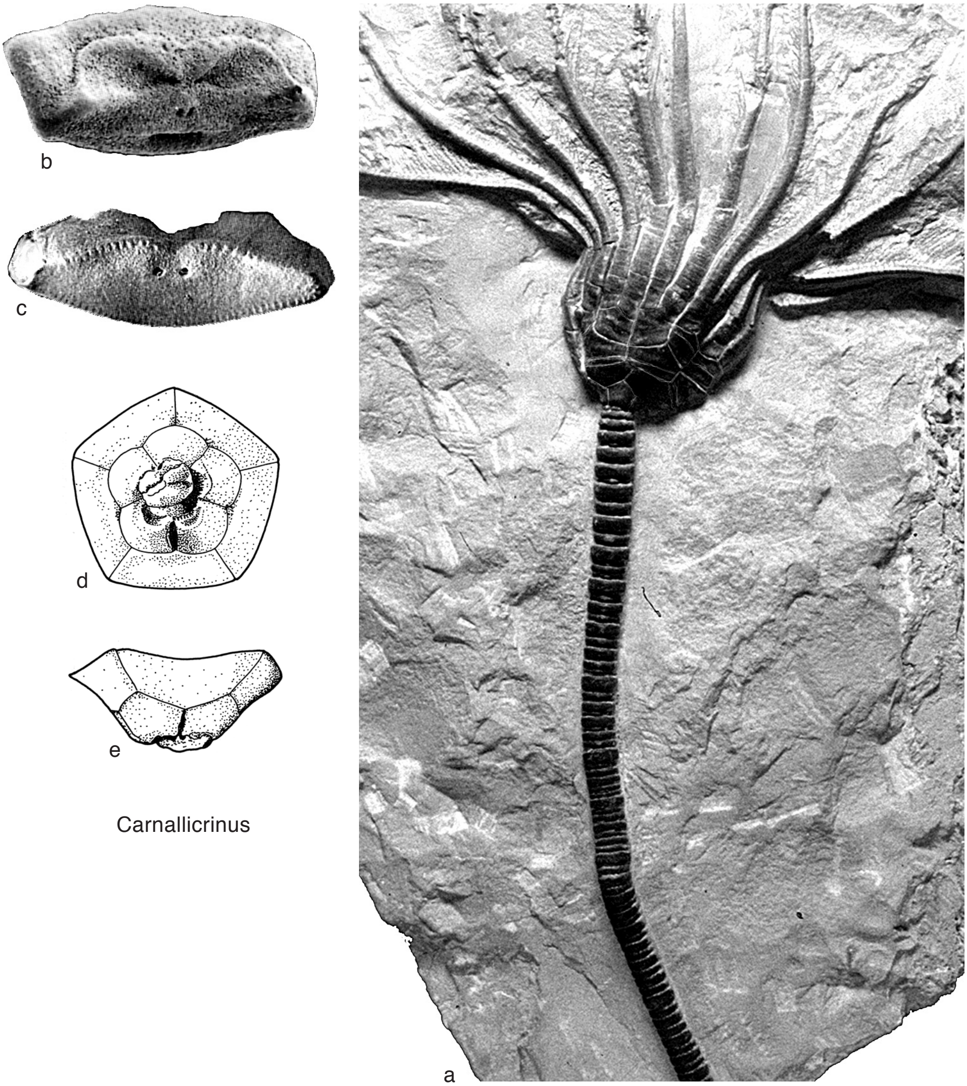


FIG. 15. Dadocrinidae (p. 35).

secundibrachial 2 axillary in juveniles, in adults, second arm branching after indefinite number of irregularly biserial secundibrachials, isotomous branching in 4 major arms. Armlets may branch at axillary; these axillaries with long aboral spine. Major arms and armlets biserial. Radial and brachial articulations syzygial, with grooves (fossulae) opening along aboral sutures in circular pores (articulations between brachials similar to articulations between columnals); bands of short crenulae between fossulae. Pinnulars with distal spine. Tegmen with polygonal plates, anal tube short, with polygonal plates. Column long to very long, proximally with distinct nodals and internodals; nodals without cirri. Columnals very low, circular to elliptical, articular facets with multiradiate rows of granules or very short crenulae that may be arranged as sets of chevrons; number of rows increasing toward the margin by bifurcation and intercalation. Terminal column with articulated radicular cirri with multiradiate facets. [DITTMAR (1866) proposed 3 species of his genus: *Porocrinus caudex* DITTMAR, *P. ornatus* DITTMAR, and *P. reticulatus* DITTMAR. However, these represent pluricolumnals from different column parts of a

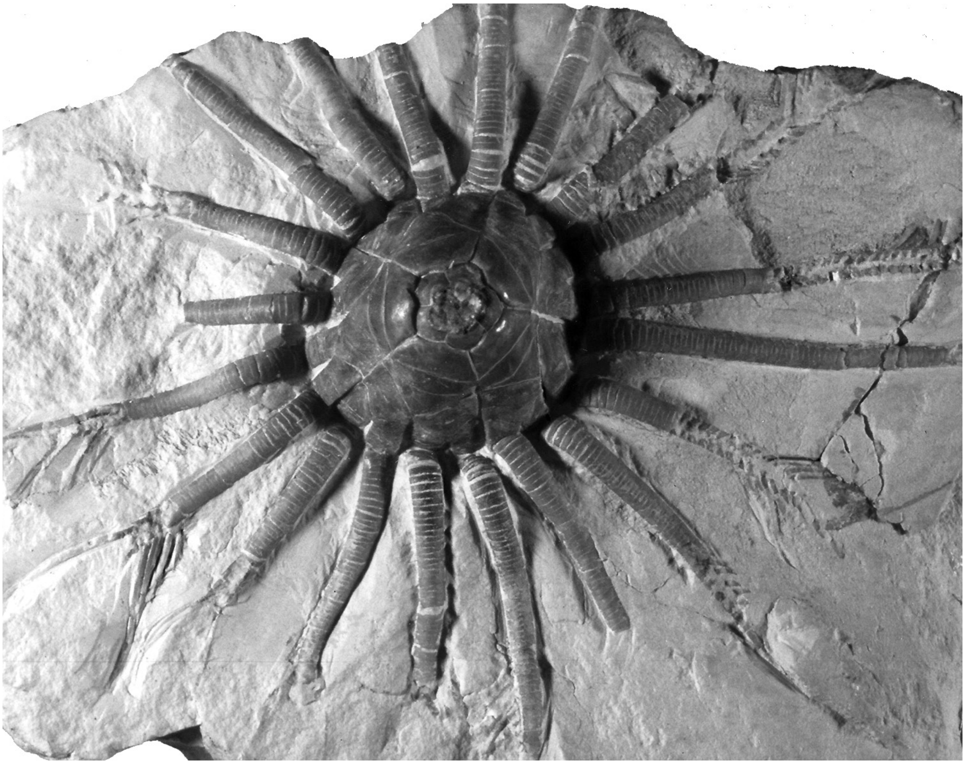


Fig. 16. Dadocrinidae (p. 35).

single species. *T. caudex*, a large distal pluricolumnal, has page priority (Hagdorn, Wang, & Wang, 2007). Mu (1949) established 3 species (*T. hsui*, *T. uniformis,* and *T. kueichouensis*) for the excellently preserved Chinese material; Kristan-Tollmann and Tollmann (1983) and Klikushin (1983) treated these species as junior synonyms of *T. caudex*. Hagdorn, Wang, and Wang (2007) left the question open whether the fragmentary type material from Europe and the intact specimens from China constitute separate species. *T. hsui* is, herein, tentatively treated as a separate species. Wang and others (2008), described complete colonies from Southwest China with columns exceeding 11 m and attached to driftwood. *Traumatocrinus* is a highly specialized offshoot of Anisian-Ladinian Encrinidae, with characters that occur in taxa from the upper Ladinian–lower Carnian Cassian Formation; *Cassianocrinus* has endotomous arm branching and up to 40 arms, and *Zardinicrinus* has a reduced cup and columns with pores and articular facets resembling those of *Traumatocrinus* (Hagdorn, 1998, 2004a).] *Middle Triassic (upper Ladinian)–Upper Triassic (lower Carnian):* Austria, Germany, Italy, Romania, Turkey, Afghanistan, Iran, India, Timor, Vietnam, China, ?New Zealand.——Fig. 17*a–d*. **T. caudex* (Dittmar); *a,* polished cross section of proximal columnal showing tubuli and fossulae, lower Carnian, North Afghanistan, MHI 1885/1, ×2 (Hagdorn, new); *b–c*, column, *b,* lateral, *c,* proximal facet, Austria, holotype, MNHB MB.E 2286, ×0.7 (Dittmar, 1866); *d*, lateral view of cup with small basals and top columnal, note large sculptured aboral ligament area of radials, upper Ladinian, Iran, GBA 1985/6/27, ×3 (Kristan-Tollmann, 1991).——Fig. 18*a–b. T. hsui* Mu, lower Carnian, China; *a,* crown and proximal column, YIGMR XT3xH-10, ×0.35; *b*, adoral view of semiadult crown with tegmen, anal cone, and distal arms, MHI 1882/3, ×1.5 (Hagdorn, new).——Fig. 17*e–h. T. hsui* Mu, lower Carnian, China; *e,* terminal column with radicular cirri, MHI 1882/1, ×1.75; *f,* cirrus sockets with multiradiate facets on side of column, MHI 1882/2, ×6; *g–h*, proximal column, *g*, lateral with nodal-internodal sequence, ×3, *h*, interior

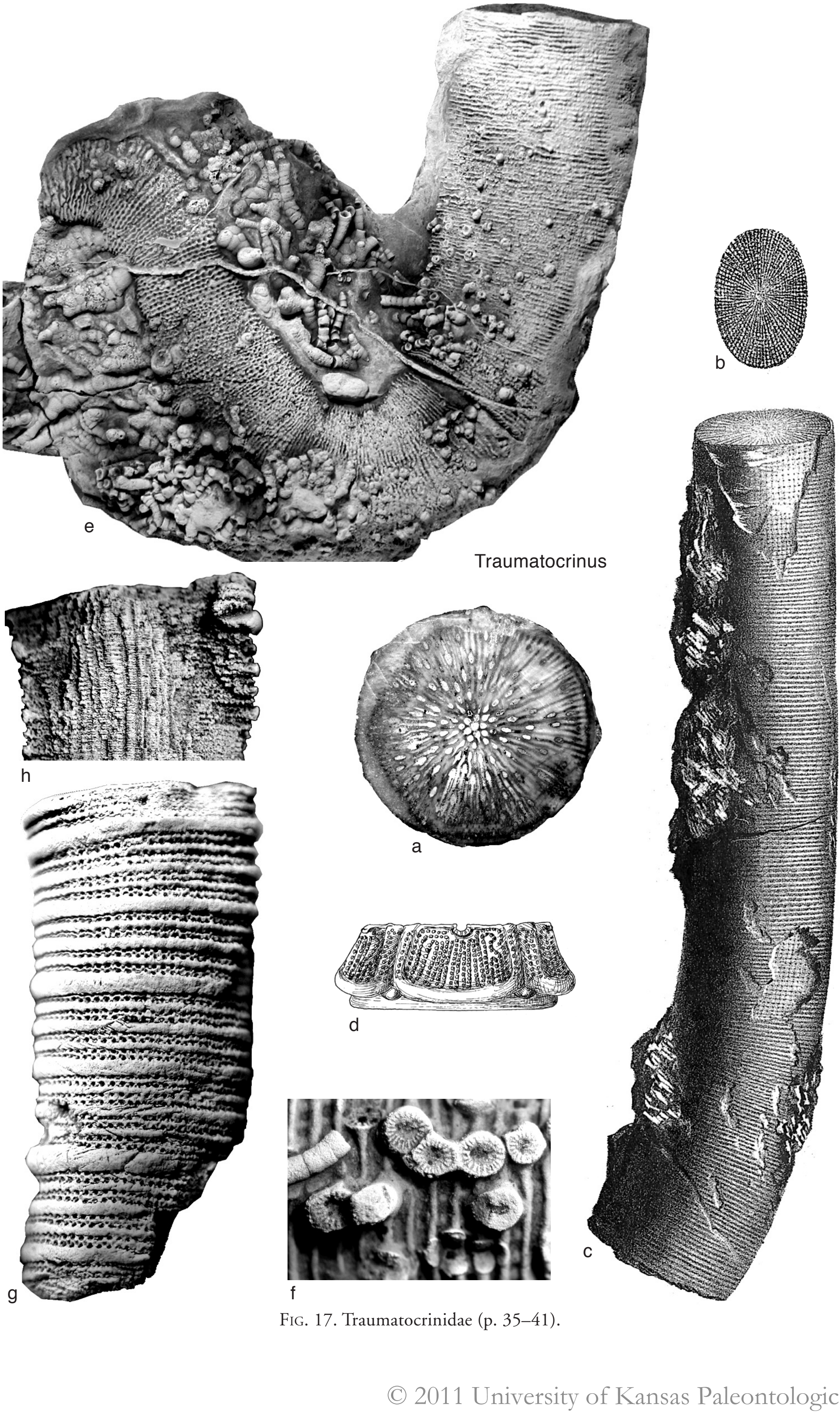


FIG. 17. Traumatocrinidae (p. 35–41).

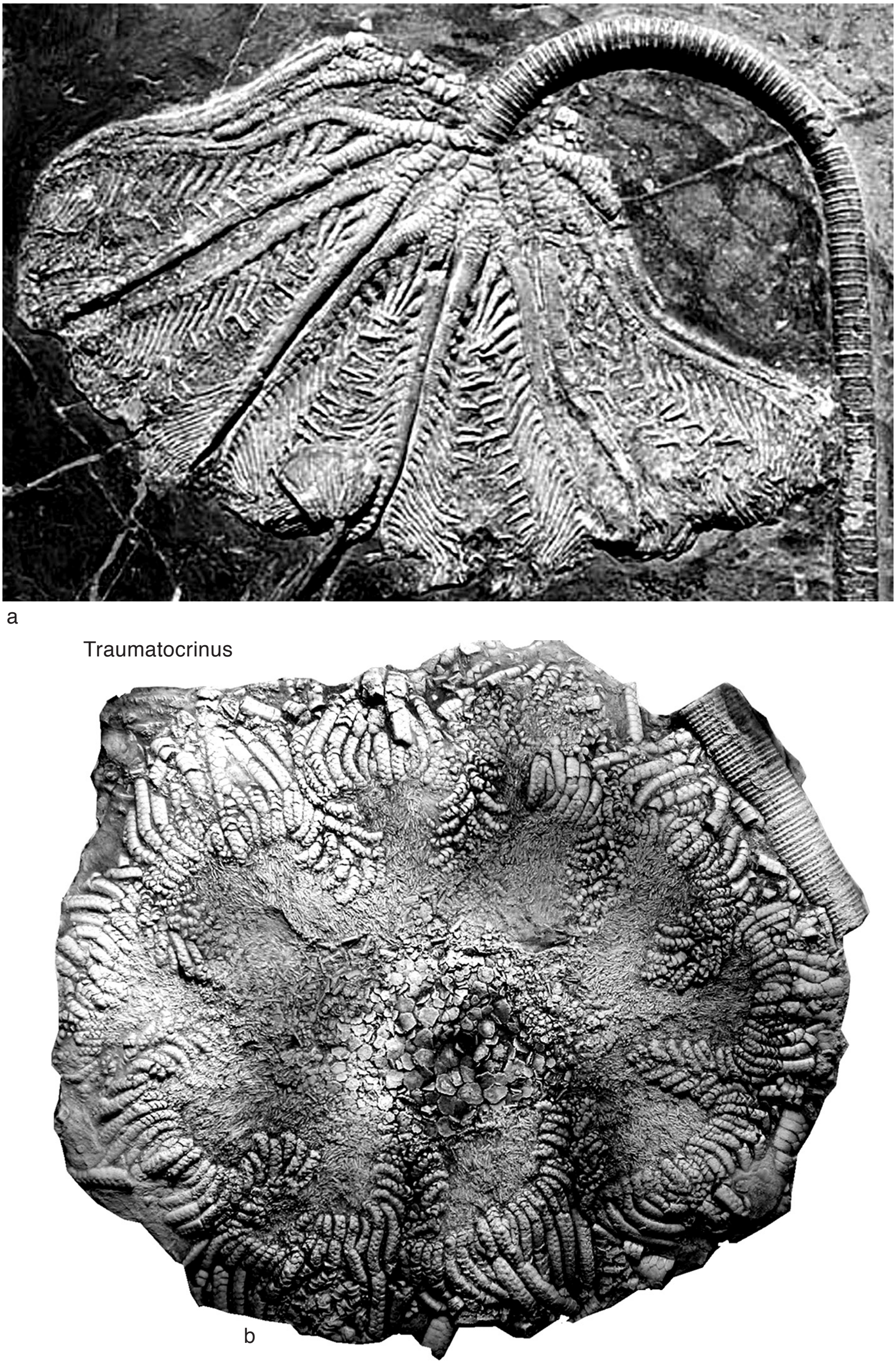


FIG. 18. Traumatocrinidae (p. 35–41).

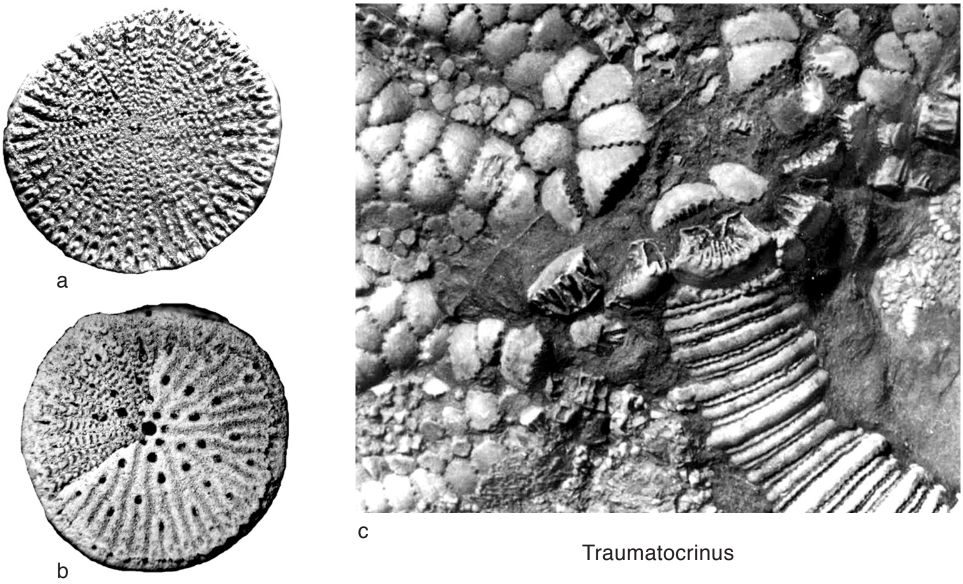


Fig. 19. Traumatocrinidae (p. 35–41).

view of weathered side with tubuli, MHI 1880/2, ×5 (Hagdorn, new).——Fig. 19*a–c. T. hsui* Mu; *a,* facet of proximal columnal, lower Carnian, China, MHI 1880/5, ×5; *b*, facet of immature internodal with fossulae overlying mature nodal with crenulate loops, lower Carnian, China, MHI 1880/4, ×5 (Hagdorn, new); *c*, proximal column and proximal part of crown with radial articular facet exposed, MHI 1850, ×1 (Hagdorn, Wang, & Wang, 2005).

Vostocovacrinus Yeltisheva & Polyarnaya, 1986, p. 114 [**V. boreus*; M]. Cup unknown. Arms extremely biserial, brachials very low, without axillary knots and spines. *Middle Triassic (Ladinian):* Russia (Novosibirsk Islands, Kotel Island), Spitsbergen, North America, Greenland.——Fig. 13,*2a–c.* **V. boreus*; *a,* crown, Russia, ×0.6 (Ausich & others, 1999); *b–c*, pluricolumnal from mesistele, *b,* lateral, *c,* facet, Spitsbergen, MHI 1684/5, ×3 (Hagdorn, new).

ISOCRINIDA

HANS HESS

[Natural History Museum Basel, Switzerland, e-mail: hans.hess@bluewin.ch]

Order ISOCRINIDA Sieverts-Doreck, 1952

[Isocrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952, p. 614, *partim*, excluding Holocrinidae]

Cup cryptodicyclic, wider than high, low cone or bowl shaped; radial cavity wide, cup elements not extremely thick. Basals commonly much lower than radials. Radial articular facet directed outward, muscle fossae large but may be small in Lower Jurassic Pentacrinitina. Axial canals between brachials single. Columnal articula petaloid. [Subdividing the Isocrinida has been highly controversial. BOURSEAU and ROUX (1989) and BOURSEAU and others (1991) treated the isocrinids as a homogeneous group classified as the family Pentacrinidae D'ORBIGNY. They rejected the notion of 2 families, the uniquely fossil Pentacrinidae (with *Seirocrinus* and *Pentacrinites*) and the Isocrinidae (including the living representatives); thus, they also rejected a classification of Isocrinida into 2 suborders (Pentacrinitina and Isocrinina). The pentacrinitids, herein classified in the suborder Pentacrinitina, differ by some easily recognizable characters from isocrinids classified in the suborder Isocrinina, such as endotomous arm branching, highly cirriferous columns with laterally compressed cirri, and columnal articular facets with a distinctive pattern. Isocrinines, on the other hand, constitute a rather homogeneous group subdivided by relatively minor character differences.] *Middle Triassic (Anisian)–Holocene.*

Suborder PENTACRINITINA Gray, 1842

[*nom. transl.* HESS, herein, *ex* Pentacrinitidae GRAY, 1842, p. 119]

Radials large and projected outward or downward, lower edge of basals more or less curved downward, overhanging the top of the column. Arms divided at primibrachial 2 and further divided several times; division at primibrachials and secundibrachials isotomous, succeeding divisions endotomous. Interradial plates present in Pentacrinitidae and continuing in numerous plates of high tegmen, or absent in Eocomatulidae. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Syzygies absent, but cryptosyzygies present in Eocomatulidae. Highly cirriferous juvenile column that may become very long with intercalated internodals in adults. Column varying in length from a few columnals in *Eocomatula* to more than 20 m in *Seirocrinus*. Articular facet of columnals with very narrow or elliptical to pyriform petals surrounded by a slightly crenulated edge and separated by large, more or less triangular, smooth or rugose radial areas. Cirri commonly laterally compressed and long in *Pentacrinites* but shorter and more circular in *Seirocrinus,* although differences are smaller in juvenile specimens. *Middle Triassic (Anisian)–Upper Jurassic (Oxfordian).*

Family PENTACRINITIDAE Gray, 1842

[Pentacrinitidae GRAY, 1842, p. 119] [=Pentacrinidae D'ORBIGNY, 1852 in 1850–1852, p. 147; *emend.*, GISLÉN, 1924, p. 218]

Brachials with weakly developed muscle fossae in pseudoplanktonic species. Ligamentary brachial articulations absent or restricted to secundibrachials 6 and 7, additional ligamentary articulations in *Pentacrinites dargniesi.* Column with persistent alternation and indefinite intercalation of columnals, small intercolumnals may be concealed by nodals. [Intact specimens of *Pentacrinites fossilis*, *P. dichotomus* (M'COY), and *Seirocrinus subangularis*, attached to driftwood, occur in Lower Jurassic black shale deposits of England and southern Germany (HESS, 1999a; SIMMS, 1999). Intact specimens of the benthic *Pentacrinites dargniesi* TERQUEM & JOURDY are widely distributed in Middle Jurassic oolitic sedi-

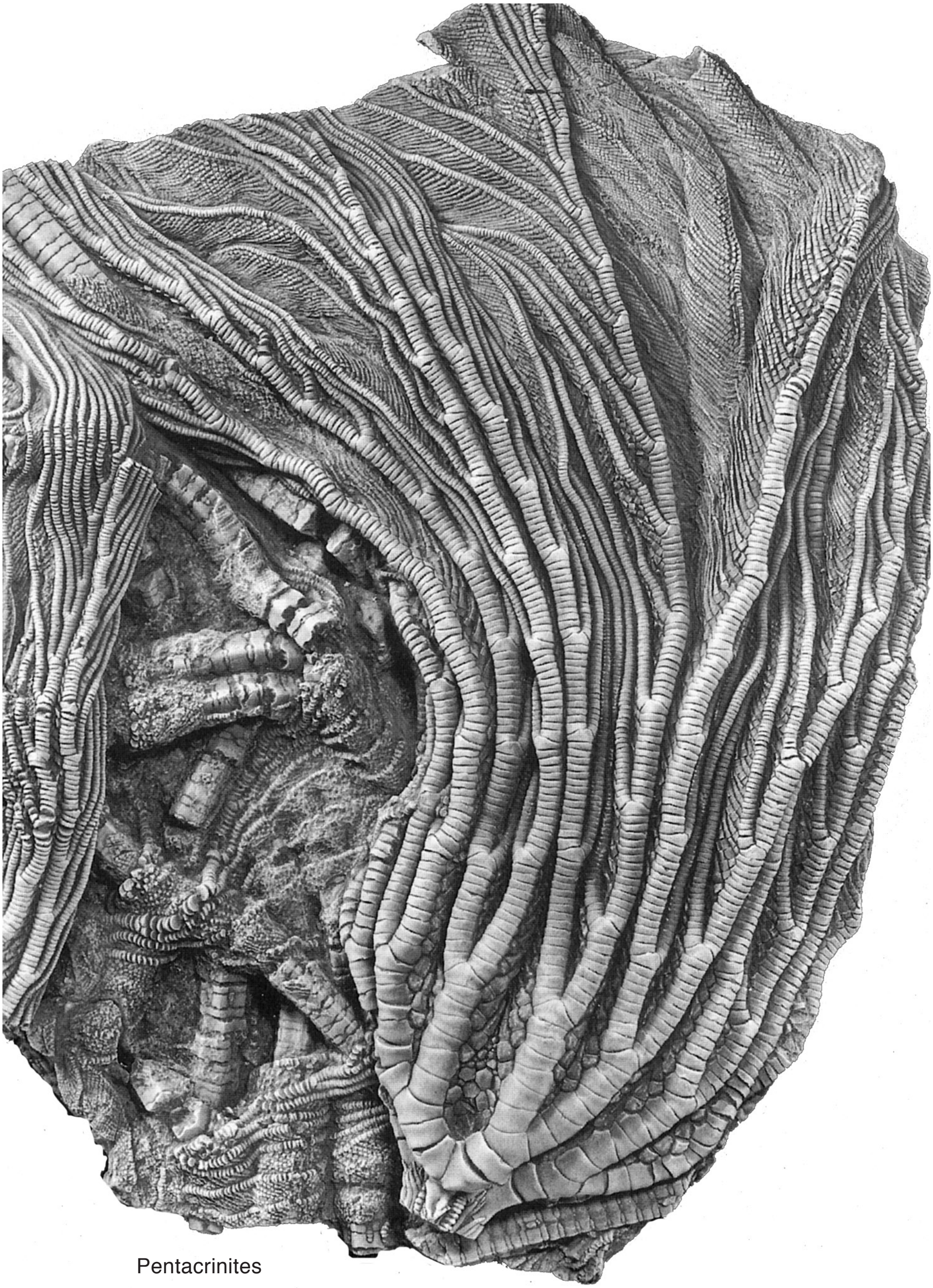


FIG. 20. Pentacrinitidae (p. 43–46).

ments of France, England, and Switzerland (DE LORIOL, 1888–1889 in 1882–1889; HESS, 1999b).] *Middle Triassic (Anisian)–Upper Jurassic (Oxfordian).*

Pentacrinites BLUMENBACH, 1804 in 1802–1804, Heft 7, no. 70, *nom. nov. pro Pentacrinis lapis* AGRICOLA, 1546, p. 262, *emend.,* BATHER, 1898, p. 245 [**P. fossilis;* M; =*P. britannicus* VON SCHLOTHEIM, 1813, p. 100, obj.; =*P. briareus* MILLER, 1821,

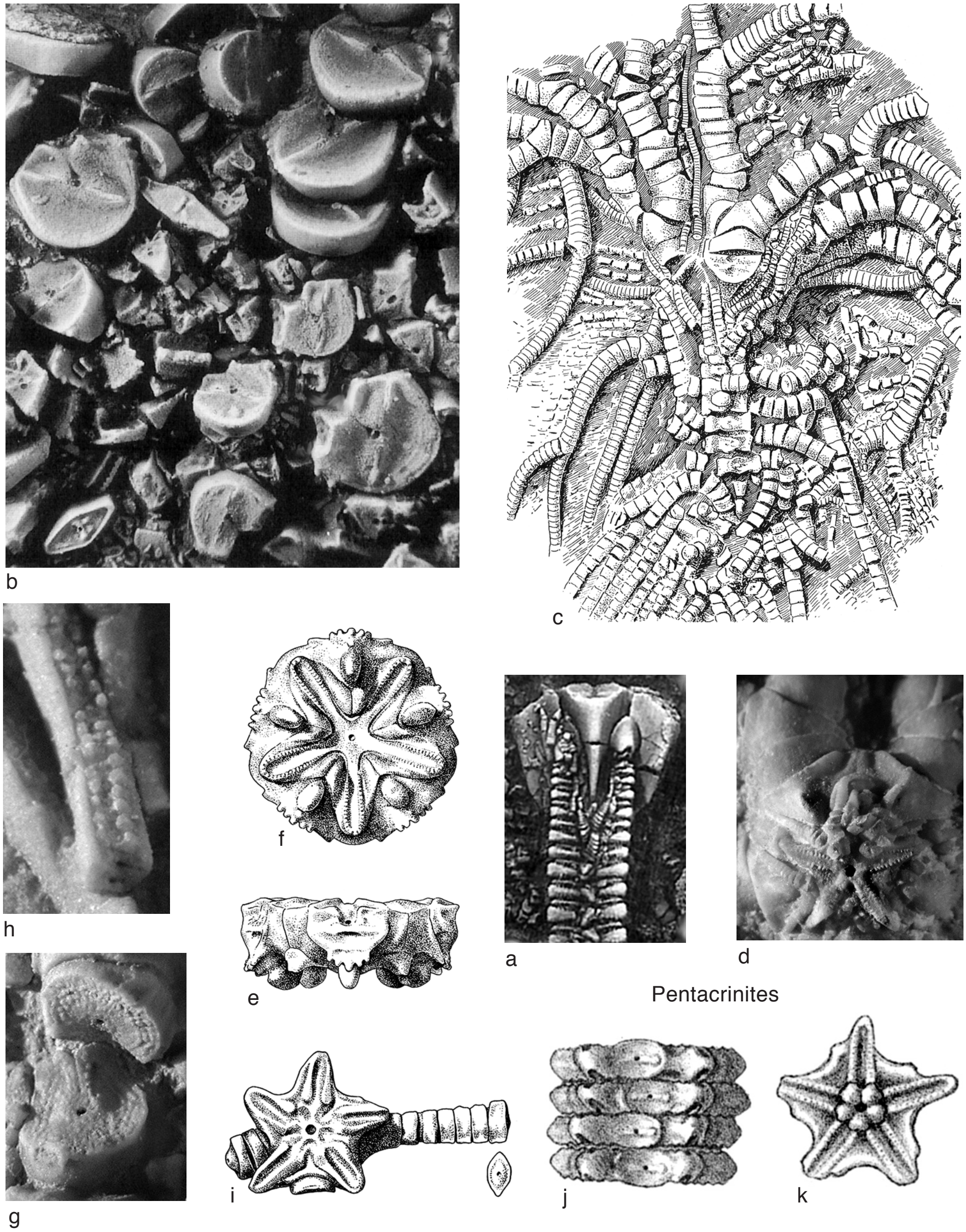
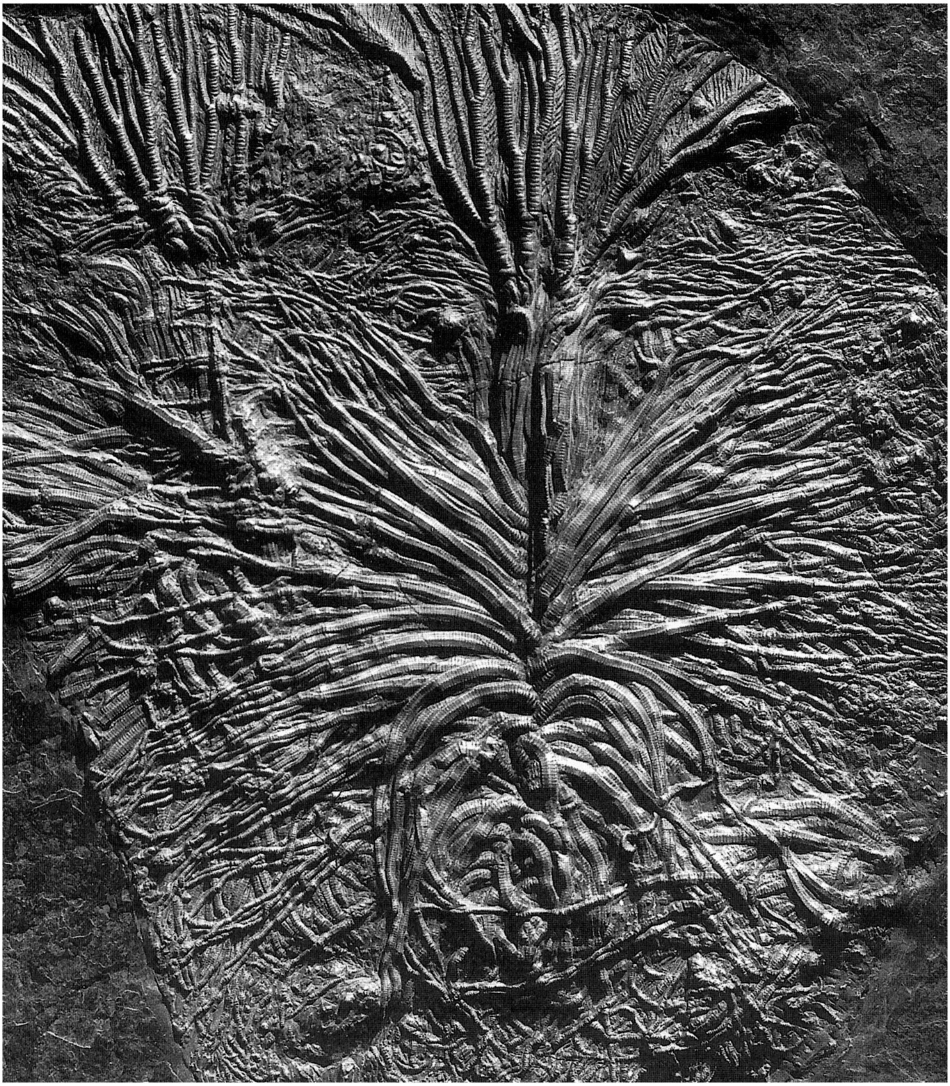


FIG. 21. Pentacrinitidae (p. 43–46).

p. 56] [=*pentacrinite* GUETTARD, 1761, p. 227, *nom. null.;* =*Pentacrinus* MILLER, 1821, p. 45, *nom. van.;* =*Extracrinus* AUSTIN & AUSTIN, 1847 in 1843–1849, p. 95 (type, *P. briareus* MILLER, 1821, p. 107, OD); =*Pentracinus* WIEGMANN, 1838, p. 334, *nom. null.*, *error pro Pentacrinus*; =*Heterocrinus* FRAAS, 1858, p. 327, obj.,, *non* HALL, 1847, p. 278]. Cryptosyzygy or synostosis between secundibrachials 6 and 7 in *P. dichotomus* and *P. dargniesi,* respectively, where synostoses also occur between brachials 2 and 3 in succeeding division series. Synarthry between secundibrachials 3 and 4 in *P. dargniesi*. Tegmen moderately high, with anal pyramid of elongate platelets in *P. dargniesi*. Column short, generally much less than 0.5 m, but may reach 1 m in *P. fossilis*, pentalobate to stellate



Pentacrinites

FIG. 22. Pentacrinitidae (p. 43–46).

or subpentagonal in section. Internodes very short, proximal part of column with only nodals exposed, distal part with a few internodals, commonly 3 or 4 larger and intercalated smaller internodals. Symplectial areolae narrow. Columnal articular facets with smooth radial areas. Cirri numerous and very long, commonly narrow, elliptical to rhombic in section with aboral and adoral ridge. Cirri directed more or less upward, commonly covering column and cup completely. Pinnules all free. Pinnule grooves protected by 2 rows of granular platelets present in *P. dargniesi.* [AUSTIN and AUSTIN (1847 in 1843–1849) incorrectly considered *Pentacrinus* established by MILLER (1821), with *P. caput-medusae* as type species, and used the name *Pentacrinus* for all Isocrinidae. They were followed by most authors until BATHER (1898) and some later authors.] *Middle Triassic (Anisian)–Upper Jurassic (Oxfordian):* Austria, Czech Republic, England, France, Germany, Poland, Switzerland, Russia, *Norian–Oxfordian;* New Zealand, *Anisian.*——FIG. 20. **P. fossilis*; crown, Sinemurian, England, BMNH E35056, ×1 (Simms, 1999).——FIG. 21*a–b.* **P. fossilis,* Sinemurian, England; *a,* cup and proximal column, BMNH E70315, ×3; *b*, brachial facets, BMNH E69872, ×3 (Simms, 1989a).——FIG. 22. *P. dichotomus* (M'COY); intact columns and base of crowns, Toarcian, Germany, SMNS 7389, ×0.45 (Hess, 1999a).——FIG. 21*c–k*. *P. dargniesi* TERQUEM & JOURDY, Bajocian; *c,* proximal column and base of crown, Switzerland, NMB M9661, ×2 (Hess, 1975); *d*, base of cup with topmost columnals, Switzerland, NMB M10568, ×3.5 (Hess, new); *e–f*, cup, *e,* lateral, *f,* proximal, Switzerland, NMB M9324, ×2.5 (Hess, 1975); *g*, secundibrachials 6 and 7 with cryptosyzygy or synostosis, Switzerland, NMB M10569, ×6 (Hess, new); *h*, adoral view of pinnules with cover plates, Switzerland, NMB M10570, ×15 (Hess, new); *i*, nodal with cirrus and cirral facet, Switzerland, NMB M9315, ×2.3 (Hess, 1975); *j–k*, column, *j*, lateral, *k*, facet of nodal with small internodal, France, ×4 (de Loriol, 1889 in 1882–1889).

Seirocrinus GISLÉN, 1924, p. 218 [**Pentacrinites subangularis* MILLER, 1821, p. 59; OD; =*Pentacrinites fasciculosus* VON SCHLOTHEIM, 1813, p. 56, *nom. nud.*, and *P. bollensis* VON SCHLOTHEIM, 1813, p. 56, *nom. nud.*, based on figures in KNORR, 1755, pl. 11b and c, but listed as *Pentacrinites subangularis* MILLER by VON SCHLOTHEIM, 1822 in 1822–1823, p. 80, and 1823 in 1822–1823, p. 106; =*Pentacrinus hiemeri* KOENIG, 1825, p. 2; =*Extracrinus lepidotus* AUSTIN & AUSTIN, 1847 in 1843–1849, p. 106; =*Pentacrinites briaroides* QUENSTEDT, 1852, p. 607; =*Pentacrinites colligatus* QUENSTEDT, 1852, p. 608]. Radials barely in contact or separated by basals. Radial articular facet with very large aboral ligament area and small interarticular ligament and muscle fossae, inclined to aboral part at an angle of approximately 40 degrees. Aboral ligament fossa of proximal brachials indistinct, L-shaped. Tegmen very high; proximal pinnules reduced and included in tegmen. Column rounded subpentagonal to circular in section. Length of internodes gradually increasing to more than 100 internodals in distal part of long columns. Nodals with 5 very small cirrus sockets, circular or subelliptical in outline, facing outward or upward. Symplectial areolae narrow elliptical to pyriform, with maximum width toward outer end, bordered by numerous very small crenulae; radial areas highly rugose. Cirri short and slender, with weakly compressed, rounded rhomboidal section. Cirri may be adpressed in oblique furrows in surface of column. *Upper Triassic (Norian)–Middle Jurassic:* Russia (New Siberian Islands, Siberia), England, Germany, Italy, Bulgaria, Portugal, Switzerland, Turkey, Indonesia, Japan, USA (Alaska), Canada.——FIG. 23,*1a–f*. **S. subangularis* (MILLER); *a,* radial articular facet, Pliensbachian, England, BGS 91097, ×3.3; *b*, facet of proximal secundibrachial, Pliensbachian, England, BGS 91097, ×4 (Simms, 1989a); *c*, columns with facet, Toarcian, Germany, Werkforum Dotternhausen, ×0.9 (Hess, 1999a); *d*, proximal column and cup, radials black, Toarcian, Germany, Hauff, ×1.5 (Seilacher & Hauff, 2004); *e–f*, top of column, *e*, lateral, *f*, proximal, Toarcian, Germany, ×1.5 (Quenstedt, 1876).——FIG. 23,*1g*. *S. klikushini* SIMMS, 1989a; proxistele (left) and mesistele, Rhaetian, Kotelny Island, ×1 (Klikushin, 1982a).

Family EOCOMATULIDAE
Simms, 1988

[Eocomatulidae SIMMS, 1988a, p. 284]

Cryptosyzygies common throughout arm, facets with numerous fine marginal culmina. Short, untapered column retaining distinct symplectial articulum on terminal columnal. [SIMMS (1989a, p. 29) assigned Eocomatulidae, type species *Eocomatula interbrachiata,* to the Paracomatuloidea on the basis of its short column. He considered *Eocomatula* to be an almost perfect transition between the Pentacrinitidae and Paracomatulidae. As discussed by HAGDORN and CAMPBELL (1993), *Eocomatula* differs from *Paracomatula* in some major characters. *Eocomatula* still has a thick column, consisting of 6 to 7 pentastellate nodals, with constant diameter down to the terminal columnal, the axial canal of which is not sealed. The cirrals have rhomboidal articula, and the arms branch endotomously beyond the tertibrachials. Thus, *Eocomatula* shares more characters with the Pentacrinitidae, some of which are apomorphic: endotomous arm branching and rhomboidal cirrals. The column of *Eocomatula*, unlike the reduced column of *Paracomatula*, is a short version of a pentacrinitid column. Column shortening occurred repeatedly in crinoid history, either caused by traumatic events such as in *Chelocrinus schlotheimii* from the Upper Muschelkalk (Middle Triassic) of Germany (HAGDORN, 1982) or among the millericrinids independent of traumatic events, such as in *Ailsacrinus* (TAYLOR, 1983). In both cases the terminal columnals have sealed axial canals, which is not true for *Eocomatula*. *Eocomatula* is regarded herein to be related more closely to the pentacrinitids, sharing with these the symplectial lower nodal articula and the apomorphic characters of rhomboidal cirrals and endotomous arm branching. The cups of both *Eocomatula* and *Pentacrinites* have radials with pyramidal projections, whereas the

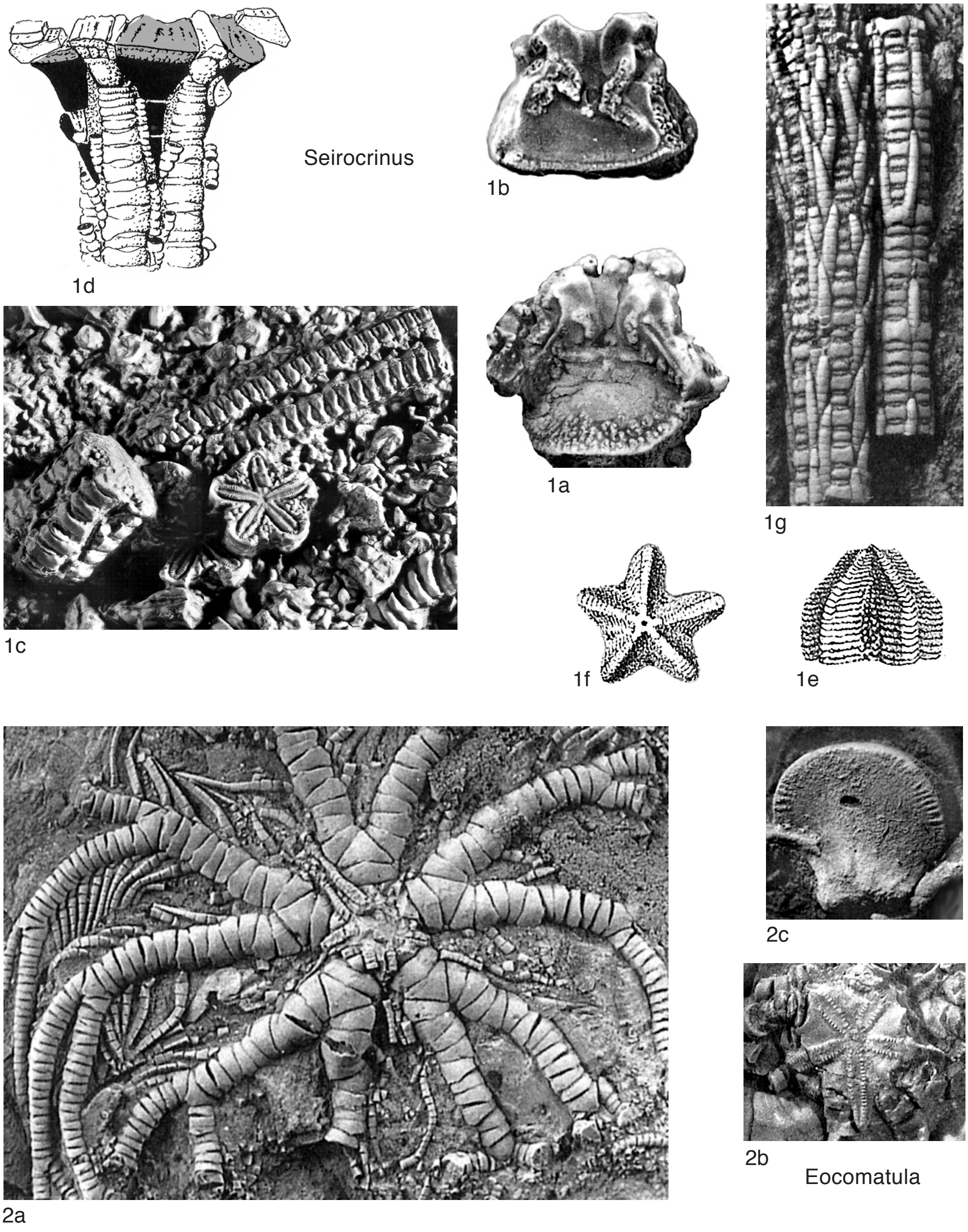


FIG. 23. Pentacrinitidae and Eocomatulidae (p. 46–48).

radials of *Paracomatula* are undifferentiated. Like its presumed Middle Triassic holocrinid ancestors, *Eocomatula* still has cryptosyzygial brachial articulations, a character largely lost in pentacrinitids.] *Upper Triassic (Norian)–Lower Jurassic (Pliensbachian).*

Eocomatula SIMMS, 1988a, p. 274, 284 [*_Pentacrinus interbrachiatus_ BLAKE in TATE & BLAKE, 1876, p. 445; OD]. Characters as for family. *Upper Triassic (Norian)–Lower Jurassic (Pliensbachian):* Peru, *Norian–Rhaetian;* England, *Pliensbachian.*——FIG. 23,*2a–c*. *_E. interbrachiata_ (BLAKE), Pliensbachian, England; *a,* aboral view of crown, CAMSM J.37264, ×1; *b,* facet of nodal, CAMSM J.37265,

×3; *c*, cryptosyzygy on secundibrachial, BMNH 1858, ×5 (Simms, 1989a).

Suborder ISOCRININA Sieverts-Doreck, 1953

[Isocrinina Sieverts-Doreck in Ubaghs, 1953, p. 758, *partim,* excluding Holocrinidae and Thiolliericrinidae] [=suborder Isocrinina Simms, 1988a, p. 284, *partim*, excluding Marsupitidae]

Arms long, slender, branching mostly isotomous. Facets of brachials with well-developed muscle fossae. Whorls of mostly circular cirri at regular intervals along the pentaradiate column. Facets of columnals with petaloid pattern. Cryptosymplectial to synostosial articulation beneath cirrinodals as preformed rupture point (autotomy plane) between nodal and infranodal; in Proisocrinidae all columnal articulations symplectial and attachment by cementing disk. [Simms (1988a) designated the suborder Isocrinina for all Isocrinida formerly included within the family Isocrinidae Rasmussen & Sieverts-Doreck (1978). However, he also included the Marsupitidae, which are assigned herein to the Comatulida, suborder Comatulidina. Isocrinina share the synapomorphy of cryptosymplectial or synostosial articulations beneath the cirrinodals (Hagdorn, 1983; Donovan, 1984). Rasmussen (1978) recognized 15 genera, but this number has now increased to 24. Earlier attempts to subdivide this large group of similar-looking crinoids largely failed to gain acceptance due to the conflicting results obtained by using different characters. Most schemes have been based either on the configuration or microstructure of columnal articulations (Roux, 1970, 1974, 1977a), including the pattern of ligamental pores (tubuli) on the facets (Klikushin, 1979a, 1982a), or on the type of articulation between primibrachials 1 and 2 (Carpenter, 1882c, 1884a; Rasmussen, 1978; Oji, 1985; Oji & others, 1996). Simms (1988a, 1989a) rejected the use of columnal articulations and the arrangement of ligamental pores as characters to determine phylogenetic relationships above the generic level because of considerable variation between, or even within, individuals in a given species. He also pointed out that morphological changes associated with heterochronous evolution may produce apparently quite distinct and morphologically dissimilar articulation patterns in 2 very closely related genera, as demonstrated for *Isocrinus (Chladocrinus)* and *Balanocrinus*. Ignoring columnal articulations and considering only the proximal brachial articulations reveals a much clearer pattern of relationships within the Isocrinina. With the exception of the fossil *Raymondicrinus* and *Eometacrinus*, all genera with a synarthry between primibrachials 1 and 2 also have a synarthry between secundibrachials 1 and 2. Similarly, most genera with a cryptosyzygy between primibrachials 1 and 2 also have a cryptosyzygy between secundibrachials 1 and 2. Both Carpenter (1879a) and A. H. Clark (1908f) considered the articulations between primibrachials 1 and 2 and secundibrachials 1 and 2 to be homologous. However, this is not supported by those forms of Isocrinina in which the articulation between primibrachials 1 and 2 is cryptosyzygial, but the articulation between secundibrachials 1 and 2 is synarthrial. Based on brachial articulations, Simms (1988a) distinguished 3 distinct groups among the Isocrinina. The first group retains the ancestral condition, with synarthries between both primibrachials 1 and 2 and secundibrachials 1 and 2. It corresponds to the so-called Old Group of Oji (1985), and, because it includes the genus *Isocrinus*, it constitutes Simms's (1988a) emended family Isocrinidae. All Triassic and Jurassic genera belong here, together with the extant genera *Hypalocrinus* and *Neocrinus*. The Isocrinidae is divided into 2 subfamilies on the basis of the columnal articulations: Isocrininae Gislén, 1924 (Roux, 1981) and Balanocrininae Roux, 1981. The second group, the Cainocrinidae Simms, 1988a, have a cryptosyzygy (or synostosis) between primibrachials 1 and 2 but retain a synarthry between secundibrachials 1 and 2. It comprises 3 genera: *Nielsenicrinus* from the Cretaceous, *Cainocrinus* from the Eocene, and *Teliocrinus* ranging from Miocene to Holocene (Oji & others, 1996). The third and final group, the Isselicrininae Klikushin, 1977, and Isselicrinidae Simms, 1988a, comprises Isocrinina, with a cryptosyzygy between primibrachials 1 and 2. Three genera have a muscular articulation between secundibrachials 1 and 2 and more than 2 primibrachials; they constitute the Metacrininae Roux, 1981. The Isselicrininae have a cryptosyzygy between secundibrachials 1 and 2 and nodals with fewer than 5 cirrus sockets. The Diplocrininae Roux, 1981, also have a cryptosyzygy between secundibrachials 1 and 2, but nodals have 5 cirrus sockets. It should be noted that cryptosyzygies with a number of fine ridges along the aboral edge are at times difficult to distinguish from synostoses. True syzygies with coarse ridges are very rare in Isocrinina but occur in the Lower Jurassic *Balanocrinus ticinensis* (Hess, 2006; see Fig. 6,*6*) and in Oxfordian species of *Balanocrinus* (Hess, personal observations, 2009). A large number of fossil isocrinid species are based on columnals that are difficult to classify. However, intact isocrinids have repeatedly been reported from Mesozoic and Tertiary sediments. Examples are from Lower Jurassic shales of England and Germany (Rosenkranz, 1971; Sieverts-Doreck, 1979; Simms, 1989a), Upper Jurassic marls of France (Bourseau & others, 1998), Lower Cretaceous sandstone of Japan (Oji, 1985), Upper Cretaceous mudstone of Japan (Oji & others, 1996), and Paleogene sandstones and siltstones of Antarctica (Baumiller & Gaździcki, 1996). Especially noteworthy are the rich Middle Jurassic occurrences in oolitic limestones of France and Switzerland (Bigot, 1938; Hess, 1999b) and those in tuffaceous siltstones from the Paleogene of Oregon, United States (Moore & Vokes, 1953; Hess, 1999e). Members of 3 genera in 2 families as construed here (*Neocrinus* in Isocrinidae and *Cenocrinus* and *Endoxocrinus* in Isselicrinidae) are able to lie along the seafloor and crawl using their arms, at least sometimes in association with autotomy of a distal portion of the column. This crawling behavior is apparently a means of escaping from cidaroid echinoid predators (Messing & others, 1988; Baumiller & Messing, 2007; Baumiller, Mooi, & Messing, 2008).] *Middle Triassic (?Anisian, Ladinian)–Holocene:* bathyal.

Family ISOCRINIDAE Gislén, 1924

[Isocrinidae Gislén, 1924, p. 218]

Synarthry between primibrachials 1 and 2. [Subdivison of the large family Isocrinidae as represented by Rasmussen (1978) has been the subject of several proposals, but the one based on the proximal brachial articulations is followed herein (Simms, 1988a); however, columnal articulations and arm branching are used as secondary characters. Roux (1981) defined 4 subfamilies: Isocrininae, Balanocrininae, Diplocrininae, and Metacrininae. He also suggested a fifth subfamily, Pentacrininae, for *Pentacrinus* (=*Pentacrinites*) and *Seirocrinus*. Previously, Klikushin (1977) established subfamilies on the basis of the articulation between primibrachials 1 and 2, Isocrininae with a synarthry, Metacrininae with a syzygy (=cryptosyzygy), and Isselicrininae with a synostosis. Later, Klikushin (1982a, 1992) accepted the Balanocrininae as defined by Roux (1981). Herein, the Isocrinidae are subdivided into 2 subfamilies, and Roux's remaining subfamilies (Diplocrininae and Metacrininae) are assigned to the Isselicrinidae.] *Middle Triassic (?Anisian, Ladinian)–Holocene.*

Subfamily ISOCRININAE Gislén, 1924

[*nom. transl.* Roux, 1981, p. 481, *ex* Isocrinidae Gislén, 1924, p. 218]

Two primibrachials; synarthry between secundibrachials 1 and 2, in *Raymondicrinus* muscular articulation between secundibrachials 1 and 2. [*Neocrinus* and *Hypalocrinus* were placed by Klikushin (1992) in this subfamily; but according to Bourseau and others (1998), they belong to the Balanocrininae based on properties of the column. Roux (1981, p. 481) assigned the extant genus *Cenocrinus* and the fossil genera *Isocrinus*, *Chariocrinus*, and *Nielsenicrinus* to

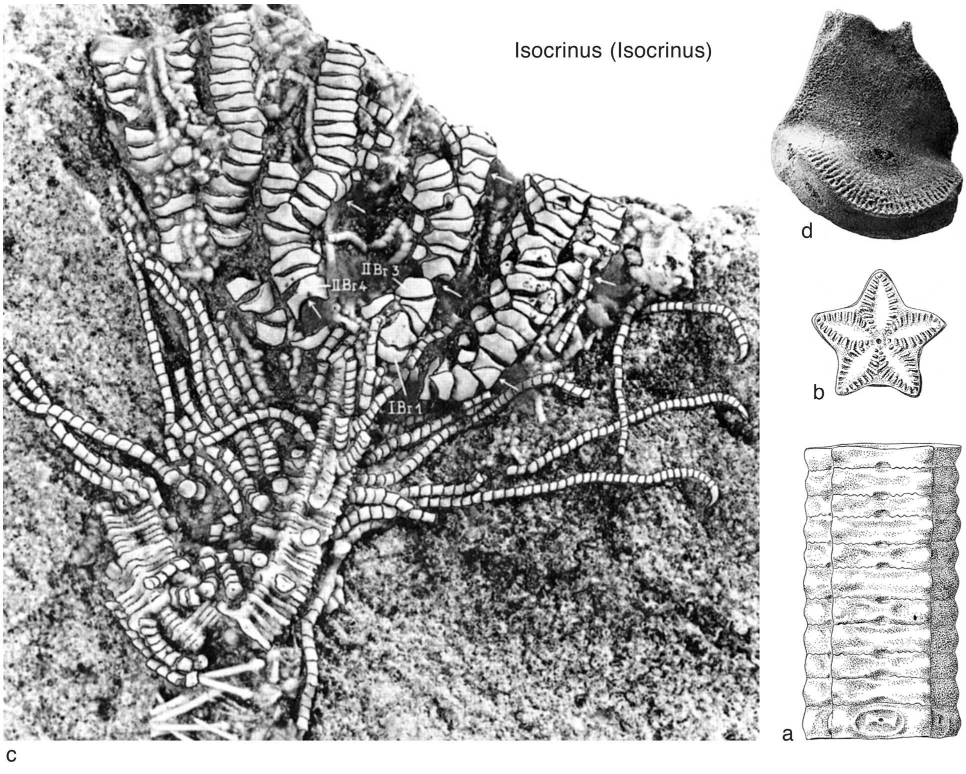


FIG. 24. Isocrinidae (p. 50–51).

this subfamily. Herein, *Cenocrinus* is assigned to Isselicrinidae, subfamily Diplocrininae, because of the cryptosyzygies between primibrachials 1 and 2 and secundibrachials 1 and 2. *Nielsenicrinus* is placed in Cainocrinidae because of the cryptosyzygy between primibrachials 1 and 2.] *Middle Triassic (?Anisian, Ladinian)–Holocene.*

Isocrinus von Meyer in Agassiz, 1836, p. 195, *non* Phillips, 1841, p. 30 [**Isocrinites pendulus* von Meyer, 1836, p. 57; M; =?*Pentacrinus amblyscalaris* Thurmann in Thurmann & Étallon, 1861, p. 351] [=*Isocrinites* von Meyer, 1836, p. 57, *nom. van.*]. Basals small, visible from outside, not forming contiguous circlet. Columnals low, except in distalmost part of column, cirrus sockets large, as high as nodals. [The type species, *I. pendulus*, is based on a crown that originally had a fragment of column attached and was so figured by von Meyer, but this fragment was subsequently lost (de Loriol, 1887 in 1882–1889, p. 246 and pl. 174,*3*). It is extremely probable that the crown belongs to the same species as the numerous columnals of *I. amblyscalaris* (Thurmann) from coeval sediments (de Loriol, 1887 in 1882–1889, p. 247; Hess, 1972a, p. 198).] *Upper Triassic (?Carnian), Lower Jurassic–Lower Cretaceous*: Europe, Russia, Crimea, Caucasus, Japan.

I. (**Isocrinus**). Symmorphy between secundibrachials 3 and 4. Column with fewer than 10 (mostly 7) internodals except in proximalmost part. [True *Isocrinus* are most common in the Middle and Upper Jurassic. Klikushin (1982a, p. 306) mentioned *I. annulatus* (Roemer) from the Berriasian of the Crimea, and Hess and Gale (2010) described *Isocrinus legeri* (Repelin) from the Albian of England. According to Rasmussen (1961, p. 110), the majority of the Cretaceous isocrinids are known only from columns, and most of those from the Upper Cretaceous belong to *Nielsenicrinus*. The best preserved species of *Isocrinus s.s.* is *I. nicoleti* from the Middle Jurassic, known from numerous intact specimens. It has a well-developed symmorphy between secundibrachials 3 and 4 and may be regarded as a typical representative of this genus.] *Lower Jurassic–Lower Cretaceous:* Europe, Crimea, Caucasus, Russia.——Fig. 24*a–b*. **I. (I.) pendulus* (von Meyer), Oxfordian, Switzerland; *a,* column, NMB M9594, ×3; *b*, facet of internodal,

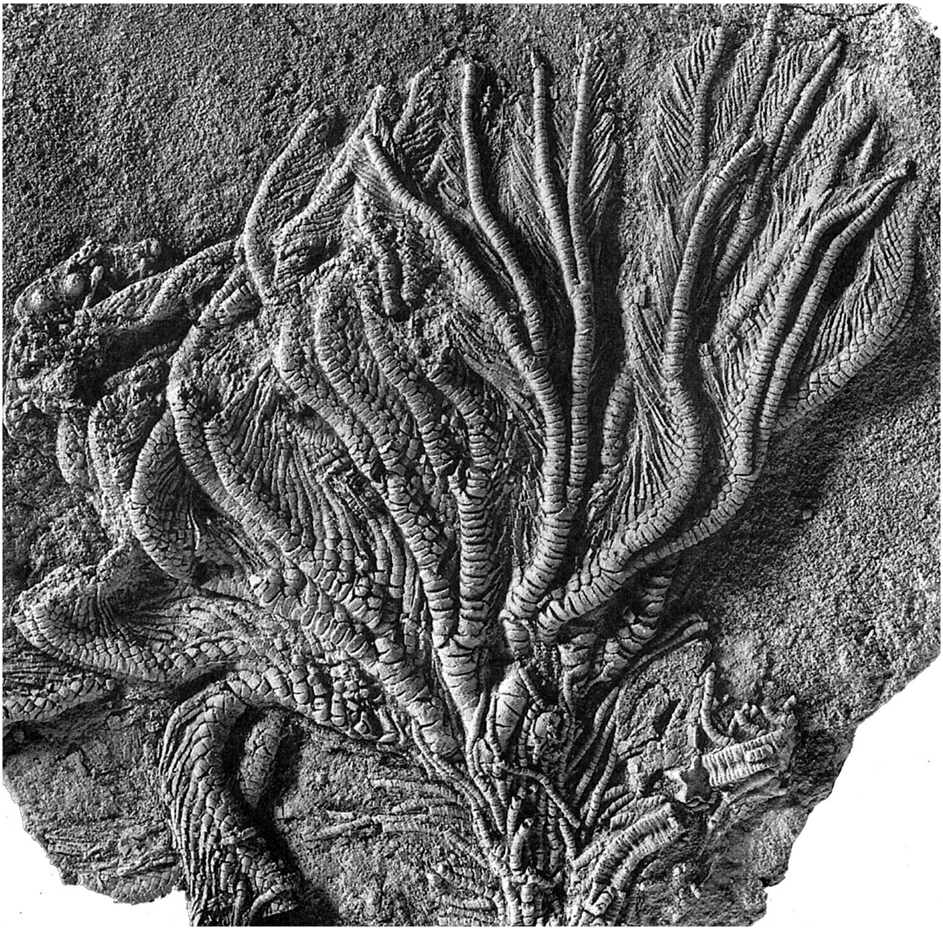


FIG. 25. Isocrinidae (p. 50–51).

NMB M9595, ×3 (Hess, 1972a).——FIG. 24*c–d. I. (I.) nicoleti* (THURMANN in THURMANN & ÉTALLON, 1861), Bajocian, Switzerland; *c,* column and base of crown, NMB M9892, ×2 (Hess, 1972a); *d*, symmorphial cryptosyzygial brachial facet, NMB M10748, ×8 (Hess, 1975).——FIG. 25. *I. (I.) nicoleti* (THURMANN in THURMANN & ÉTALLON, 1861); intact crown with proximal column, Bajocian, Switzerland, NMB M10585, ×1.4 (Hess, 1999b).

I. (**Chladocrinus**) AGASSIZ, 1836, p. 195, *emend.*, SIEVERTS-DORECK, 1971, p. 314 [**Pentacrinites basaltiformis* MILLER, 1821, p. 62; SD SIEVERTS-DORECK, 1971, p. 318]. Straight cryptosyzygy between secundibrachials 3 and 4. Internodes long, with as many as 20 columnals. [*Chladocrinus* was introduced for species of *Pentacrinus* with greater distance between nodals, thus corresponding to the definition of *Seirocrinus* GISLÉN (1924), and also included the later type of *Seirocrinus*. SIEVERTS-DORECK (1971) emended the genus and designated a type species. RASMUSSEN (1978) listed *Neocrinus* as a synonym of *Chladocrinus,* but *Neocrinus* is herein treated as a valid genus. As discussed by SIMMS (1989a, p. 35), *Isocrinus* s.s. and *Chladocrinus* are distinguished on the basis of a single character transformation: the presence of symmorphial as opposed to cryptosyzygial articulation on *Isocrinus* brachials. Therefore, SIMMS (1989a) treated *Chladocrinus* as a subjective synonym of *Isocrinus*. Species of *Chladocrinus* are distinctive fossils in the Lower Jurassic, some represented by more or less intact specimens. Thus, *Chladocrinus* is retained herein as a subgenus. A number of species, including 2 from the Upper Triassic (KLIKUSHIN, 1982a), are based on material insufficient for final classification. *Isocrinus (Chladocrinus)*

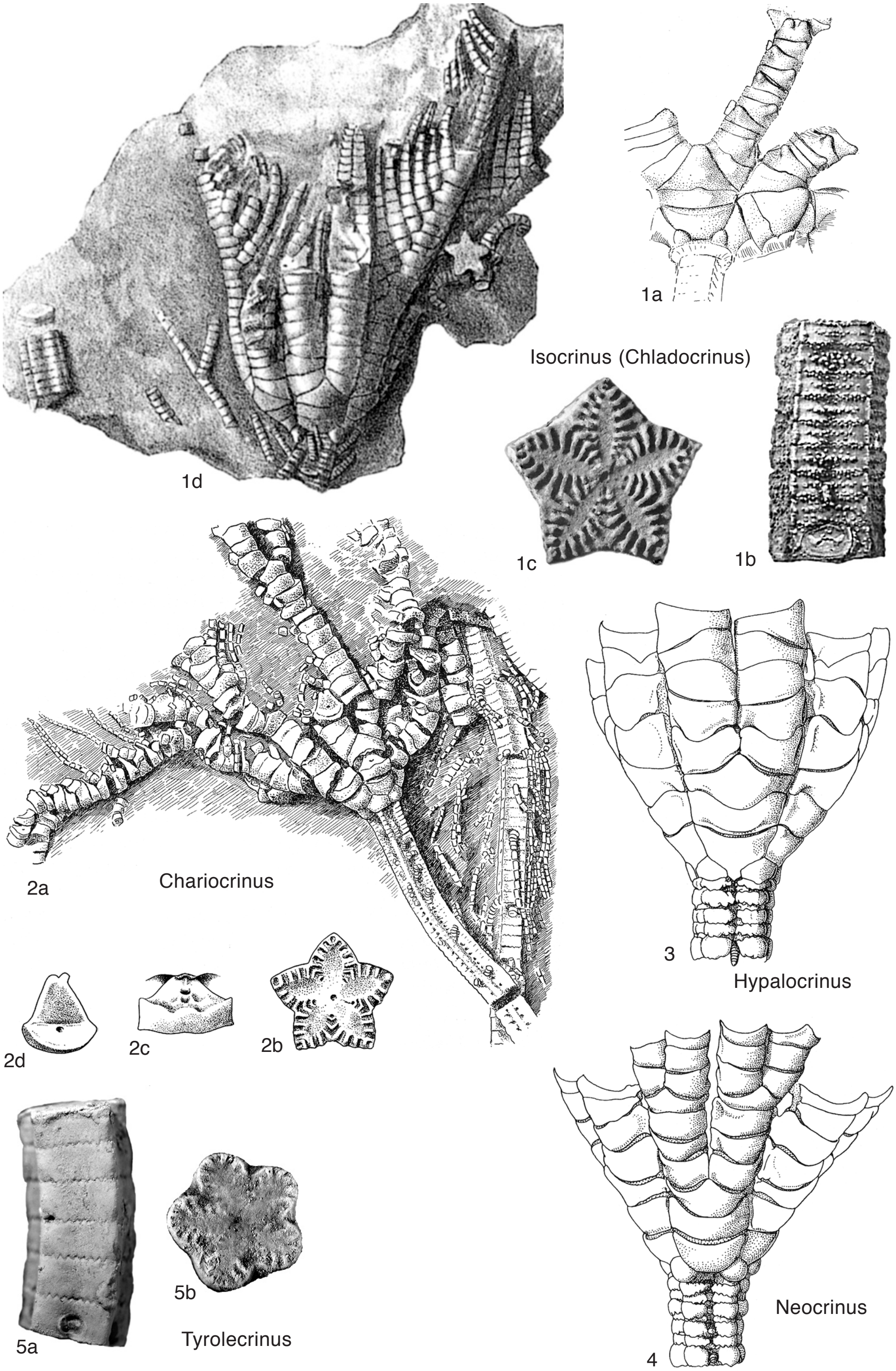


FIG. 26. Isocrinidae (p. 51–56).

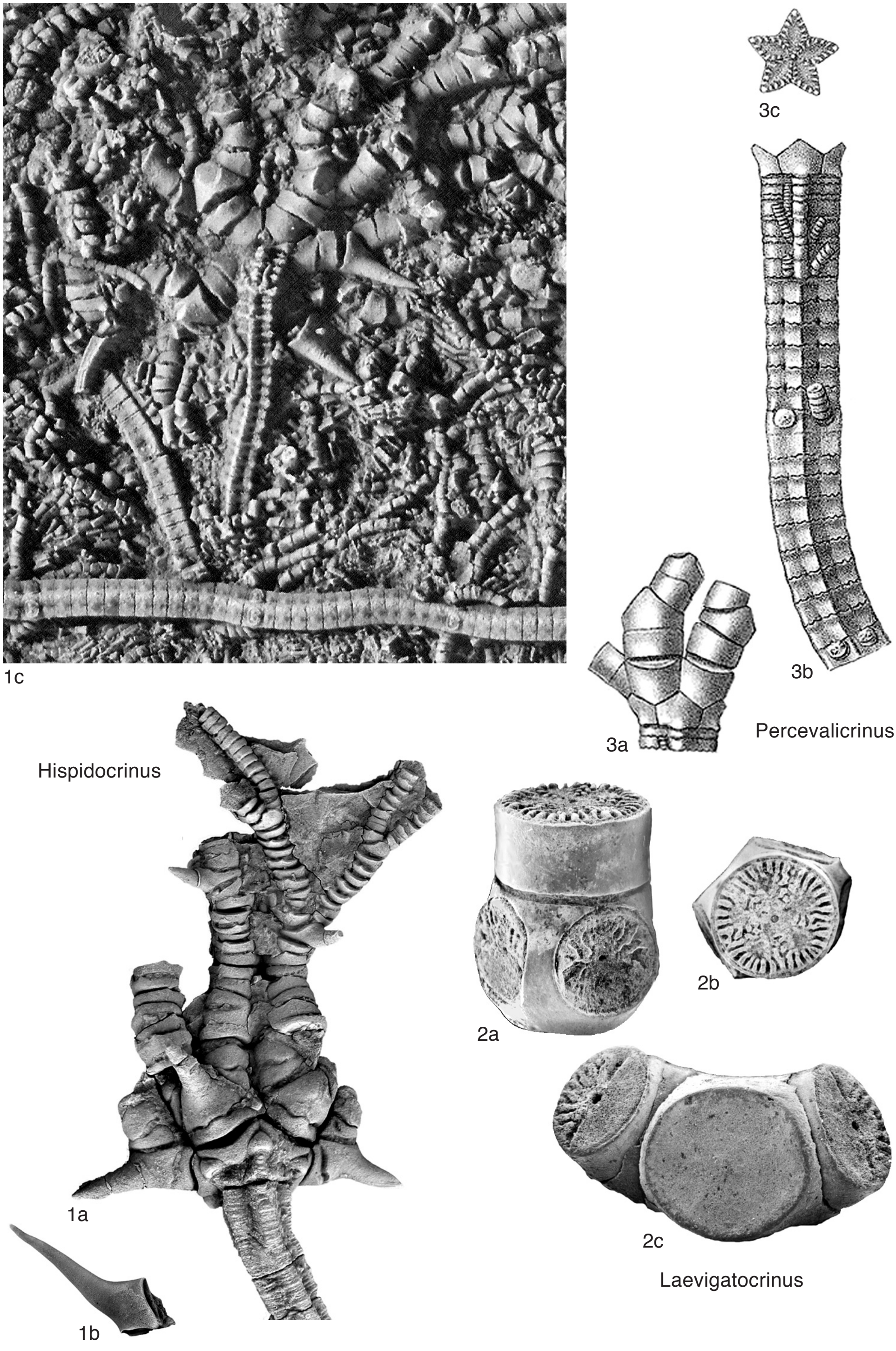


FIG. 27. Isocrinidae (p. 55–58).

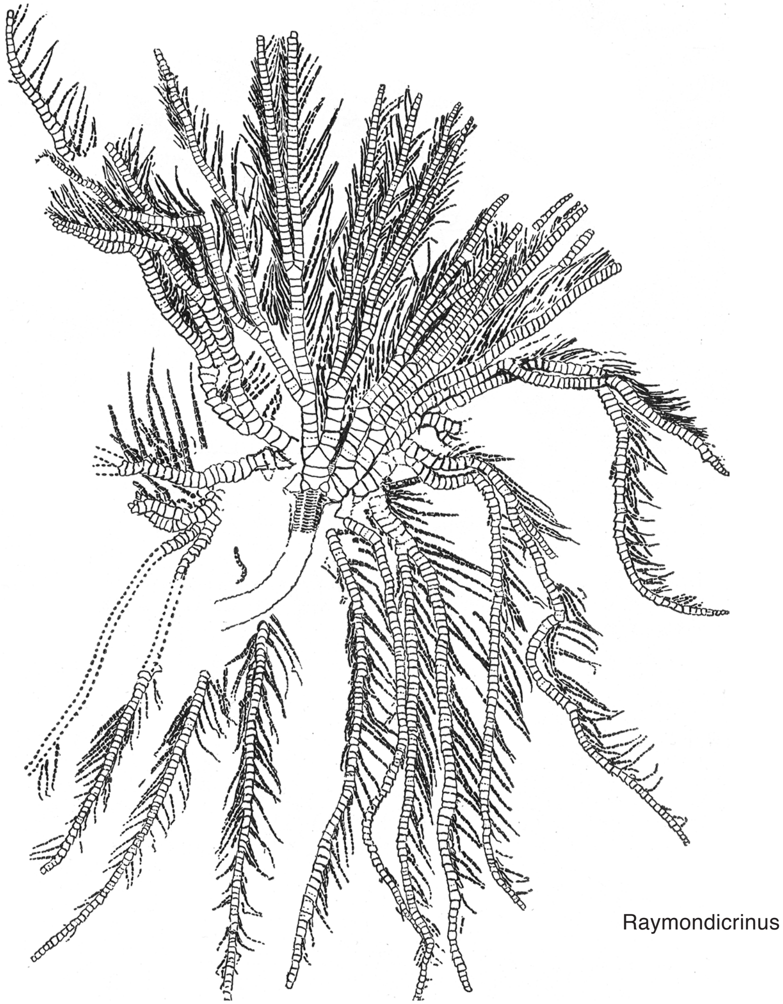


FIG. 28. Isocrinidae (p. 56).

hanaii OJI (1985), from the Lower Cretaceous, has slightly embayed cryptosyzygies between brachials 3 and 4 in each brachitaxis as well as large cirrus sockets, but internodes are short, of 8 or 9, or rarely 10 columnals.] *Upper Triassic (?Carnian), Lower Jurassic (Hettangian)–Lower Cretaceous (Aptian):* Austria, Belgium, Bulgaria, England, France, Germany, Hungary, Ireland, Italy, Scotland, Spain, Switzerland, Russia; Japan, *Aptian.*——FIG. 26,*1a–c.* **I. (C.) basaltiformis* (MILLER), Pliensbachian; *a,* part of base of crown, Germany, Collection Deppe, ×2 (Sieverts-Doreck, 1971); *b*, column, England, BMNH E70323, ×2 (Simms, 1989a); *c*, facet of internodal, Germany, ×4 (Sieverts-Doreck, 1971).——FIG. 26,*1d. I. (C.). tuberculatus* (MILLER); partly preserved crown with proximal column, Lower Jurassic, France, EM 12 126, ×1 (de Loriol, 1882 in 1882–1889).

Chariocrinus HESS, 1972a, p. 204 [**Isocrinus andreae* DESOR, 1845, p. 213; OD]. Moderately large to small Isocrininae. Basals rather large, forming a contiguous circlet. Weakly embayed synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Cryptosyzygy to weak symmorphy between secundibrachials 3 and 4. Column pentagonal to stellate with rather high columnals; proximal columnals pentalobate, low; latera smooth; distalmost part of column subcircular in section. Internodes rather short, of as many as 14 but commonly fewer than 10 columnals. Nodals slightly larger than internodals, with 5 rather small cirrus sockets, small cupule above and slight lip below each cirrus socket. Columnal articular

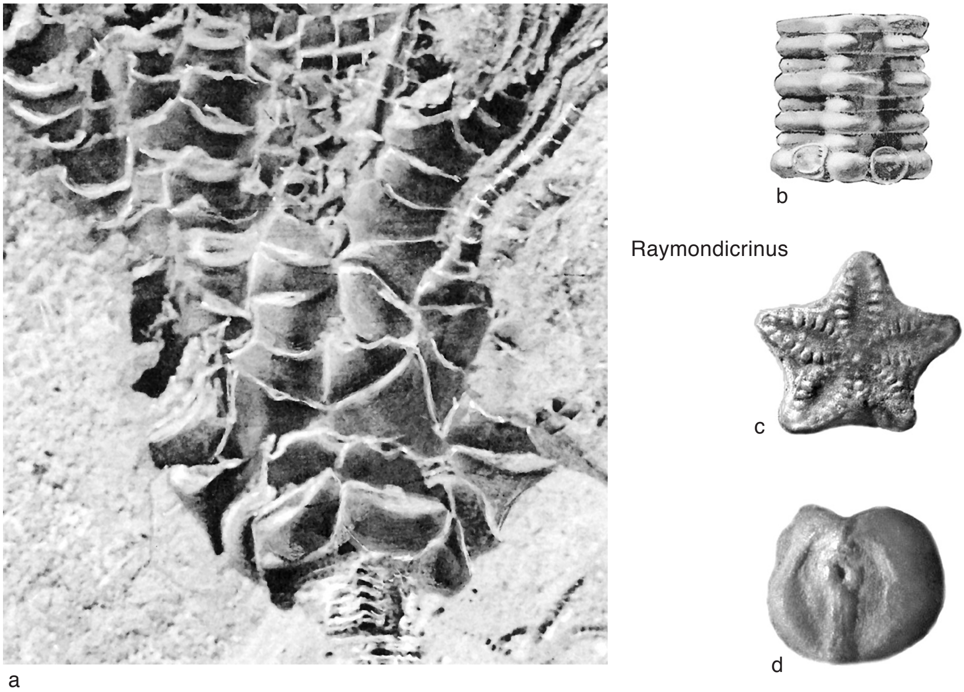


FIG. 29. Isocrinidae (p. 56).

facets with small marginal and interradial crenulae, rapidly diminishing toward center of facet, pattern in some species approaching that of *Balanocrinus. Lower Jurassic (Toarcian)–Upper Jurassic (Oxfordian):* Eurasia, Antarctica.——FIG. 26,*2a–d.* **C. andreae* (DESOR), Bajocian, Switzerland; *a,* proximal crown and column, NMB M9891, ×2; *b*, facet of internodal, NMB M9891, ×5; *c*, distal facet of primibrachial 1, NMB M9891, ×5; *d*, distal facet of secundibrachial 3, NMB M9891, ×5 (Hess, 1972a).

Hispidocrinus SIMMS, 1988d, p. 43 [**Pentacrinites scalaris* GOLDFUSS, 1831 in 1826–1844, p. 173; OD]. Basals small, separated, projecting slightly to overhang top of column. Radials may be very low. Large conical spines on some or all axillaries up to tertibrachials. Column pentastellate to pentalobate. Internodes short, with fewer than 10 columnals. Radial pores on proximal columnals indistinct. Cirrus sockets small, directed outward and slightly upward. Symplectial areolae elongate elliptical; adradial crenulae of adjacent areolae separated by furrow and smooth band. [The small Middle Jurassic *Hispidocrinus leuthardti* (DE LORIOL) is known from intact specimens. It is tentatively assigned to the genus based on the presence of axillary spines. Other characters, such as the proximally pentastellate and distally pentagonal column, basals that are just in contact, and secundibrachials 3 and 4 articulated by a weak symmorphy resemble those of *Chariocrinus andreae.* However, internodes are of 15 columnals and, thus, longer than in *C. andreae* and *H. scalaris.*] *Lower Jurassic (Sinemurian)–Upper Jurassic (Oxfordian):* Eurasia.——FIG. 27,*1a–b.* **H. scalaris* (GOLDFUSS), Sinemurian, England; *a,* partial crown and proximal column, BMNH E69928, ×1.5; *b,* axillary brachial, BMNH E69896, ×2 (Simms, 1989a).——FIG. 27,*1c. H. leuthardti* (DE LORIOL, 1894); proximal column and crown, mesistele, Bathonian, Switzerland, topotype, NMB M9770, ×2.2 (Hess, 1999b).

Hypalocrinus A. H. CLARK, 1908i, p. 152 [**Pentacrinus naresianus* CARPENTER, 1882c, p. 167; M]. Arms 10. Symmorphy between secundibrachials 3 and 4 and more distally. *Holocene*: western tropical Pacific Ocean.——FIG. 26,*3.* **H. naresianus* (CARPENTER); proximal column and base of crown, MNHN EcPs203, ×3 (Roux, Messing, & Améziane, 2002; photo courtesy of the *Bulletin of Marine Science*).

Neocrinus THOMSON, 1864, p. 7 [**Pentacrinus decorus* THOMSON, 1864, p. 7; M]. Base of crown conical, commonly more than 10 arms. Secundibrachials 3 and 4 united by symmorphy in *Neocrinus blakei* (CARPENTER) and by synostosis in *N. decorus*. [RASMUSSEN (1978) listed *Neocrinus* as a synonym of *Chladocrinus*, but *Chladocrinus* is herein treated as a Mesozoic subgenus of *Isocrinus*.] *Holocene*: western tropical Atlantic Ocean (bathyal).——FIG. 26,*4.* **N. decorus* (THOMSON); proximal column and base of crown, NSU, ×3 (Roux, Messing & Améziane, 2002; photo courtesy of the *Bulletin of Marine Science*).

Raymondicrinus KLIKUSHIN, 1982a, p. 306 [**Isocrinus oregonensis* MOORE & VOKES, 1953, p. 124; OD]. Arms bifurcating 3 times. Muscular articulation between secundibrachials 1 and 2, cryptosyzygy between secundibrachials 3 and 4. Internodes of 6 or 7 columnals; nodals very similar in size to internodals; cirrus sockets small. Cirri with terminal claw. *Paleogene (Oligocene):* North America.——FIG. 28. **R. oregonensis* (MOORE & VOKES); intact crown, Oregon, holotype, USNM 560790, ×0.7 (Moore & Vokes, 1953).——FIG. 29*a–d*. **R. oregonensis* (MOORE & VOKES), Oregon; *a*, proximal part of crown, holotype of *Isocrinus nehalemensis* MOORE & VOKES, USNM 560792K, ×3; *b*, column, paratype, USNM 560903A, ×2.5 (Moore & Vokes, 1953); *c*, proximal facet of nodal, topotype, NMB M10603, ×5; *d*, distal view of primibrachial 1, topotype, NMB M10604, ×5 (Hess, new).

Tyrolecrinus KLIKUSHIN, 1982a, p. 307 [**Pentacrinus tyrolensis* LAUBE, 1865, p. 277; OD]. Crown unknown. Column pentalobate or circular, with high, smooth columnals. Internodes short, of 3 to 7 columnals. Nodals and internodals of equal size; nodals with 5 small, strongly depressed cirrus sockets, directed outward and downward. Columnal facets with large crenulae directed more or less radially. *Middle Triassic (?Anisian, Ladinian)–Upper Triassic (Carnian):* Austria, Bulgaria, Germany, Hungary, Italy, Afghanistan, China.——FIG. 26,*5a–b*. **T. tyrolensis* (LAUBE), Ladinian, Italy; *a*, column, lateral, holotype, GBA 1865/3/83, ×6; *b*, facet of internodal, syntype, GBA 1865/3/83, ×7 (Kroh, new).

Subfamily BALANOCRININAE Roux, 1981

[Balanocrininae ROUX, 1981, p. 482]

Synarthry between secundibrachials 1 and 2, flat articulation between primibrachials 1 and 2 in *Percevalicrinus.* Cryptosyzygy or weak symmorphy between secundibrachials 3 and 4. Arms divided at primibrachial 2. Columnal facets with short and uniform radiating crenulae along margin and narrow radial ridges. [ROUX (1981) established the subfamily solely on the basis of the columnal facets, with characters of the crown identical to Isocrininae. *Balanocrinus maritimus* is from the Kimmeridgian of France and is known from intact specimens. It has weak synarthrial articulations between primibrachials 1 and 2 and secundibrachials 1 and 2 (BOURSEAU & others, 1998). In *B. gracilis*, also known from intact specimens, cryptosyzygies occur between secundibrachials 3 and 4, secundibrachials 8 and 9 or 9 and 10, and between brachials 2 and 3 of more distal brachitaxes (SIMMS, 1989a). Thus, the main difference between the subfamilies Isocrininae and Balanocrininae is the articular facet of the column; in addition, columnals are relatively higher in Balanocrininae. Typical Isocrininae, such as *I. pendulus* and *I. nicoleti*, commonly have diameter/height ratios of 6 or more in columnals from the mesistele, whereas those of typical Balanocrininae (*B. subteres* and *B. pentagonalis*) are commonly below 3. BOURSEAU and others (1998, p. 222) recorded diameter/height ratios ranging from 2.2 to 3.4 during the ontogeny of *Balanocrinus maritimus*.] *Middle Triassic (?Anisian, Ladinian)–Lower Cretaceous (Albian), Upper Cretaceous (?Cenomanian, ?Santonian).*

Balanocrinus AGASSIZ in DESOR, 1845, p. 214 [**Pentacrinites subteres* MÜNSTER in GOLDFUSS, 1831 in 1826–1844, p. 176; OD; genus proposed by AGASSIZ in DESOR, 1845, for a column of *P. subteres* with deformation, incorrectly interpreted as a cup] [=*Margocrinus* KLIKUSHIN, 1979b, p. 94 (type, *Pentacrinites pentagonalis* GOLDFUSS, 1831 in 1826–1844, p. 176, OD); =*Terocrinus* KLIKUSHIN, 1982a, p. 303 (type, *Pentacrinites subteroides* QUENSTEDT, 1858, p. 197, OD)]. Basals small to well developed, separate or in contact. Arms slender. Moderate to long brachitaxes. Cryptosyzygy between secundibrachials 3 and 4; symmorphy absent or only weakly developed. Column circular to subpentalobate to pentagonal; may be pentalobate in proximal columnals; cupule above and lip below each cirrus socket. Internodes apparently long in most species but may have only 7 columnals. Nodals slightly larger than internodals, commonly with 5 rather small cirrus sockets facing outward or slightly upward. Columnal facets with short and uniform radiating crenulae along margin and with narrow radial ridges or ribbons of minute crenulae or granules. Small adradial crenulae, where present, perpendicular to marginal crenulae and without any gradual transition, except that a single crenular pair may form an intermediate angle in some specimens. [The type species has cylindrical and rather high columnals. KLIKUSHIN (1979b) divided *Balanocrinus* into 2 subgenera, *Balanocrinus*, with *subteres* (GOLDFUSS) as type species, and *Margocrinus*, with *pentagonalis* (GOLDFUSS) as type species. He distinguished *Margocrinus* from *Balanocrinus* by columnals with pentagonal rather than circular outline, cirrus sockets toward the proximal rather than the distal margin of the nodal, greater width

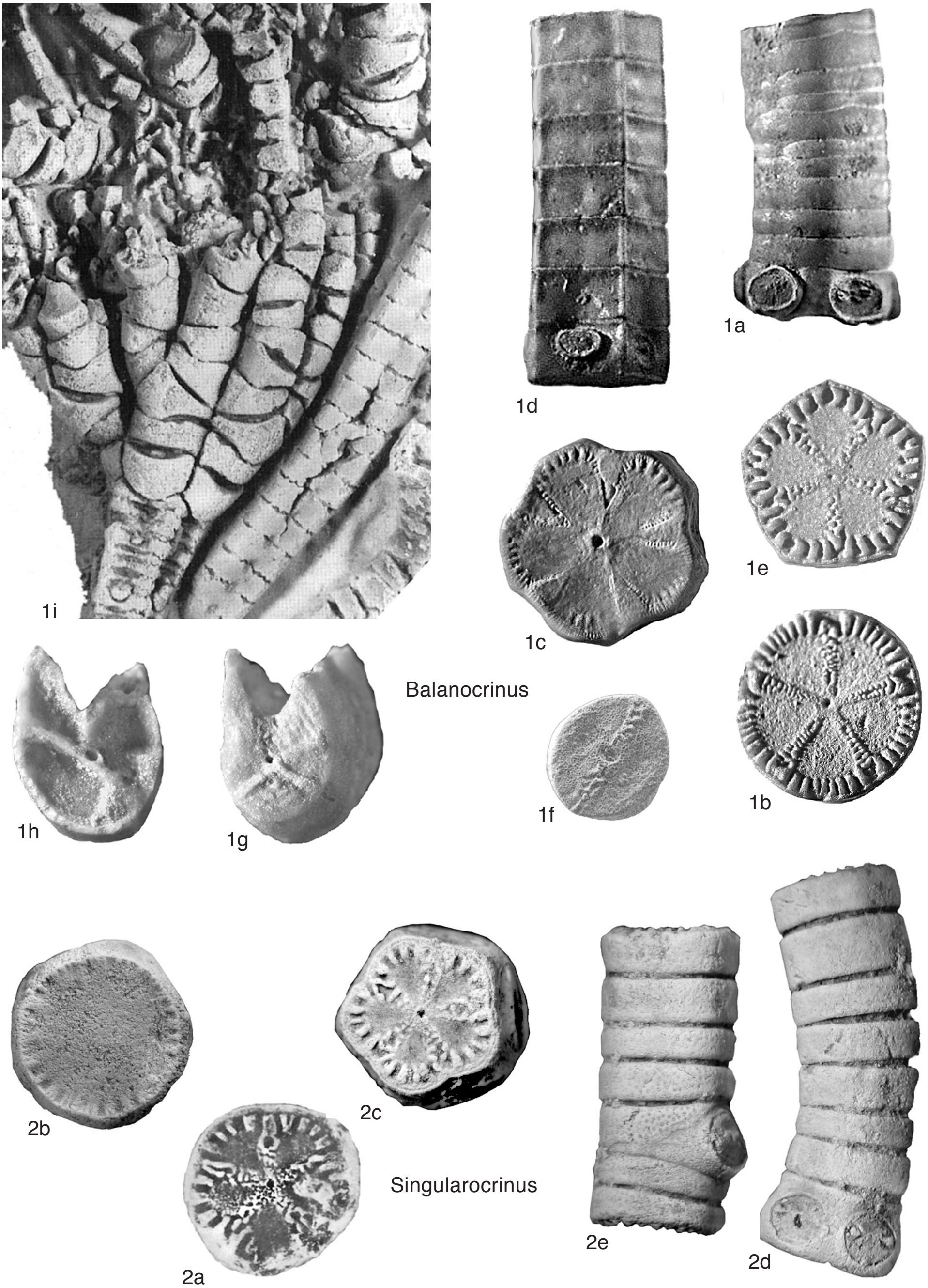


FIG. 30. Isocrinidae (p. 56–58).

in the bands of adradial crenulae, and in having fewer than 20 rather than supposedly more than 30 internodals per noditaxis (see SIMMS, 1989a, p. 56). KLIKUSHIN (1982a) subsequently raised both to generic status and created a third genus, *Terocrinus,* to accommodate several Lower Jurassic and one Triassic species, with *Pentacrinites subteroides* QUENSTEDT (1858) as type species. *Terocrinus* has a slender column, larger marginal crenulae than in *Balanocrinus,* and the petals correspondingly surround small, droplike areolae rather than large triangular areolae. However, the features distinguishing *Margocrinus* and *Terocrinus* from *Balanocrinus*, such as the column cross section, are not consistent enough to warrant generic status. Following SIMMS (1989a, p. 56), both are considered herein to be subjective junior synonyms of *Balanocrinus*. A Triassic existence of *Balanocrinus* species has been questioned by SIMMS (1988d), who suggested that the lineage evolved as a paedomorphic offshoot from *Isocrinus* during the Early Jurassic.] *?Middle Triassic, Lower Jurassic (Sinemurian)–Lower Cretaceous (Albian), Upper Cretaceous (?Cenomanian, ?Santonian):* England, France, Germany, Hungary, Italy, Poland, Portugal, Spain, Switzerland, Russia, Algeria, Tunisia; France, Madagascar, *?Cenomanian, ?Santonian.*——FIG. 30,*1a–c.* **B. subteres* (MÜNSTER), Oxfordian, Switzerland; *a,* column, NMB M10586, ×4; *b*, facet of internodal, NMB M10587, ×6; *c*, distal, cryptosymplectial facet of nodal, NMB M10588, ×6 (Hess, new).——FIG. 30,*1d–e. B. pentagonalis* (GOLDFUSS), Oxfordian, Switzerland; *d,* lateral view of column, NMB M10579, ×10; *e*, facet of internodal, NMB M10622, ×13 (Hess, new).——FIG. 30,*1f. B. subteroides* (QUENSTEDT); synarthrial facet on larval columnal, Pliensbachian, England, BMNH E70451, ×30 (Simms, 1989a).——FIG. 30,*1g–h. B. ticinensis* HESS; epizygal secundibrachial; *g*, proximal syzygy; *h*, distal oblique muscular articulation with pinnule socket, Pliensbachian, Switzerland, syntype, NMB M10403, ×10 (Hess, 2006).——FIG. 30,*1i. B. gracilis* (CHARLESWORTH); proximal column and crown, Pliensbachian, England, BMNH E70344, ×2.5 (Simms & Sevastopulo, 1993).

Laevigatocrinus KLIKUSHIN, 1979b, p. 88 [**Pentacrinus laevigatus* MÜNSTER, 1841, p. 50; OD]. Crown unknown. Column cylindrical, distal columnals very high. Articular facets with large peripheral crenulae and small petals. Cirrus sockets 2 to 4, rarely 1 or 5, large, directed outward. [KLIKUSHIN (1982a, p. 302) placed *Laevigatocrinus* in the subfamily Balanocrininae, although the facets resemble those of *Austinocrinus*. However, assignment of *Laevigatocrinus* to the Isselicrinidae seems problematic because of the wide stratigraphic gap between this Late Triassic form and remaining Isselicrinidae, which are all from the Upper Cretaceous. Preservation potential of such forms is so good that intermediate forms should be preserved.] *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* Austria, Bulgaria, Italy, Poland, Russia, Amur Basin, Afghanistan, China, New Zealand.——FIG. 27,*2a–c.* **L. laevigatus* (MÜNSTER), Italy; *a–b,* pluricolumnal, *a*, oblique lateral with 2 cirrus sockets, *b*, proximal facet, lectotype, BSP As VII 912, ×6; *c*, distal view of nodal with cirrals, IGPT, ×9 (Hagdorn, new).

Percevalicrinus KLIKUSHIN, 1977, p. 88, *nom. nov. pro Picteticrinus* DE LORIOL in DE LORIOL & PELLAT, 1875, p. 298, *non* ÉTALLON, 1857, p. 282, *nom. nud.* [**Picteticrinus beaugrandi* DE LORIOL in DE LORIOL & PELLAT, 1875, p. 298; M]. Basals large, forming contiguous circlet; lower edge of basals with inconspicuous median prolongation partly covering edge of uppermost columnal. Arms divided at primibrachial 2, some arms divided further once or twice with variable intervals. Flat articulation between primibrachials 1 and 2. Column stellate, with radial pores in sutures; proximal columnals alternating in height. Internodes of 5 to 17 columnals. Columnal facets with short and uniform marginal and adradial crenulae. Cirrus sockets small, strongly depressed, directed obliquely upward. [The genus and attributed species were diagnosed and described in detail by KLIKUSHIN in 1979c and 1981. *Picteticrinus* DE LORIOL in DE LORIOL & PELLAT, 1875, p. 298 is junior homonym of *Picteticrinus* ÉTALLON, 1857, p. 282, *nom. nud.* The genus was rejected as a homonym by DE LORIOL (1878 in 1877–1879, p. 111), and the type species was transferred to *Cainocrinus* FORBES, 1852, p. 33. BIESE (1930) incorrectly made *P. beaugrandi* the type species of *Cainocrinus*.] *Upper Jurassic (Tithonian)–Lower Cretaceous (Valanginian):* France, Russia, Siberia, ?North America.——FIG. 27,*3a–c.* **P. beaugrandi* (DE LORIOL), Portlandian, France; *a,* base of crown and column with basals; *b*, column, lectotype, ×3; *c*, facet of columnal, ×3 (de Loriol, 1887).

Singularocrinus KLIKUSHIN, 1982a, p. 303 [**S. singularis*; M]. Cup low cone shaped, with convex base and large basals visible in side view. Column circular, facets with short, strong crenulae along margin; adradial crenulae wider and continuing toward lumen as band of small crenulae or granules; nodals 2 to 3 times higher than internodals. Internodes long, as many as 17 columnals. Cirrus sockets large, directed outward, specimens with less than 5 sockets occur. [KLIKUSHIN (1982a, p. 303) distinguished this genus from other balanocrinines by the extraordinarily large nodals and by the "complex hypozygal ridge;" however, KLIKUSHIN did not illustrate the latter feature. SIMMS (1990a, p. 73) suggested that it may be a continuation of the *Laevigatocrinus* lineage.] *Upper Triassic (Carnian–Norian):* Caucasus, China.——FIG. 30,*2a–e.* **S. singularis*; *a,* facet of internodal, Norian, Russia, holotype, LGI TB-5-6, ×6 (Klikushin, 1992); *b–c*, nodal, *b*, distal, *c*, proximal facet, Carnian, China, MHI 1603/1/4, ×6; *d*, column with nodal, Carnian, China, MHI 1603/1/2, ×6; *e*, column with nodal, Carnian, China, MHI 1603/1/3, ×6 (Hagdorn, new).

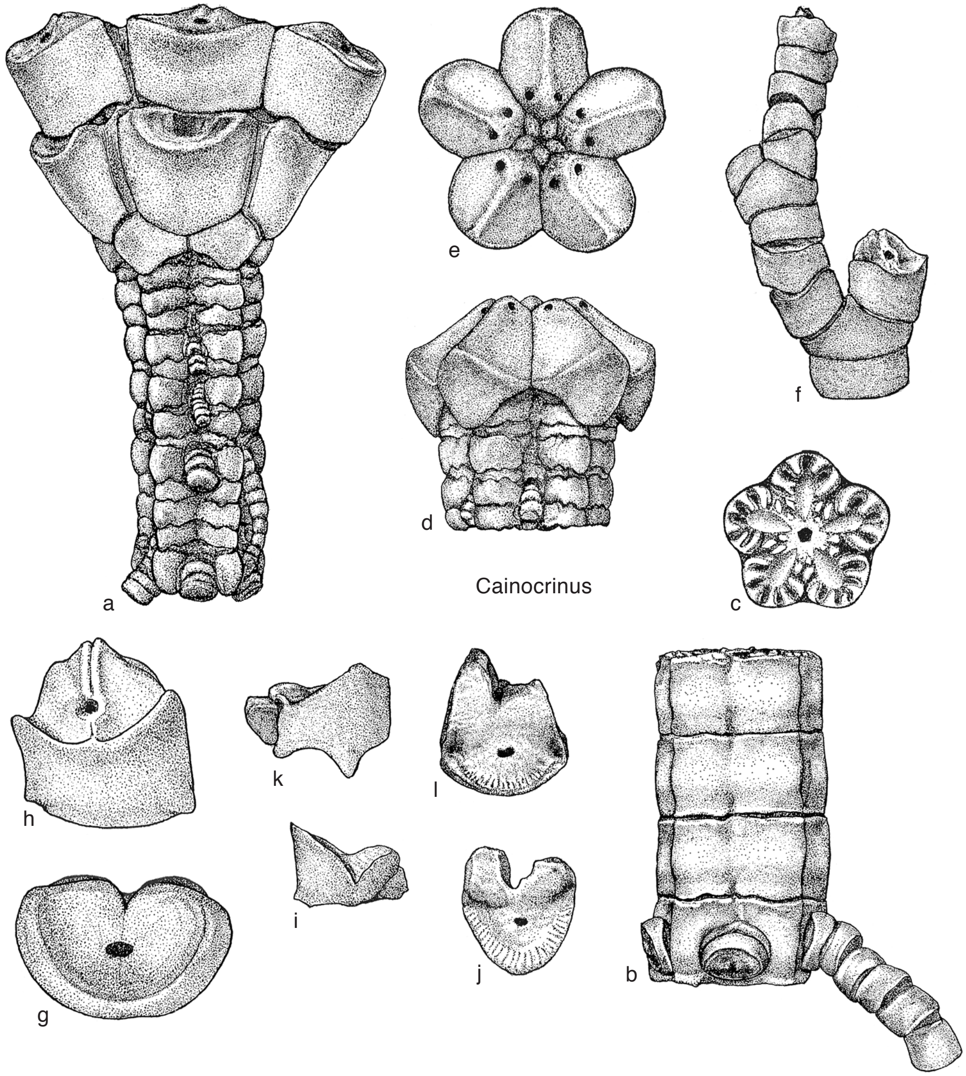


FIG. 31. Cainocrinidae (p. 59–61).

Family CAINOCRINIDAE Simms, 1988

[Cainocrinidae SIMMS, 1988a, p. 275, 284]

Cryptosyzygy or synostosis between primibrachials 1 and 2; flat synarthry between secundibrachials 1 and 2; cryptosyzygy or symmorphy between secundibrachials 3 and 4. *Lower Cretaceous (Hauterivian)–Holocene.*

Cainocrinus FORBES, 1852, p. 33 [**C. tintinnabulum;* M; *emend.*, RASMUSSEN, 1972a, p. 26]. Symmorphy between secundibrachials 3 and 4; muscular articulation between tertibrachials 1 and 2, and symmorphy between tertibrachials 2 and 3. Further symmorphies may occur distally, all other brachial articulations muscular. Arms divided at primibrachial 2 and secundibrachial 4; no further divisions. First pinnule on secundibrachial 2. Nodals with 5 circular to elliptical cirrus sockets. [*Picteticrinus beaugrandi* DE LORIOL in DE LORIOL & PELLAT, 1875, p. 298, was referred to *Cainocrinus* by DE LORIOL (1878 in 1877–1879, p. 111) and was incorrectly designated the lectotype of this genus by BIESE (1930). RASMUSSEN (1972a) described new specimens of the type species.] *Paleogene (Eocene), ?Paleocene:* England, Italy, Crimea, *Eocene;* Poland, *?Paleocene.*——FIG. 31*a–l.* **C. tintinnabulum*,

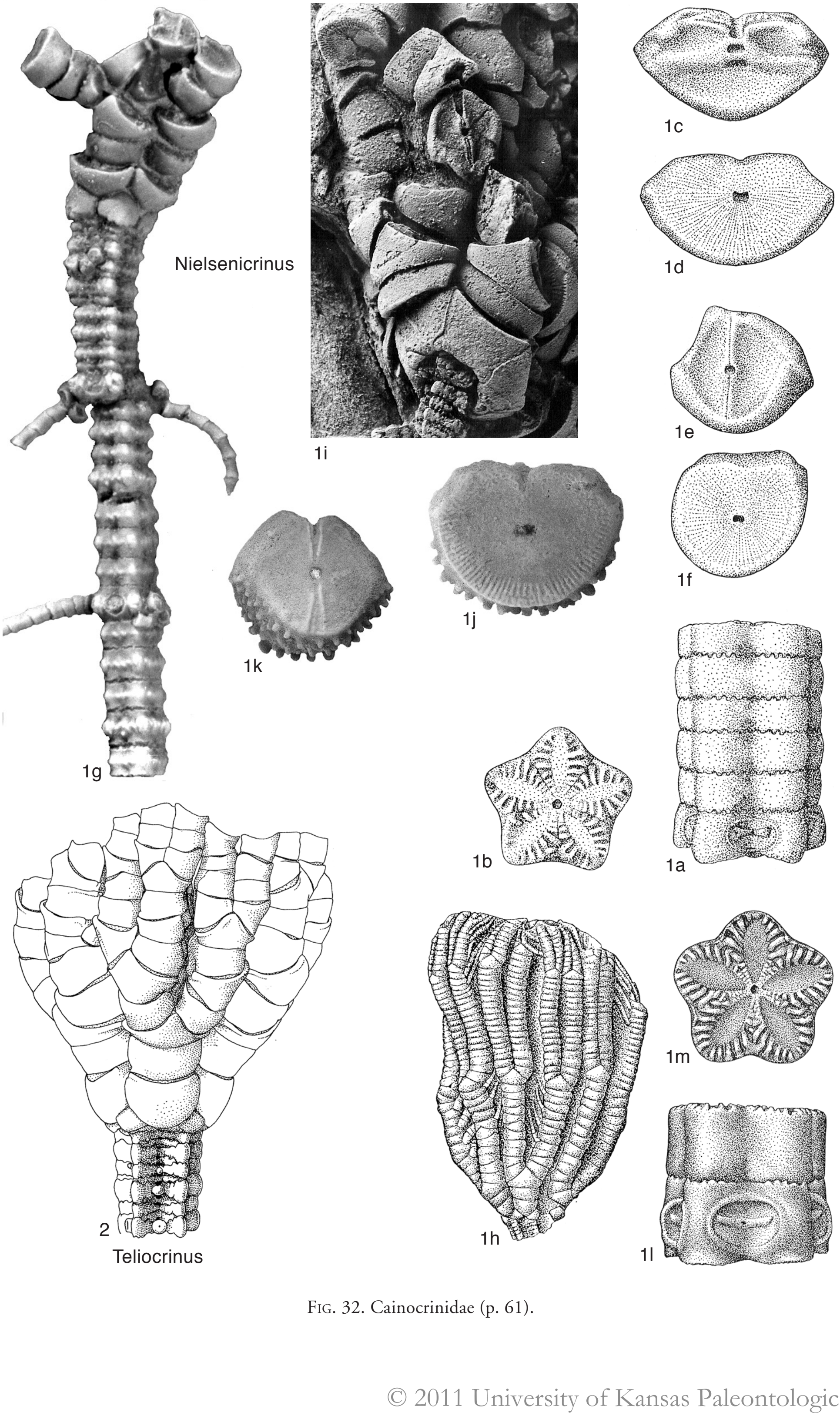


FIG. 32. Cainocrinidae (p. 61).

Eocene, England; *a,* proximal column and crown, MGUH 12759, ×11; *b–c*, column with cirrus, *b*, lateral, *c*, facet of internodal, MGUH 12760, ×8; *d–e*, basal circlet and proximal column, *d*, lateral, *e*, distal, MGUH 12763, ×10; *f*, arm from primibrachial 1 to tertibrachial 5, MGUH 12768, ×5; *g*, proximal view of primibrachial 2, MGUH 12767, ×10; *h*, oblique distal view of secundibrachial 1 (synarthry), MGUH 12769, ×10; *i–j*, tertibrachial 2, *i*, lateral, *j*, distal, MGUH 12774, ×10; *k–l*, tertibrachial 3, *k*, lateral, *l*, proximal, MGUH 12775, ×10 (Rasmussen, 1972a).

Nielsenicrinus Rasmussen, 1961, p. 94 [**Pentacrinus obsoletus* Nielsen, 1913, p. 97; OD]. Cryptosyzygy between secundibrachials 3 and 4, no symmorphy. [Columnals of this genus have also been reported from the Upper Cretaceous to upper Oligocene in Crimea, Kazakhstan, India, Australia, and New Zealand (see Oji & others, 1996). However, the wide variability in columnal morphology of these specimens renders assignment to *Nielsenicrinus* doubtful.] *Lower Cretaceous (Hauterivian)–Paleogene (Oligocene):* Denmark, England, France, Germany, Netherlands, Sweden, Switzerland, Japan, *Hauterivian–Maastrichtian;* New Zealand, *Oligocene.*——Fig. 32,*1a–f.* **N. obsoletus* (Nielsen), Danian, Denmark; *a–b,* column, *a*, lateral, *b*, facet of internodal, MGUH 8884, ×5; *c–d*, primibrachial 1, *c*, proximal, *d*, distal (cryptosyzygy), MGUH 8889, ×5; *e*, distal view of secundibrachial 1, MGUH 8891, ×5; *f*, distal view of secundibrachial 3 (cryptosyzygy), MGUH 8893, ×5 (Rasmussen, 1961).——Fig. 32,*1g. N. cretaceus* (Leymerie, 1842), proximal column and part of crown, Cenomanian, England, BMNH E22104, ×2 (Smith & Wright, 2002).——Fig. 32,*1h. N. chavannesi* (de Loriol, 1879 in 1877–1879), crown, Hauterivian, Switzerland, lectotype, MHNG 28548, ×2.5 (Rasmussen, 1961).——Fig. 32,*1i. N. japonicus* Oji & others, 1996, proximal part of crown, Upper Cretaceous, Japan, holotype, UMUT ME19811, ×4 (Oji & others, 1996).——Fig. 32,*1j–k. N. carinatus* (Roemer, 1840 in 1840–1841), Campanian, Netherlands; *j,* proximal view of primibrachial 2 (cryptosyzygy), NHMM MB 1044p, ×7; *k*, distal view of secundibrachial 1 (weak synarthry), NHMM MB 1044r, ×7 (Jagt, 1999a).——Fig. 32,*1l–m. N. fionicus* (Nielsen, 1913), Danian, Denmark; column, *l*, lateral, *m*, facet of internodal, MGUH 8896, ×4 (Rasmussen, 1961).

Teliocrinus Döderlein, 1912, p. 22 [**T. asper;* M; =*Hypalocrinus springeri* A. H. Clark, 1909j, p. 650] [=*Comastrocrinus* A. H. Clark, 1912c, p. 252 (type, *Hypalocrinus springeri* A. H. Clark, 1909j, OD)]. Arms divided at primibrachial 2 and further divided at variable intervals of 1 to 6 brachials. Cryptosyzygy between primibrachials 1 and 2 and generally between brachials 2 and 3 or brachials 3 and 4 of succeeding brachial series, also in undivided distal branches more distally. Number of arm divisions increasing during growth by augmentative regeneration, each division generally following a cryptosyzygy. Synarthry may occur between brachials 1 and 2 in each brachial series. Nodals larger than internodals, with 5 subcircular cirrus sockets facing outward and commonly reaching lower edge of the nodal. [Roux (1981) placed the genus in the Isocrinidae, subfamily Diplocrininae, and Roux, Améziane, and Eléaume (2009) placed the genus in the Pentacrinitidae, subfamily Diplocrininae. According to Roux, Améziane, and Eléaume (2009), the specimens from the Miocene of Japan, named *T. springeri* by Oji (1990) and renamed *T. ojii* Roux, Améziane, & Eléaume (2009), may belong to *Endoxocrinus*.] *Neogene (lower Miocene)–Holocene:* Japan, *lower Miocene;* northern Indian Ocean, *Holocene.*——Fig. 32,*2.* **T. springeri* (A. H. Clark); proximal column and base of crown, Holocene, USNM 36068, ×3 (Roux, Messing, & Améziane, 2002; photo courtesy of the *Bulletin of Marine Science*).

Family ISSELICRINIDAE
Klikushin, 1977

[*nom. transl.* Simms, 1988a, p. 275, *ex* Isselicrininae Klikushin, 1977, p. 89]

Cryptosyzygy between primibrachials 1 and 2 and secundibrachials 1 and 2, in Metacrininae muscular articulation between secundibrachials 1 and 2. [Articular facet between primibrachials 1 and 2 has also been called synostosial (Klikushin, 1982a). Simms (1988a, p. 275) included the following genera: *Annacrinus*, *Austinocrinus*, *Cenocrinus*, *Diplocrinus*, *Doreckicrinus*, *Endoxocrinus*, *Isselicrinus*, *Metacrinus*, and *Saracrinus*. The family is herein divided into 3 subfamilies.] *Upper Cretaceous (Campanian)–Holocene.*

Subfamily ISSELICRININAE
Klikushin, 1977

[Isselicrininae Klikushin, 1977, p. 89]

Nodals widely separated; fewer than 5 cirrus sockets, may rarely be 5 in *Austinocrinus. Upper Cretaceous (Campanian)–Neogene (Miocene).*

Isselicrinus Rovereto, 1914, p. 177, *emend.*, Rasmussen, 1954, p. 553 [**I. insculptus;* M; =?*Pentacrinus didactylus* d'Archiac, 1846, p. 200] [=*Lipocrinus* Rasmussen, 1953, p. 416 (type, *Pentacrinites subbasaltiformis* Miller, 1821, p. 140, OD); =*Buchicrinus* Klikushin, 1977, p. 92 (type, *Pentacrinites buchii* Roemer, 1840 in 1840–1841, p. 27; SD Klikushin, 1977, p. 92)]. Cup large, forming wide, low bowl. Small infrabasals concealed, completely surrounded by basal circlet. Basals large, lower edge with median projection

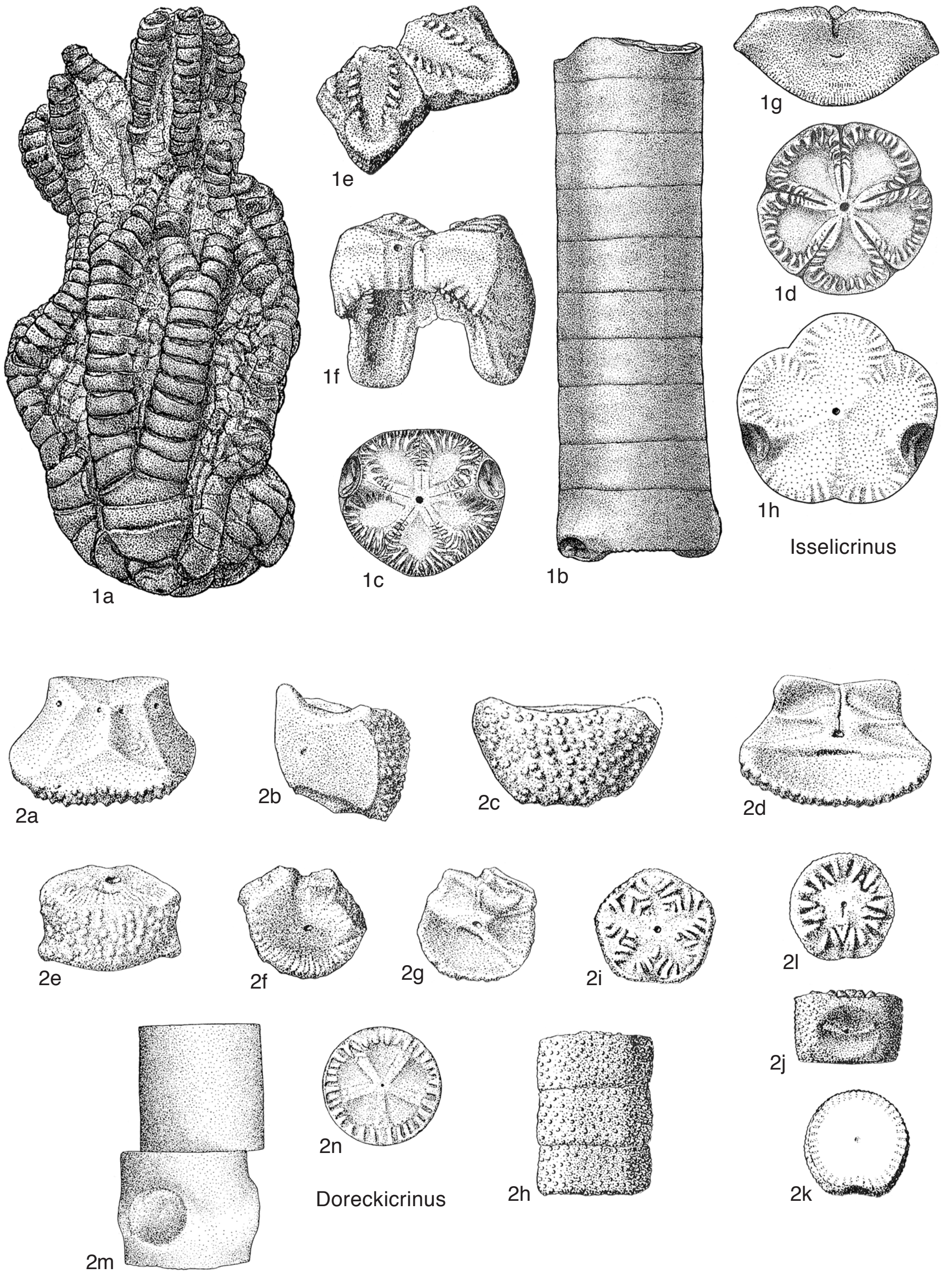


FIG. 33. Isselicrinidae (p. 61–65).

covering interradial edge of uppermost columnals. Upper ends of basals forming bottom of wide and shallow central cavity, outer sides of basals more or less covered by surrounding large radials. Arms divided at primibrachial 2 and may be further divided at long intervals. Muscular articulations between secundibrachials 2 and 3 and secundibrachials 3 and 4. Succeeding brachial articulations may all be muscular, but isolated brachials indicate that cryptosyzygial and symmorphial articulations may be present in some species. Column cylindrical, pentalobate, or pentagonal to stellate in cross section. Columnal facets in most species similar to *Balanocrinus*, with uniform marginal crenulae and with adradial ridges or ribbons of minor crenulae or granules. However, some specimens, especially with small or pentalobate columnals, have a more or less gradual transition from marginal to adradial crenulae similar to *Isocrinus*, although petals are generally wide, drop shaped, and almost subtriangular. Cirrus sockets rather small, facing downward from lower edge of nodal. Cirri short and slender. [Genus based on crushed column presumably of *P. didactylus* but interpreted by Rovereto (1914) as proximal part of conical column. Klikushin (1977, p. 92) proposed the subgenera *Isselicrinus* and *Buchicrinus,* and later Klikushin (1982a, p. 304) raised the latter to generic status. Following Oji (1990) and Jagt (1999a, p. 76), *Buchicrinus buchii* (Roemer) is herein regarded as a species of *Isselicrinus*. Upright, bundled columns of *I. ariakensis* (Yokoyama, 1911) from upper Eocene mudstones of western Japan suggest a relay strategy in which individuals attached themselves to a preexisting, autotomized column of the same individual (Fujiwara & others, 2005).] *Upper Cretaceous (Maastrichtian)–Neogene (Miocene):* Armenia, Austria, Denmark, England, France, Germany, Hungary, Italy, Spain, Sweden, Switzerland, Yugoslavia, Caucasus, Crimea, Iran, Tunisia, Algeria, Borneo, Japan, Greenland, USA (New Jersey), South America (Tierra del Fuego), Cuba, Haiti.——Fig. 33,*1a–d*. **I. subbasaltiformis* (Miller), Eocene, Denmark; *a,* crown, MGUH 12755, ×1.8; *b–c*, column, *b*, lateral, *c*, distal facet of nodal, MGUH 12753, ×4; *d*, facet of internodal, MGUH 12754, ×4 (Rasmussen, 1972a).——Fig. 33,*1e–h*. *I. paucicirrhus* (Nielsen, 1913), Danian, Denmark; *e–f,* 2 basals, *e*, lower (proximal) side, *f,* lateral, MGUH 1198, ×5; *g*, proximal view of primibrachial 2, Coll. Geol. Survey Denmark, ×2.5; *h*, distal facet of nodal, MGUH 1163, ×3 (Rasmussen, 1961).

Austinocrinus de Loriol, 1889a, p. 153 [**A. komaroffi;* M; =*Pentacrinus erckerti* Dames, 1885, p. 219; =?*Pentacrinus sulcifer* Eichwald, 1871, p. 83, sp. indet.] [=*Austinocrinus (Penroseocrinus)* Sieverts-Doreck, 1953, p. 114 (type, *Balanocrinus mexicanus* Springer, 1922b, p. 1, OD)]. Column stout, up to several meters long. Columnals low, rounded subpentagonal to circular in section, proximal columnals pentalobate. Internodes long, of 15 to 37 columnals. Nodals slightly enlarged, mainly where cirri are attached. Cirri reduced in proxistele but thick and long in dististele. Commonly 1 or 2 cirrus sockets. In proximal, pentalobate nodals sockets directed strongly upward, almost reaching edge between nodal and supranodal. In more distal nodals, sockets very large, almost circular, facing outward or slightly upward, generally covering entire height of nodal and most of supranodal, and in some specimens also part of infranodal. Columnal facets with 5 elliptical petals and stout crenulae, which may be more or less restricted to radial marginal area in proximal, pentalobate columnals, strongly reduced toward center of articular facet, and missing interradially of petals. In more distal, cylindrical columnals, this petaloid pattern occupies only the central part of articular facet and is surrounded by a secondary zone with a large number of very long and fine, radiating crenulae, which may be closely placed or form small, isolated groups, or crenulae may be interrupted and form 2 or 3 concentric zones. [Sieverts-Doreck (1953, p. 113) proposed 2 subgenera, *Austinocrinus* s. str., and *Penroseocrinus*. Following Rasmussen (1961, p. 28), this subdivison is not followed herein. Jaekel (1904) referred an isolated crown from the lower Campanian of northern Germany with reservation to *A. rothpletzi* Stolley (1892). Basals are stout, but separated on the side of the cup by the lower point of the radials. Arms are divided at primibrachial 2. There is no division at secundibrachial 2; more distal brachials are unknown. Articulation between primibrachials 1 and 2 is slightly biconcave and almost smooth, with indistinct radiating crenulae (cryptosymplectial or cryptosyzygial). Some columnals of the Triassic *Laevigatocrinus laevigatus* (Münster, 1841) and *Eckicrinus radiatus* (Schauroth, 1859) may have very long radial, marginal crenulae resembling the pattern of columnals of *Austinocrinus* (see for example, Klikushin 1979b, fig. 1b; Hagdorn, Głuchowski, & Boczarowski, 1996, pl. 5,*g*).] *Upper Cretaceous (Campanian–Maastrichtian):* Denmark, England, Germany, Netherlands, Spain, Turkey, Caucasus, Turkmenistan, Tunisia, Mexico, Cuba.——Fig. 34,*1a–b*. **A. erckerti* (Dames), Maastrichtian; *a,* facet of cirral, Spain, MHNG 28473, ×2.5 (Rasmussen, 1961); *b*, proximal facet of supranodal (nodal with 5 cirri), Turkmenistan, LGI KT-48-17, ×2.5 (Klikushin, 1985b).——Fig. 34,*1c–h*. *A. rothpletzi* Stolley, 1892; *c,* base of crown, Senonian, Germany, ×1 (Jaekel, 1904); *d*, facet of proximal internodal, Campanian, Germany, Hamburg coll. 218, ×5 (Rasmussen, 1961); *e–g*, column (nodal with 3 cirrus sockets), *e*, lateral, *f,* distal facet, *g*, proximal facet, Campanian, Turkmenistan, NMB M10589, ×3; *h*, facet of distal internodal, Campanian, Turkmenistan, NMB M10590, ×4 (Hess, new).

Doreckicrinus Rasmussen, 1961, p. 75 [**Pentacrinus miliaris* Nielsen, 1913, p. 97; OD]. Radials and proximal brachials referred to type species indicate cup rather large with radials more or less

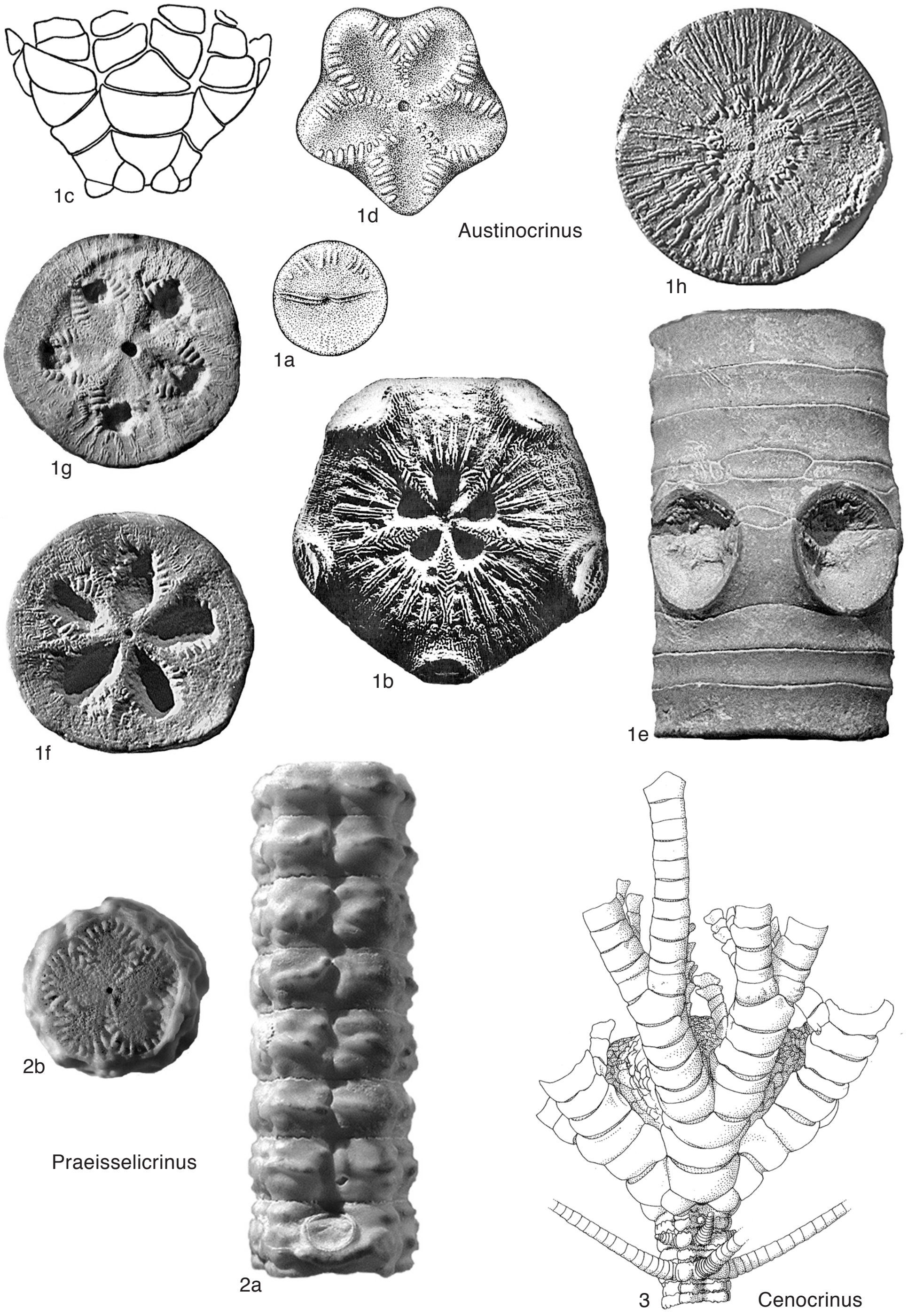


FIG. 34. Isselicrinidae (p. 63–65).

overhanging basals. Arms divided at primibrachial 2 but apparently not at secundibrachial 2. First pinnule on secundibrachial 2. Column circular to rounded subpentagonal, rarely pentalobate in section. Columnals moderate to high. Articulation between nodal and infranodal cryptosymplectial to smooth synostosial. Cirrus sockets circular to elliptical in outline, centrally placed on the sides and commonly considerably smaller than height of nodal. Columnal facets with uniform marginal crenulae and faint adradial ridges, or few large crenulae more or less restricted to radial marginal areas, rarely with narrow elliptical petals surrounded by numerous crenulae. [There is a great resemblance of this genus to the living species *Endoxocrinus (Diplocrinus) alternicirrus* (Carpenter, 1884a, p. 321) in structure of column, articular facet of columnals, nodals having less than 5 cirri, and cryptosyzygial articulations in proximal brachials. However, arm branching is different in *Endoxocrinus*.] *Upper Cretaceous (Maastrichtian)–Paleogene (Danian):* Denmark, Italy, Netherlands.——Fig. 33,*2a–l.* **D. miliaris* (Nielsen), Danian, Denmark; *a–d,* radial, *a*, proximal, *b*, lateral, *c*, aboral, *d*, distal, MGUH 8867, ×5; *e*, aboral view of primibrachial 1, MGUH 8866, ×5; *f–g*, secundibrachial, presumably 2, *f*, proximal, *g*, distal, MGUH 8868, ×5; *h–i*, pluricolumnal, *h*, lateral, *i*, facet, Coll. Wind No. 64, ×5; *j–l*, nodal, *j*, lateral, *k*, distal facet, *l*, proximal facet, MGUH 8864, ×5 (Rasmussen, 1961).——Fig. 33,*2m–n. D. italicus* Rasmussen, 1961; pluricolumnal, *m*, lateral, *n*, facet of internodal, Senonian, Italy, syntype, NMB M3068 (not No. 9278, as listed in Rasmussen, 1961), ×4 (Rasmussen, 1961).

Praeisselicrinus Klikushin, 1977, p. 92 [**Isselicrinus atabekjani* Klikushin, 1973, p. 43; OD] [=*Isselicrinus (Praeisselicrinus)* Klikushin, 1977, p. 92 (type, *Isselicrinus atabekjani* Klikushin, 1973, p. 43, OD)]. Crown unknown. Column pentalobate in section. Sutures proximally serrate, crenulae small. Cirrus sockets 1 or 2, directed upward. Internodes of 15 or 16 columnals. *Upper Cretaceous (Campanian, ?Maastrichtian):* Turkmenistan, *Campanian;* Netherlands, *?Maastrichtian.*——Fig. 34,*2a–b.* **P. atabekjani* (Klikushin), Campanian, Turkmenistan; *a*, column, NMB M10591, ×3.5; *b*, facet of internodal, NMB M10592, ×3 (Hess, new).

Subfamily DIPLOCRININAE
Roux, 1981

[Diplocrininae Roux, 1981, p. 482]

Brachitaxes typically with fewer than 5 brachials beyond secundaxil (more in *Cenocrinus*). Symplectial facets of columnals with lanceolate areolae opened outward and with relatively few crenulae (fewer than 8). Nodals always with 5 cirrus sockets, except in *Endoxocrinus (Diplocrinus) alternicirrus* (Carpenter, 1882c) in which nodals have only 2 or 3 cirri. [Roux, Améziane, and Eléaume (2009) included *Doreckicrinus*, *Endoxocrinus* (with *Endoxocrinus* and *Diplocrinus* as subgenera), *Nielsenicrinus,* and *Teliocrinus* in the subfamily.] *Holocene.*

Cenocrinus Thomson, 1864, p. 2–3 [**Isis asteria* Linné, 1767, p. 1288; M; =*Encrinus caput medusae* Lamarck, 1816, p. 435; ICZN Opinion 636, 1962]. Cup bowl shaped. Basals rather small, separated on surface of cup. Arms divided at primibrachial 2; approximately 6 secundibrachials; further divisions with variable intervals, and distal brachitaxis series with more than 6 brachials. Cryptosyzygy between brachials 1 and 2 of brachitaxes, all other brachial articulations muscular. Proximal columnals pentalobate, alternating in size and with radial pores in the suture; distal column subcylindrical. Internodes of 13 to 21 internodals, less in proximal part of column; nodals slightly larger than internodals, and with 5 large, elliptical cirrus sockets facing outward; cirri long. *Holocene:* Western tropical Atlantic Ocean.——Fig. 34,*3.* **C. asterius* (Linné); proximal column and base of crown, NSU, ×2 (Roux, Messing, & Améziane, 2002; photo courtesy of the *Bulletin of Marine Science*).

Endoxocrinus A. H. Clark, 1908i, p. 151 [**Encrinus parrae* Gervais, 1835, p. 49; OD; =*Pentacrinus muelleri* Örsted, 1857, p. 202; David and others (2006, p. 34) designated Örsted's specimen of *Pentacrinus müllleri* as the neotype of *E. parrae*, thus treating *muelleri* as a junior objective synonym of *parrae*.] [=*Isocrinus (Diplocrinus)* Döderlein, 1912, p. 21 (type, *Pentacrinus maclareanus* Thomson, 1877b, p. 113, SD A. H. Clark, 1923a, p. 11); =*Annacrinus* A. H. Clark, 1923a, p. 11 (type, *Pentacrinus wyvillethomsoni* C. W. Thomson, 1872, p. 767, OD)]. Cup rather low. Basals small and separated to rather large, forming contiguous basal circlet; lower edge of basals more or less covering uppermost columnals. Radials with or without median projection of lower edge, separating basals. Arms divided at primibrachial 2 and secundibrachial 2 and further divided with intervals of 2 or 3 brachials, but all divisions after either primibrachial 2 or secundibrachial 2 heterotomous, restricted to outer branches, inner branches remaining undivided. Cryptosyzygy between all first and second brachials in a brachial series, and sometimes occurring also more distally in undivided arms of some species. Column commonly rather short, rounded pentagonal to pentalobate in section. Proximal columnals pentalobate, strongly alternating and with radial pores. Nodals with generally 5 elliptical to almost circular cirrus sockets facing outward or slightly downward, occupying generally entire height of nodal and sometimes extending to infranodal or supranodal. *E. (D.) alternicirrus* (Carpenter,

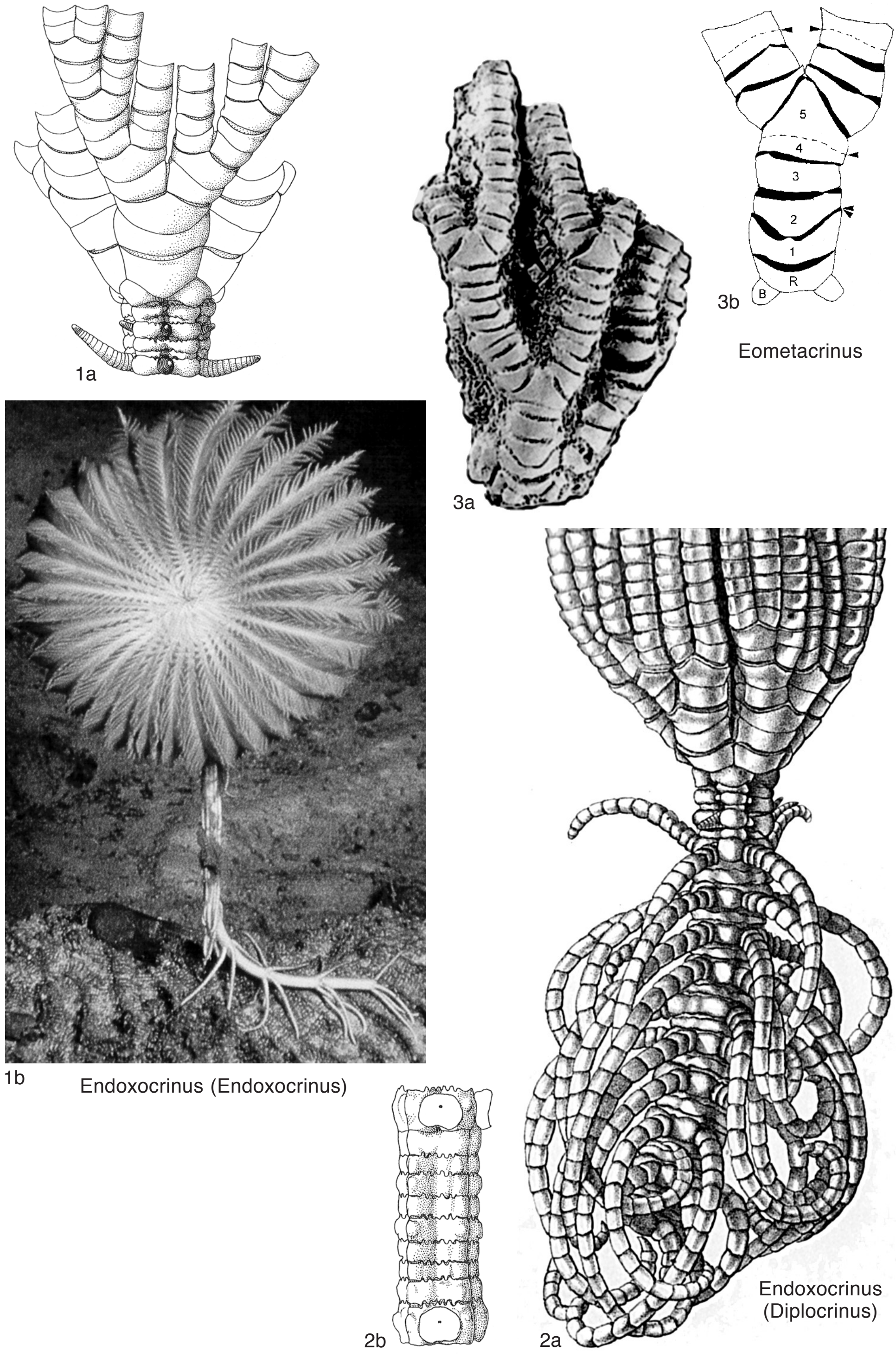


FIG. 35. Isselicrinidae (p. 67–69).

1882c) has less than 5 cirri per nodal. Articular facet of columnals similar to *Isocrinus*, commonly with rather uniform crenulae. [*Endoxocrinus* and *Diplocrinus* have been distinguished by the pattern of brachial ramification and number of brachials separating each division, but both characters vary within the species or specimens. Therefore, they were considered by RASMUSSEN (1978) as subgenera, and *Annacrinus* was treated as a separate genus. *Annacrinus* was treated as a subgenus of *Endoxocrinus* by ROUX, 1977a, and ROUX, MESSING, and AMÉZIANE, 2002. Following DAVID and others (2006), *Pentacrinus wyvillethomsoni* is herein classified with the subgenus *Diplocrinus.*] *Holocene:* tropical to subtropical western Atlantic Ocean (bathyal).

E. (**Endoxocrinus**). Secundibrachial series from 1 to 4 brachials, usually 2; tertibrachials to pentabrachials from 1 to 5 brachials, exceptionally up to 7; commonly 3 rather than 2 in the tertibrachitaxis, typically 3 in quartibrachitaxis and pentabrachitaxis. Number of internodals per mature noditaxes 3 to 16; rarely, a distal callus at end of column; number of cirrals typically more than 30. *Holocene:* western tropical Atlantic Ocean (bathyal).——FIG. 35,*1a–b*. **E. (E.) parrae* (GERVAIS); *a,* proximal column and base of crown, NSU CRI 614, ×2.5 (Roux, Messing, & Améziane, 2002; photo courtesy of the *Bulletin of Marine Science*); *b,* living specimen of **E. (E.) parrae* in feeding position on coral, crown with 32 arms deploying parabolic filtration fan, oral view with current from behind, Bahamas at 692 m (Hess, 1999e).

E. (**Diplocrinus**) DÖDERLEIN 1912, p. 21 [**Pentacrinus maclareanus* THOMSON, 1877b, p. 113; SD A. H. CLARK, 1923a, p. 11]. Second brachial axillary in all brachitaxes, very rarely first or third. Number of internodals per mature noditaxis strongly variable; column typically with distal callus; number of cirrals per cirrus typically fewer than 30, cirrals relatively long. *Holocene:* western tropical Atlantic Ocean, northeastern Atlantic Ocean, central and western Pacific Ocean (bathyal).——FIG. 35,*2a*. **E. (D.) maclareanus* (THOMSON, 1877b), proximal column with cirri and base of crown, western Atlantic off Brazil at 640 m, ×2 (P. H. Carpenter, 1884a, pl. 16,*1*).——FIG. 35,*2b*. *E. (D.) alternicirrus* (CARPENTER, 1882c); portion of column between 2 nodals, ×2 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

Subfamily METACRININAE Klikushin, 1977

[Metacrininae KLIKUSHIN, 1977, p. 89; *emend.,* ROUX, 1981, p. 482]

Cryptosyzygy or synarthry between primibrachials 1 and 2, muscular articulation between secundibrachials 1 and 2. More than 2 primibrachials. Nodals with 5 cirrus sockets. [KLIKUSHIN (1977) assigned the following genera to this subfamily: *Metacrinus*, *Saracrinus*, *Diplocrinus,* and *Teliocrinus*; but later (KLIKUSHIN, 1992) assigned *Cenocrinus*, *Metacrinus*, *Nielsenicrinus,* and *Saracrinus* instead. ROUX (1981, p. 482) restricted the Metacrininae to only *Metacrinus* and *Saracrinus*, forms with more than 2 primibrachials. *Eometacrinus* BAUMILLER & GAŹDZICKI, 1996, is similar to *Metacrinus* and *Saracrinus* in having 5 primibrachials and muscular articulation between secundibrachials 1 and 2, but it differs in the synarthrial articulation between primibrachials 1 and 2.] *Paleogene (Eocene)–Holocene.*

Metacrinus CARPENTER, 1882c, p. 167 [**M. wyvillii* CARPENTER, 1884a, p. 358; SD A. H. CLARK, 1908d, p. 527]. Cup low and wide. Basals generally large, forming contiguous basal circlet; lower edge with median projection covering interradial edge of uppermost columnals. Typically 7 primibrachials (range: 2 to 11). Arms divided at primibrachials 4 to 7 and further divided 2 or more times. Cryptosyzygy between primibrachials 1 and 2, in species with 7 primibrachials also a cryptosyzygy between primibrachials 4 and 5 or primibrachials 5 and 6, in secundibrachitaxis cryptosyzygy between secundibrachials 2 and 3 or 3 and 4, and in more distal parts of arms. Other brachial articulations muscular. No synarthry. All axillaries follow an oblique muscular articulation. First pinnule on primibrachial 2. Column pentagonal or pentalobate to rounded subpentagonal. Columnal facets similar to *Isocrinus*, crenulae rather short. Internodes of 5 to 13 internodals, fewer in proximal part of column. Nodals larger than internodals, with 5 rather large, elliptical to circular cirrus sockets facing outward or slightly upward. Cirri long. *Paleogene (Eocene)–Holocene:* Antarctic Peninsula, *Eocene;* western Pacific Ocean (sublittoral–bathyal), *Holocene.*——FIG. 36,*1a*. **M. wyvillii;* proximal column and part of crown, Holocene, Kermadec Islands at 1152 m, ×1.2 (Carpenter, 1884a, pl. 48,*1*).——FIG. 36,*1b. M. fossilis* RASMUSSEN, 1979; crown, Eocene, Antarctic Peninsula, USNM 459260, loc. 500, ×1.5 (Meyer & Oji, 1993).——FIG. 36,*1c. M. levii* AMÉZIANE-COMINARDI in AMÉZIANE & others, 1990; cryptosyzygy on proximal facet of primibrachial 2, Holocene, MNHN EcPh50, ×8 (Améziane, new).

Eometacrinus BAUMILLER & GAŹDZICKI, 1996, p. 106 [**E. australis;* M]. Primibrachials 5. Synarthry between primibrachials 1 and 2, cryptosyzygy between primibrachials 4 and 5. *Paleogene (Eocene):* Antarctic Peninsula.——FIG. 35,*3a–b*. **E. australis*; *a,* proximal part of crown, ×2, *b,* cup plates and proximal brachials (*B,* basal; *R,* radial; *1–5,* IBr1–5; *single arrows,* syzygies; *double arrow,* synarthry),

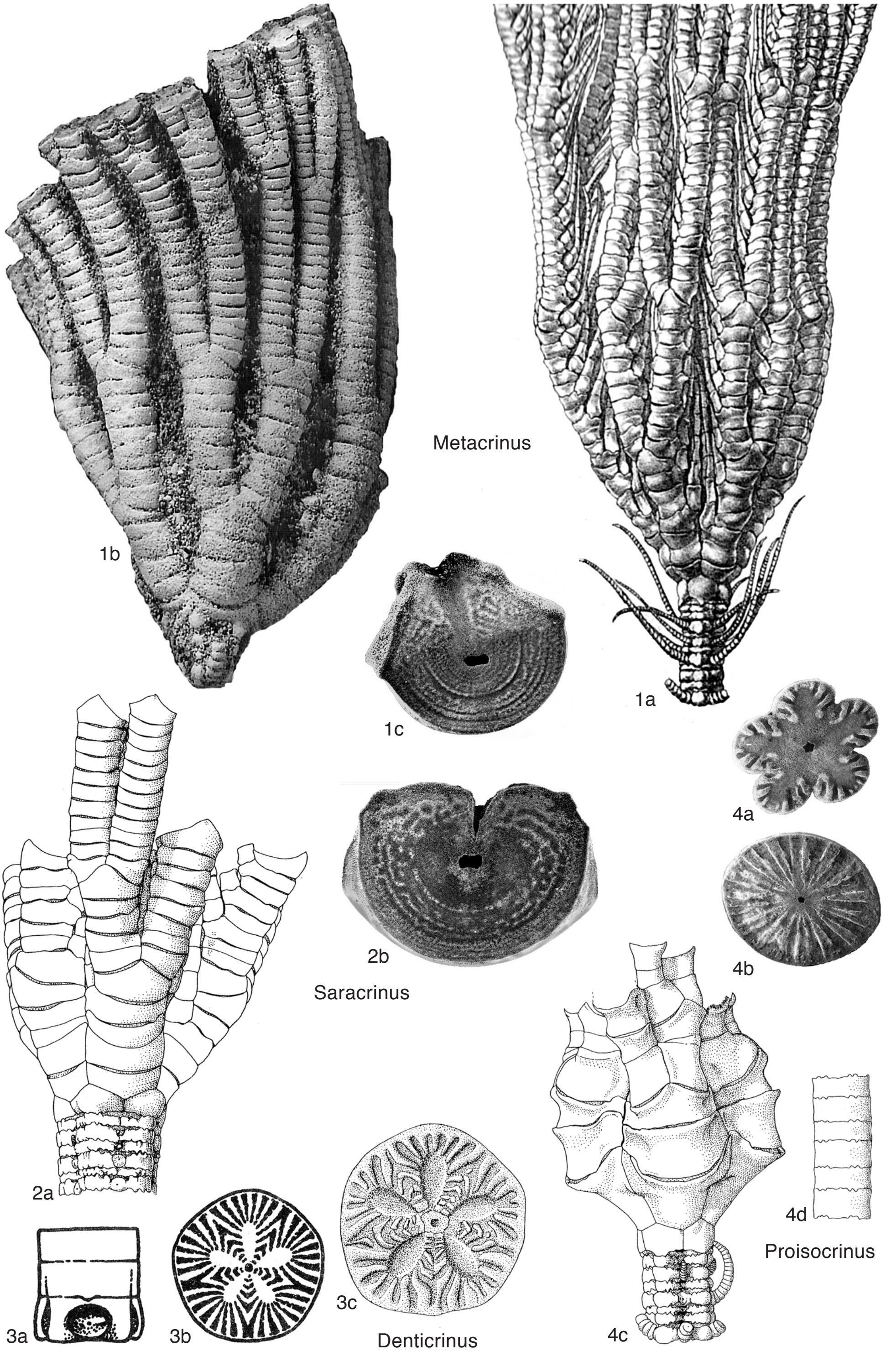


FIG. 36. Isselicrinidae and Proisocrinidae (p. 67–69).

Eocene, Antarctic Peninsula, ZPAL Ca.V/3, ×3 (Baumiller & Gaździcki, 1996).

Saracrinus A. H. CLARK, 1923a, p. 9 [**Metacrinus nobilis* CARPENTER, 1884a, p. 351; OD]. Typically 4 primibrachials (range: 3 to 6), only primibrachials 1 and 2 united by cryptosyzygy. [This genus is closely related to *Metacrinus* but is treated herein separately in accordance with the recent literature (MEYER & OJI, 1993; AMÉZIANE, 1997; ROUX, MESSING, & AMÉZIANE, 2002).] *Neogene (Miocene)–Holocene:* New Zealand, *Miocene;* western Pacific Ocean, *Holocene.*——FIG. 36,*2a.* **S. nobilis* (CARPENTER); proximal column and base of crown, Holocene, MNHN EcPs156, ×2.5 (Roux, Messing, & Améziane, 2002; photo courtesy of the *Bulletin of Marine Science*).——FIG. 36,*2b. S. moosai* AMÉZIANE; cryptosyzygy on proximal facet of primibrachial 2, Holocene, Kai Islands, Indonesia at approximately 300 m, MNHN EcPh6, ×8 (Améziane, 1997).

Subfamily UNCERTAIN

Denticrinus KLIKUSHIN, 1985a, p. 46 [**D. dentifer*; OD]. Crown unknown. Column circular distally. Nodals somewhat larger than internodals. Cirrus sockets 5, large, strongly depressed and directed outward, restricted to columnal. Columnal facets with long, thick, peripheral crenulae almost perpendicular to edge of facet, crenulae begin immediately at small petals and passing into periphery without bifurcating; length of culmina reaching half or more of width of radius. [KLIKUSHIN (1985a) assigned *Denticrinus* to Metacrininae, but it differs from other genera of this group by the strongly depressed cirrus sockets and columnal facets closely resembling those of *Austinocrinus*. Five cirrus sockets restricted to one columnal distinguish it from *Austinocrinus.*] *Paleogene (Danian):* Russia, Bulgaria.——FIG. 36,*3a–b.* **D. dentifer*, Russia; *a,* pluricolumnal, ×2; *b*, facet of internodal, ×2 (Klikushin, 1992).——FIG. 36,*3c. D. gocevi* (SIEVERTS-DORECK, 1951a); facet of internodal, Bulgaria, holotype, ×4 (Rasmussen, 1961).

Family PROISOCRINIDAE
Rasmussen, 1978

[Proisocrinidae RASMUSSEN, 1978, p. 866]

Cup with a rather low, cylindrical circlet of 5 basals and a larger, broadly conical circlet of 5 radials, pentalobate in outline. Radial articular facet wide, occupying entire upper edge of cup. Arms divided at primibrachial 2 and secundibrachial 2. Proximal brachials broad, meeting laterally. Nonmuscular (synostosial) articulations between primibrachials 1 and 2 and secundibrachials 1 and 2; all other articulations muscular. First pinnule on tertibrachial 2. Column very long, pentalobate in section proximally, with columnals alternating in size. Rudimentary, cirrus-bearing nodals restricted to proximal column; cirrus sockets obliterated distally. Middle and distal column cylindrical; columnals not alternating in size. Facets of proximal columnals with petaloid crenulae, those of middle and distal columnals with rather large, radiating crenulae, not reaching lumen. All articulations symplectial, no cryptosymplexies between nodals and infranodals. Attachment by cementing disk. [RASMUSSEN (1978, p. 866) assigned the family to the Isocrinida based on the structure of the crown and the presence of nodals with cirri. BOURSEAU and others (1991, p. 265) suggested affinities with the Millericrinidae due to the absence of cryptosymplexies, the multiradiate facets in the distal column, and the resemblance to species of *Angulocrinus*. However, a recent phylogenetic study (ROUSE, JERMIN, & MESSING, 2006) confirms RASMUSSEN's original assignment. Synostosial articulation between the primibrachials suggests that *Proisocrinus* is probably derived from Isocrinina with cryptosyzygial or synostosial, rather than synarthrial, articulation between the primibrachials (OJI & KITAZAWA, 2008). The proximal column of *Proisocrinus* resembles the column of *Holocrinus*. Holocrinids have massive cup elements, and their distal columnals (internodals) may be cylindrical with radiating crenulae, as in the Middle Triassic *Holocrinus meyeri* and *Eckicrinus radiatus* (HAGDORN, GŁUCHOWSKI, & BOCZAROWSKI, 1996, fig. 5; pl. 3,*n;* pl. 5,*g,n,u*). Thus, *Proisocrinus* may be representative of an ancestral form on the path from holocrinids to millericrinids, a process induced by preferential attachment to hardgrounds by a terminal disk.] *Holocene.*

Proisocrinus A. H. CLARK, 1910d, p. 387 [**P. ruberrimus*; M]. Characters as for family. *Holocene:* western and central Pacific Ocean (bathyal).——FIG. 36,*4a–d.* **P. ruberrimus*; *a,* facet of proximal columnal, holotype, USNM 24308, ×4; *b,* facet of distal columnal, holotype, USNM 24308, ×4 (Bourseau & others, 1991); *c*, proximal column and base of crown, Bishop Museum 1992.340, ×1.5; *d*, portion of mesistele, MNHN EcPs 10247, ×1.5 (Roux, Messing, & Améziane, 2002; photos courtesy of the *Bulletin of Marine Science*).

COMATULIDA

HANS HESS and CHARLES G. MESSING

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Order COMATULIDA A. H. Clark, 1908

[Comatulida A. H. CLARK, 1908h, p. 135] [=Comatuladae FLEMING, 1828, p. 494; =Comatulidae D'ORBIGNY, 1852 in 1850–1852, p. 138, including Uintacrinida and excluding Thiolliericrinidae A. H. CLARK, 1908b, p. 209]

Larval column with synarthrial articulations that may persist in adult columns without true cirri (suborder Bourgueticrinina). Attachment by radix or terminal disk (suborders Bourgueticrinina and Guillecrinina). Reduction of column to cirri-bearing centrodorsal or complete loss of attachment structure (suborder Comatulidina). [Comatulida A. H. CLARK, 1908h, was established as an order to cover the family Comatuladae FLEMING, 1828, =Comatulidae D'ORBIGNY, 1852 in 1850–1852, p. 138), including Uintacrinida and excluding Thiolliericrinidae CLARK, 1908b. Herein, Thiolliericrinidae are included in the order. Bourgueticrinina are included in the order because of their relationship with Thiolliericrinidae, a family that bridges the gap between bourgueticrinids and comatulids proper. This follows the classification of SIMMS and others (1993, p. 501), but raises the Bourgueticrinidae to subordinal status. Also included are the extant stalked Guillecrinina, previously assigned to the Hyocrinida by MIRONOV and SOROKINA (1998b). Recent molecular analyses suggested that they belong to a clade including bourgueticrinids and comatulids (COHEN & others, 2004).] *Upper Triassic (Norian)–Holocene.*

The following discussion is based on RASMUSSEN (1978, p. 867). In comatulids proper (suborder Comatulidina), the cirriferous uppermost columnal or series of coalesced proximal columnals becomes enlarged during the stalked postlarval stage (pentacrinoid) and attached to the cup as a centrodorsal with cirri. The postlarval column distal to the centrodorsal is autotomized, and the juvenile takes up a nonsessile existence, anchoring to substrates via the cirri but still being free to creep and, in some families, swim. Cirri are secondarily reduced or lost in some genera of Comasteridae. Thiolliericrinidae, Bourgueticrinina, and Guillecrinina retain the column as adults, apparently via paedomorphosis.

A. H. CLARK (1915a in 1915–1950) interpreted the centrodorsal as a single nodal, not a series of coalesced nodals, and this may be correct insofar as no new columnals develop proximal to the centrodorsal. However, after the first 5 radially oriented (as in other dicyclic or cryptodicyclic crinoids) cirri form, the centrodorsal continues to grow at its proximal (adoral, upper) margin, adding new cirrus sockets and cirri. Among modern comatulids, additional single columnals never form. However, in the Upper Triassic to Middle Jurassic Paracomatuloidea, the centrodorsal is composed of a series of closely joined, very low columnals separated by distinct sutures and articulated by a more or less distinct petaloid pattern of crenulae, similar to the column of *Pentacrinites*. Each of these columnals have 5 cirri positioned either midradially, in 5 vertical columns, or adradially, alternating in position with cirri on the columnal below, thus forming 10 vertical columns. Many fossil and modern comatulids develop a more or less conical centrodorsal with cirri arranged in 10 columns, which may be a primitive feature. The socket arrangement may be modified, most simply by intercalation of new sockets radially, increasing the number of columns from 10 to 15 or 20. Sockets in adjacent columns alternate in position along the oral-aboral axis rather than lying side by side. In many others, alternating the addition of new sockets at or near the centrodorsal margin produces diagonal whorls of sockets rather than columns. Increasing diameter relative to height with growth often produces a truncated or discoidal centrodorsal with apical cirri and sockets reduced (obsolete) or obliterated and commonly with a cirrus-free, flattened-to-concave aboral apex. Crowded marginal sockets are generally described as lying in irregular horizontal rows, circles, or verticils.

After some cirri develop in the uppermost columnal, the pentacrinoid discards the rest of the column, and the comatulid remains without an articulated column or permanent attachment. The separation between centrodorsal and postlarval column reveals a 5-rayed perforation at the aboral pole, corresponding to the axial canal of the column. Although this opening is closed rapidly by calcareous deposits, some species retain a remnant radial, star-shaped impression in the centrodorsal cavity (so-called dorsal star). Rarely, in both extant and fossil species, the aboral apex bears a faint, petaloid impression with interradial rays, perhaps the remains of a scar from a pentagonal postlarval column. If indeed several columnals fused to form the centrodorsal, the possibility exists that exceptional autotomy of the column between two of the enlarged columnals in the juvenile centrodorsal might leave this scar.

The adoral (proximal, upper) side of the centrodorsal has a central pit, the centrodorsal cavity, which houses the chambered organ and surrounding nerve capsule. Cavity diameter varies from less than 20 to more than 50 percent of the centrodorsal diameter, decreasing relatively during growth. Modern Atelecrinidae and some of the Antedonoidea, especially Zenometridae and Pentametrocrinidae, exhibit the greatest cavity diameters. Cavity diameter is approximately 25 to 30 percent of centrodorsal diameter in adults of most other comatulids. CLARK (1909h) regarded this relative size as an important feature in subdividing Comatulida into 2 suborders: Oligophreata with proportionally smaller and Macrophreata with larger cavities. However, the distinction is neither sharp nor natural, and these suborders are not recognized here.

A fine canal runs from the centrodorsal cavity to each cirrus. The opening of these canals may form 1 to 4 vertical columns in each radial section of the centrodorsal cavity. Pores are also similarly arranged in the centrodorsal cavity in some species lacking sockets in distinct columns, but whether this is a general feature is unknown.

The adoral side of the centrodorsal is divided into 5 radial sections by 5 interradial ridges or furrows. Some comatulids (Decameridae, most Mariametroidea, Asterometridae, Notocrinoidea, and a few other comatulids such as *Antedon bifida*) bear in each radial area a pit, depression, or branched furrows for the reception of coelomic diverticulae of unknown function. In many Asterometridae and Notocrinoidea, the radial pits are very deep.

The arrangement of cirri in radial groups, the radial orientation of the first cirri formed, and the commonly pentagonal outline of the centrodorsal with interradial angles indicate that comatulids are dicyclic or cryptodicyclic, according to the rule of WACHSMUTH and SPRINGER (1886). In fact, 3 to 5 vestigial infrabasals occur in the early stage of 2 extant species, and the extant *Promachocrinus kerguelensis* bears 5 larger infrabasals (see A. H. CLARK 1915a, in 1915–1950, p. 315). Vestigial infrabasals also occur in the Upper Jurassic *Solanocrinites gresslyi* (ÉTALLON, 1862) (Fig. 38*j*) and the Lower Cretaceous *Comatulina batalleri* (ASTRE, 1925), in which they form a central star on the adoral side of the centrodorsal (Fig. 40,*2c*).

Basals are well developed in the larval and postlarval stages of all comatulids. In the paracomatulids and the oldest true comatulids (such as *Palaeocomaster*), the basals form a stellate circlet of 5 rather stout plates, exposed interradially, joined centrally, and articulated to the centrodorsal with a petaloid pattern of crenulae, similar to that in *Pentacrinites*. In living *Atelecrinus* and *Sibogacrinus* and in the fossil *Jaekelometra*, the basals maintain their postlarval character as a circlet of large plates, although they may gradually shrink during growth. In the Cretaceous Decameridae, the inner ends of the basals grow into large plates, forming a stout basal circlet surrounded by the radial circlet. In all other comatulids, the basals are more or less reduced to 5 interradial rods or tongues lodged in the shallow interradial furrows in the centrodorsal plus a central perforated plate called the rosette that roofs the centrodorsal cavity. In many Mesozoic species, the rodlike basals may have faint crenulae. Their tips may be exposed interradially between centrodorsal and radials, or they may be concealed. In Mariametroidea and most Antedonoidea, the rodlike portions are reduced, and only the rosette remains (Fig. 3,*4;* Fig. 5,*2*).

Radials occur invariably in a circlet of 5, although 2 living genera of Antedonoidea, *Promachocrinus* and *Thaumatocrinus*, have 5 additional radials (pararadials) that are interradial in position and retarded during early growth. They bear arms similar to those arising from the primary radials. The radials generally have a rather low exposed surface but may be concealed in the midradial area by the centrodorsal and first brachial. Size and shape of muscle fossae of the radial articular facets vary greatly. In living forms, the size of muscle fossae appears to be correlated with swimming activity (Janevski & Baumiller, 2010). In the swimming antedonids, arms are gracile and the muscle fossae are high, which compensates for the narrower articular facet. In contrast, the crawling comasterids have low muscle fossae.

Rays are undivided in Pentametrocrinidae, Atopocrinidae, Eudiocrinidae, and some fossil species of Solanocrinitoidea. A few fossil Solanocrinitoidea have rays divided at the first primibrachial, probably as a result of the fusion of the first and second primibrachials (Fig. 38*m–n*). In all other comatulids, rays divide at least once at primibrachial 2, and it many taxa, one to several times more at intervals of 2 to 4 brachials. Articulation between primibrachials 1 and 2 and generally also secundibrachials 1 and 2 is synarthrial, although some Solanocrinitoidea with undivided rays have muscular articulation here. The fulcral ridge and ligamentary fossae of proximal synarthries may be reduced in a few genera so that the articular surface is almost flat (cryptosynarthry). A syzygy occurs between primibrachials 1 and 2 only in Zygometridae, Eudiocrinidae, and *Comatula* (Comasteridae). Elsewhere among comatulids, syzygial articulations generally occur between brachials 3 and 4 of brachitaxes (when composed of 4 ossicles) and undivided arms. They appear at variable intervals more distally. In *Paracomatula*, a cryptosyzygy with numerous fine ridges replaces the syzygy between the secundibrachials 3 and 4. Pinnulation is generally complete, although pinnules are absent on the proximal few to as many as 17 brachials of the undivided arm in Bourgueticrinina, Guillecrinina, and Atelecrinidae. Some comatulids proper, such as *Comatilia* (Comasteridae) and *Hypalometra* (Antedonidae), may also lack one or a few proximal pinnules. Otherwise, the first pinnule occurs on the outside of the second ossicle in a secundibrachial and following-series composed of 4 ossicles and (when brachitaxes consist of 2 ossicles) the second brachial of an undivided arm. Pinnules never occur on axils or the proximal ossicle of a syzygial pair. Pinnules first appear near the tip of the arm in advanced pentacrinoid postlarvae, followed by the proximalmost pinnule on the second brachial. Pinnules on the intervening several brachials appear afterward.

The large majority of fossil comatulid species are based on isolated cups (radial and basal circlets), mostly still attached to the centrodorsal (Gislén, 1924). This causes taxonomic problems because diagnostic features of extant forms also include ray branching pattern and cirrus and pinnule structures (Messing, 1997). Noteworthy are the very rare occurrences of the intact comatulids *Paracomatula* in the Middle Jurassic of Switzerland (Hess, 1951, 1999b) and *Uintacrinus* in the Upper Cretaceous of North America (Springer, 1901; Hess 1999d; Meyer & Milsom, 2001). In most intact specimens from the Upper Triassic to the Upper Jurassic, centrodorsals are, unfortunately, partly hidden or indistinct (de Loriol,

1895; LEUTHARDT, 1911; MANNI, NICOSIA, & RIOU, 1985; SIMMS, 1988b; HAGDORN & CAMPBELL, 1993; BAUMILLER & GAŹDZICKI, 1996; HESS, 1999c), although some preserve details of centrodorsal structure (DE LORIOL, 1879 in 1877–1879, 1889 in 1882–1889; BIGOT, 1938).

Suborder COMATULIDINA A. H. Clark, 1908

[*nom. transl.* SIMMS, 1988a, p. 284, *ex* Comatulida A. H. CLARK, 1908h, p. 135] [=infraorder Comatulidia, *nom. transl.* SIMMS & others, 1993, p. 503, *ex* Comatulida A. H. CLARK, 1908h, p. 135]

Stalked, postlarval pentacrinoid stage followed by development of enlarged, uppermost columnal or series of fused columnals as a cirri-bearing centrodorsal that may be absent in some taxa. Thiolliericrinidae retain the column distal to the centrodorsal. Basals unmodified in most fossil forms, but modified and largely internalized in extant forms, except *Atelecrinus* and *Sibogacrinus*. Enlarged calyx present in Uintacrinoidea. *Upper Triassic (Norian)–Holocene.*

Superfamily PARACOMATULOIDEA Hess, 1951

[*nom. correct.* HESS & MESSING, herein, *pro* Paracomatulacea RASMUSSEN, 1978, p. 869, *nom. transl. ex* Paracomatulidae HESS, 1951, p. 208]

Centrodorsal rather low, composed of closely united, still articulated, 5-sided columnals; terminal columnal with sealed axial canal. Cirrus sockets without profile, offset to either side of radial midline and arranged in 5 or 10 columns. Stellate circlet of basals articulating with centrodorsal with pattern of narrow, interradial petals bordered by short, uniform crenulae (as in column of *Pentacrinites*). Radials with large exposed surface, commonly recumbent or overhanging. Radial articular facet large and steep to almost vertical; adoral muscle fossae high. Rays divided once at primibrachial 2; synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2; cryptosyzygy with numerous fine ridges between secundibrachials 3 and 4. Syzygies after secundibrachials 11 or 12 on approximately every fifth brachial and with a few coarse ridges. First pinnule on secundibrachial 2. *Upper Triassic (Norian)–Middle Jurassic (Bajocian).*

Family PARACOMATULIDAE Hess, 1951

[Paracomatulidae HESS, 1951, p. 208]

Characters as for superfamily. *Upper Triassic (Norian)–Middle Jurassic (Bajocian).*

Paracomatula HESS, 1951, p. 209 [**P. helvetica*; M]. Characters as for family and superfamily. [Characters of the genus and corresponding higher taxa are almost entirely based on intact specimens of the type species. *P. helvetica* has 3 cirriferous proximal columnals and 2 distal columnals without cirri; the distalmost columnal is sealed; brachials are finely striated. Centrodorsals and cups of the Upper Triassic *P. triadica* HAGDORN & CAMPBELL (1993) and the Lower Jurassic *P. liasica* HESS (2006) correspond in all important aspects to *P. helvetica*. However, the centrodorsal of *P. triadica* and a small centrodorsal described as *Paracomatula* sp., upper Sinemurian–lower Pliensbachian, Turkey (NICOSIA, 1991), are composed of 7 columnals. At the lower (distal) end of the latter, the axial canal is still visible so that the centrodorsal may originally have been even higher. The centrodorsal of *P. liasica* consists of only 2 columnals sealed distally.] *Upper Triassic (Norian)–Middle Jurassic (Bajocian)*: New Caledonia (HAGDORN & CAMPBELL, 1993), *Norian;* Turkey, Switzerland, *Sinemurian–Pliensbachian;* Switzerland, *Bajocian.*——FIG. 37,*1a–i*. **P. helvetica,* Bajocian, Switzerland; *a,* centrodorsal with radials and cirrals, syntype, NMB M9894, ×6 (Hess, 1951); *b,* base of crown with centrodorsal, topotype, NMB M10593, ×5.6 (Hess, new); *c*, centrodorsal with radial circlet, ×5 (Rasmussen, 1978); *d*, basal circlet on radial circlet, topotype, NMB M10594, ×5; *e*, distal facet of secundibrachial 3 (cryptosyzygy), topotype, NMB M10595, ×8; *f–g*, secundibrachial, *f*, proximal (syzygy), *g*, distal, topotype, NMB M10596, ×8; *h–i*, secundibrachial with muscular facets, *h*, proximal, *i*, distal with pinnule socket, topotype, NMB M10598, ×8 (Hess, new).——FIG. 37,*1j–k*. *P. liasica* HESS; centrodorsal with basal circlet, *j*, lateral, *k*, adoral, Pliensbachian, Switzerland, holotype, NMB M10361, ×10 (Hess, 2006).

Superfamily ATELECRINOIDEA Bather, 1899

[*nom. transl.* HESS & MESSING, herein, *ex* Atelecrinidae BATHER, 1899, p. 923; *emend.*, MESSING, 2003a, p. 280]

Centrodorsal conical; adoral rim with 5 interradial depressions or deep pits; centrodorsal cavity broad and deep. Cirrus sockets in 10 or 15 columns, bearing weak to strong, lateral, articular tubercles arising from socket rim. Basals wedge shaped, forming an externally visible ring (rarely as slightly separated, low, wide triangles) with a small central canal; rosette absent. Rays divided once at primibrachial 2. Proximal pinnules absent. [CLARK and CLARK (1967) grouped the Atelecrinidae with the Pentametrocrinidae and Antedonidae in the comatulid suborder Macrophreata, based, in part, on the relatively large centrodorsal cavity, structure of the rosette, and radial ossicles with thin-walled muscle fossae. RASMUSSEN (1978) moved the family to the superfamily Paracomatuloidea but listed no feature interpretable as a synapomorphy for the 2 included taxa (Paracomatulidae and Atelecrinidae). SIMMS (1988a) removed the family from the Paracomatuloidea, ostensibly returning it to the infraorder Comatulidia (comatulids *sensu stricto*) but without discussion. According to MESSING (2003a), Atelecrinidae, as defined by RASMUSSEN (1978) in the *Treatise* (including the extant genera *Atopocrinus* and *Sibogacrinus* and Cretaceous *Jaekelometra*), does not represent a monophyletic clade. Notwithstanding that most *Atelecrinus* have a complete basal circlet rather than just interradial triangles, the high, thin basals of *Jaekelometra* differ completely from the flattened, wedge-shaped ossicles of *Atelecrinus*. Similarly, the thin radials of *Jaekelometra*, with the plane of their low, wide, articular facets almost perpendicular to the adoral-aboral axis, also differ completely from those of *Atelecrinus*. As a result, MESSING (2003a) removed *Jaekelometra* from the Atelecrinidae and treated it as family *incertae sedis*. It is herein treated as a family of its own, Jaekelometridae, of uncertain superfamilial status. MESSING (2003a) also removed *Sibogacrinus,* based on a perceived similarity to *Jaekelometra*. However, reexamination of the unique but now deteriorated type specimen of *S. anomalus* (C. MESSING, unpublished data, 2008) reveals thick, wedge-shaped basals more similar to those of *Atelecrinus* than *Jaekelometra*. The cirrus sockets also bear weak triangular fulcral processes. It is herein retained within Atelecrinidae. MESSING (2003a, p. 291) noted that *Atopocrinus* differs from *Atelecrinus* in several respects, and new material reveals narrow, tongue-like basals rather than a complete circlet (C. MESSING, unpublished data, 2008). The genus is treated here as a family of its own, Atopocrinidae, of uncertain superfamilial status. *Pentametrocrinus varians* shares with *Atelecrinus* similarly modified, distal brachial articulations characterized by alternating, distally projecting and proximally recumbent muscle fossae, a potential synapomorphy linking *Atelecrinus* and the Pentametrocrinidae. However, these muscle fossae may also represent similar but independently developed structural solutions to a particular functional problem, perhaps associated with a specific means of swimming. Pentametrocrinidae are classified with the Antedonoidea.] *Holocene.*

Family ATELECRINIDAE Bather, 1899

[Atelecrinidae BATHER, 1899, p. 923; *emend.*, MESSING, 2003a, p. 280]

Characters as for superfamily. *Holocene.*

Atelecrinus CARPENTER, 1881c, p. 166 [**A. balanoides;* SD CARPENTER, 1888, p. 71]. Centrodorsal thin walled; centrodorsal cavity cavernous with interradial buttresses concave or hollow at their adoral ends. Lateral fulcral tubercles on cirrus sockets well developed, projecting, and producing a serrate centrodorsal profile. Basals visible externally as thin ring or low, wide triangles. Two laterally adjacent, axillary, second primibrachials have the large inner muscle fossa transformed into a process, resembling a shoe with deeply ridged sole. Proximal arm ambulacra with pseudopedicellariae and without podia; arm tip flagellate and lacking pinnules. Pinnule sockets on middle and distal brachials with a cavernous muscle fossa. [*Atelecrinus cubensis* CARPENTER (1881c, p. 166) is not conspecific with *A. balanoides* and belongs in a separate, new genus (MESSING, unpublished data, 2011).] *Holocene:* northern and tropical western Atlantic Ocean, tropical western and central Pacific Ocean (bathyal).——FIG. 37,*2a*. **A. balanoides;* interradial buttresses of centrodorsal, NSU, ×20 (Messing, 2003a).——FIG. 37,*2b–d*. *A. wyvilli* CARPENTER (1882b), MNHN IE-2009-9005 (Messing, 2003a); *b*, centrodorsal, ×10; *c*, oblique aboral-distal view of distal facet of axillary primibrachial 2, ×15; *d*, oblique proximal-lateral view of axillary primibrachial 2, ×15 (Messing, 2003a).

Sibogacrinus A. H. CLARK in CLARK & CLARK, 1967, p. 832 [**Atelecrinus anomalus* A. H. CLARK, 1912e, p. 153; OD]. Centrodorsal thick walled; centrodorsal cavity approximately half centrodorsal diameter. Interior interradial buttresses lacking,

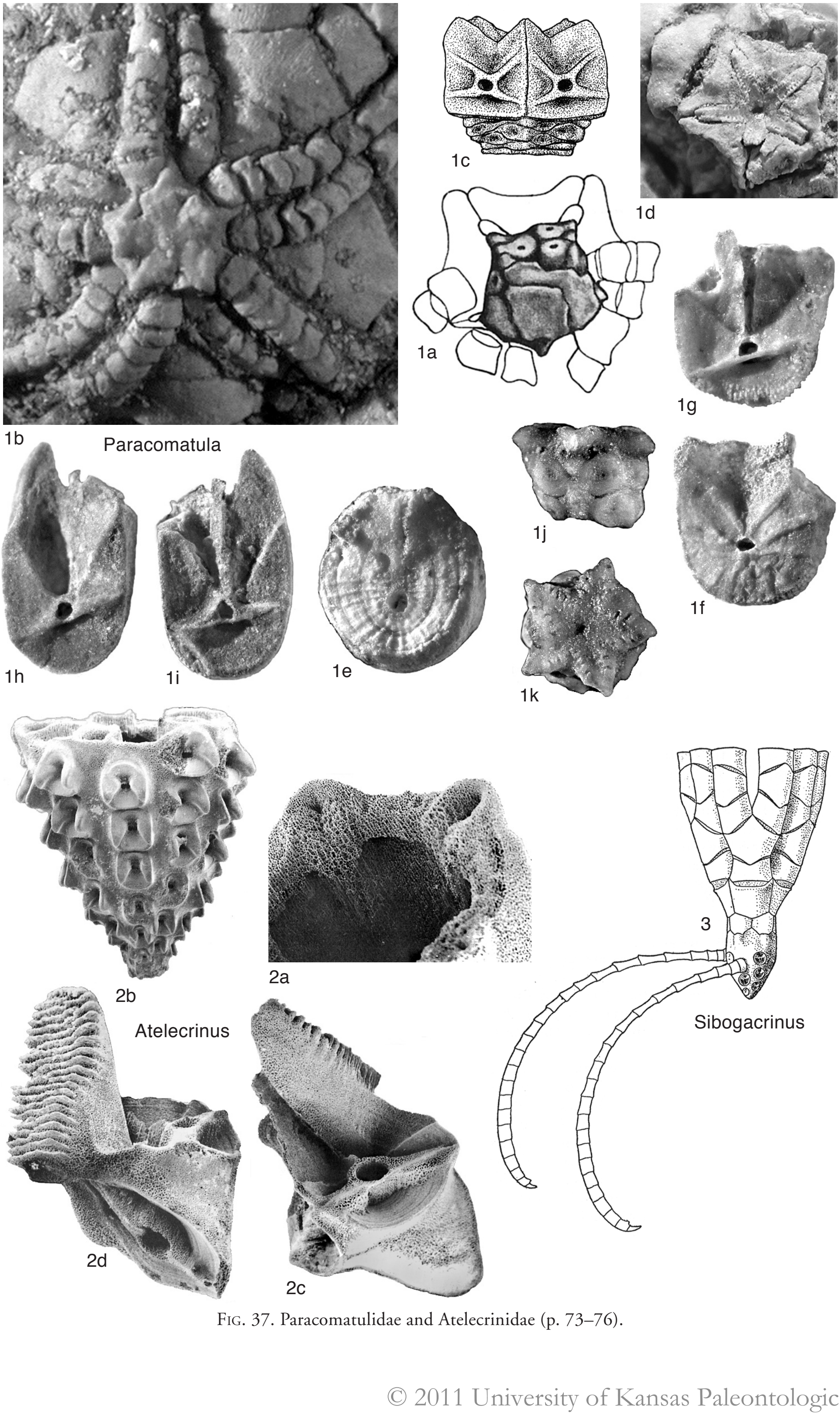

FIG. 37. Paracomatulidae and Atelecrinidae (p. 73–76).

but adoral margin with deep interradial depressions accommodating peglike, aboral projection of basals. Cirrus sockets with weak fulcral triangles not projecting. Basals moderately high, thick, and wedge shaped. Arms divided at primibrachial 2. No proximal pinnules. Middle and distal rays unknown. [Only one specimen of *Sibogacrinus* has been collected (MESSING, 2003a).] *Holocene:* tropical western Pacific Ocean (bathyal).——FIG. 37,*3*. **S. anomalus* (A. H. CLARK); centrodorsal with cirri and base of crown, holotype, ×7 (A. H. Clark, 1915a in 1915–1950).

Superfamily SOLANOCRINITOIDEA Jaekel, 1918

[*nom. correct.* HESS & MESSING, herein, *pro* Solanocrinitacea RASMUSSEN, 1978, p. 873, *nom. transl. ex* subfamily Solanocrininae JAEKEL, 1918, p. 73]

Centrodorsal truncated conical to discoidal or columnar with cirrus-free aboral apex. Postlarval column with synarthrial articulations maintained in adults of Thiolliericrinidae. Cirrus sockets arranged in 10 to 20 vertical columns or in a few irregular, marginal circles, reduced or obliterated in Thiolliericrinidae. Centrodorsal cavity very narrow. Basals stout, generally united, in Decameridae forming large rhombic plates surrounded by the radial circlet and forming bottom of large, shallow, radial cavity. In other families, basals rod shaped, visible interradially or concealed. Radial cavity large. Arms undivided or divided at first or second primibrachial. *Lower Jurassic (Hettangian)–Upper Cretaceous.*

Family SOLANOCRINITIDAE Jaekel, 1918

[*nom. correct.* RASMUSSEN, 1978, p. 873, *pro* Solanocrinidae GISLÉN, 1924, p. 145, *nom. transl. ex* subfamily Solanocrininae JAEKEL, 1918, p. 73]

Aboral side of centrodorsal flat or concave, commonly rugose or with irregular furrows. Cirrus sockets closely placed, commonly large, arranged in 10 to 15 columns (exceptionally as many as 20), or in *Palaeocomaster,* 1 or 2 irregular marginal circles. Stout, rod-shaped basals commonly exposed interradially, meeting centrally without forming large plates in bottom of radial cavity. Adoral side of centrodorsal with radiating, commonly short coelomic furrows in at least some species of *Comatulina* but not in other genera, although secondary furrows along each side of the basal rods may occur in corroded specimens. Articulation between basals and centrodorsal may be narrow petaloid and crenulate, especially in *Archaeometra*. Exposed surface of radials rather large to low or concealed. Interarticular ligament fossae and adoral muscle fossae generally low and wide, forming narrow bands in *Solanocrinites* and *Comatulina* but may be higher and triangular in *Archaeometra* and *Palaeocomaster*. Rays undivided or divided at first or second primibrachial, exceptionally at second secundibrachial or more distally. [Discoidal centrodorsal with large, cirrus-free, aboral apex, stout basal rays, large radial cavity, and, in *Palaeocomaster*, arrangement of cirrus sockets in irregular circles possibly indicate an affinity to Comasteroidea.] *Lower Jurassic (Hettangian)–Upper Cretaceous.*

Solanocrinites GOLDFUSS, 1829 in 1826–1844, p. 166 [**S. costatus*; SD DE LORIOL, 1884–1889 in 1882–1889, p. 526; *emend.*, CARPENTER, 1881a, p. 192, designating GOLDFUSS, 1831 in 1826–1844, pl. 50,*7a–b,* as lectotype of *S. costatus*] [=*Milleria* GOLDFUSS in HARTMANN, 1830, p. 45 (type, *Solanocrinites costatus* GOLDFUSS, 1829 in 1826–1844, p. 166); =*Solacrinus* AGASSIZ, 1836, p. 196, *nom. van.;* =*Solanocrinus* MÜNSTER, 1839, p. 89, *nom. van.*]. Centrodorsal moderately high discoidal or truncated conical, more or less 5-sided, with 10 columns of 1 to 3 large cirrus sockets separated by distinct ridges. Aboral apex flattened or concave, commonly rugose or with radiating irregular furrows. Rod-shaped basals generally exposed interradially. Vestigial infrabasals occur in *S. gresslyi*. Exposed surface of radials commonly moderately large and may be slightly overhanging. Interarticular ligament area rather low. Adoral muscle fossae low, forming narrow bands along adoral edge or low triangular areas separated by a median notch. First and second primibrachials fused or joined by synostosis; rays divided at primibrachial 1 in fused primibrachials or at primibrachial 2. Secundibrachials commonly wedge shaped and tumid to spinose. Arms may be biserial. Syzygies in *S. depressus* (D'ORBIGNY, 1852 in 1850–1852) but absent in *S. gresslyi* (ÉTALLON, 1862). [The holotype of the Tithonian *S. costatus* has a comparatively narrow radial cavity. Except for this character, the cups and centrodorsals of the upper Oxfordian *Solanocrinites gresslyi* (ÉTALLON) are quite similar. A series of well-preserved remains of this characteristic *Solanocrinites*, collected at a single locality in the neighborhood of Basel, are figured herein. Specimens include a basal circlet with vestigial infrabasals and separated and fused primibrachials. There are no syzygies present among 1500 brachials examined of this species. *S. lambertsi* Sieverts-Doreck (1958a), figured by Rasmussen (1978, fig. 585,*2b–d*), is considered to be a synonym of *S. gresslyi*.] *Middle Jurassic–Upper Jurassic (Tithonian):* Germany, France, Poland, Switzerland.——Fig. 38*a–b*. **S. costatus;* cup with centrodorsal, *a*, lateral, *b*, distal, Kimmeridgian, Germany, lectotype, IPB Goldfuss 378a, ×2.5 (Goldfuss, 1829 in 1826–1844).——Fig. 38*c–d*. *S. depressus* (d'Orbigny), Oxfordian, France; *c,* crown, centrodorsal missing, MNHN B11492, ×1; *d*, brachial syzygy, ×3 (de Loriol, 1889 in 1882–1889).——Fig. 38*e–s*. *S. gresslyi* (Étallon, 1862), Oxfordian, France; *e–g,* cup with centrodorsal, *e*, lateral, *f*, aboral, *g*, distal, NMB M10599, ×3.5; *h–i*, cup with conical centrodorsal and granular exposed surface of radials, *h*, lateral, *i*, aboral, NMB M10600, ×3.5; *j*, proximal view of cup with basal circlet and vestigial infrabasals, NMB M10601, ×3.5; *k–l*, fused primibrachials 1 and 2 with suture still visible, *k*, adoral, *l*, proximal, NMB M10623, ×5; *m–n*, completely fused primibrachials 1 and 2, *m*, adoral, *n*, proximal, NMB M10624, ×6; *o*, proximal view of primibrachial 2 (synostosis), NMB M10605, ×5; *p–q*, distal secundibrachial, *p*, proximal view, *q*, distal view, NMB M10606, ×5; *r–s*, proximal secundibrachial, *r*, adoral view, *s*, distal view, NMB M10607, ×5 (Hess, new).——Fig. 39. *S. thiollierei* (de Loriol, 1889 in 1882–1889); aboral view of intact specimen, Tithonian, France, holotype, MHNL 20015976, ×1 (P. Ageneau, new).

Archaeometra Gislén, 1924, p. 156 [**Solanocrinus asper* Quenstedt, 1858, p. 659; OD]. Centrodorsal similar to *Solanocrinites* but adoral diameter approximately twice that of aboral apex. Basals are stout rods, centrally united with rather large joint faces, covering considerable portion of aboral surface of radial circlet and with tips well exposed interradially. Aboral side of basals may bear short crenulae in a narrow, petaloid pattern not covering full ossicle width. Subradial cleft sometimes present. Radials large, with rather high facet. Interarticular ligament fossae triangular, slightly excavated, and smooth. Adoral muscle fossae slightly elevated and rugose, separated by a median notch. Brachials in *A. aspera* (Quenstedt) and *A. scrobiculata* (Münster in Goldfuss, 1826–1844) with synarthry or cryptosynarthry between primibrachials 1 and 2; primibrachial 2 axillary. Syzygies with very few, stout ridges; synarthries also occur on secundibrachials. *Middle Jurassic (Bajocian)–Lower Cretaceous (Valanginian):* Czech Republic, England, France, Germany, Switzerland.——Fig. 40,*1a–l*. **A. aspera* (Quenstedt), Oxfordian; *a–c,* cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, France, ×3 (de Loriol, 1889 in 1882–1889); *d*, lateral view of cup, Switzerland, NMB M10586, ×6; *e–f*, primibrachial 2, *e*, aboral, *f*, proximal (synarthry), Switzerland, NMB M10587, ×6; *g–h*, granular proximal secundibrachial, *g*, proximal view (syzygy), *h*, distal view, muscular with pinnule socket, Switzerland, NMB M10588, ×7; *i–j*, distal secundibrachial, *i*, proximal view (syzygy), *j*, distal view, muscular with pinnule socket, Switzerland, NMB M10589, ×6; *k–l*, secundibrachial, *k*, proximal view (synarthry), *l*, distal view, muscular with pinnule socket, Switzerland, NMB M10590, ×8 (Hess, new).

Comatulina d'Orbigny, 1852 in 1850–1852, p. 139 [**C. costata*; OD; *nom. nov. pro Solanocrinites costatus* Goldfuss, 1829 in 1826–1844, *partim*, taking Goldfuss, pl. 50,*7c* (=d) as type (ICZN, 1999, Article 70b); =*Antedon d'orbignyi*, invalid *nom. subst. pro* Carpenter, 1881a, p. 197]. Centrodorsal truncated conical to truncated subhemispherical, in adult specimens with more than 10 (generally 11 to 15, exceptionally as many as 20) columns of 1 to 3 large, closely placed cirrus sockets. Aboral apex of centrodorsal flat or concave, generally with irregular furrows or granulated, commonly approximately half adoral diameter of centrodorsal or less. Adoral side of centrodorsal may have irregular furrows around centrodorsal cavity. Rod-shaped basals just visible interradially or concealed and united around center, but not expanded, and not conspicuous in narrow bottom of radial cavity. Radials with moderate to low exposed surface that may be concealed or a little overhanging. Radial articular facet moderately steep, rather low. Interarticular ligament fossae low and wide, may be triangular. Adoral muscle fossae low and wide, may be triangular and separated by median notch and furrow. *Upper Jurassic (Oxfordian)–Upper Cretaceous (Coniacian):* France, Germany, Poland, Portugal, Switzerland, Algeria, *Oxfordian–Portlandian;* France, Spain, Switzerland, *Valanginian–Aptian;* Germany, *Coniacian.*——Fig. 40,*2a–b*. **C. costata;* cup with centrodorsal, *a*, lateral, *b*, aboral, Kimmeridgian, Germany, lectotype, ×2.5 (Goldfuss, 1829 in 1826–1844).——Fig. 40,*2c*. *C. batalleri* (Astre, 1925); adoral view of centrodorsal with infrabasals, Aptian, Spain, ×1.5 (Sieverts-Doreck, 1958a).

Pachyantedon Jaekel, 1891, p. 628 [**P. beyrichi*; M]. Crinoid interpreted by Jaekel as a comatulid with 10 arms composed of strongly wedge-shaped brachials. Presumed cirri stout, with short, wedge-shaped segments. Type based on impression in flint boulder, presumed Upper Cretaceous, northern Germany. [Name rejected by Rasmussen (1978, p. 927), but the form resembles specimens of *Solanocrinites* (see Fig. 39).] *Upper Cretaceous:* northern Germany.——Fig. 40,*3*. **P. beyrichi*, crown, holotype, ×1 (Jaekel, 1891).

Palaeocomaster Gislén, 1924, p. 142 [**Actinometra guirandi* de Loriol, 1889b, p. 535; OD]. Centrodorsal rather low discoidal, aboral apex commonly large, flat, and smooth or rugose. Cirrus sockets crowded, in 1 to 3 irregular marginal circles, not forming distinct columns. Rod-shaped basal rays commonly exposed interradially. Exposed surface of radials very low or concealed. Radial articular facet moderately high, wide, steep to vertical. Interarticular ligament fossae triangular. Adoral muscle fossae moderate to small, triangular, or reduced to narrow bands

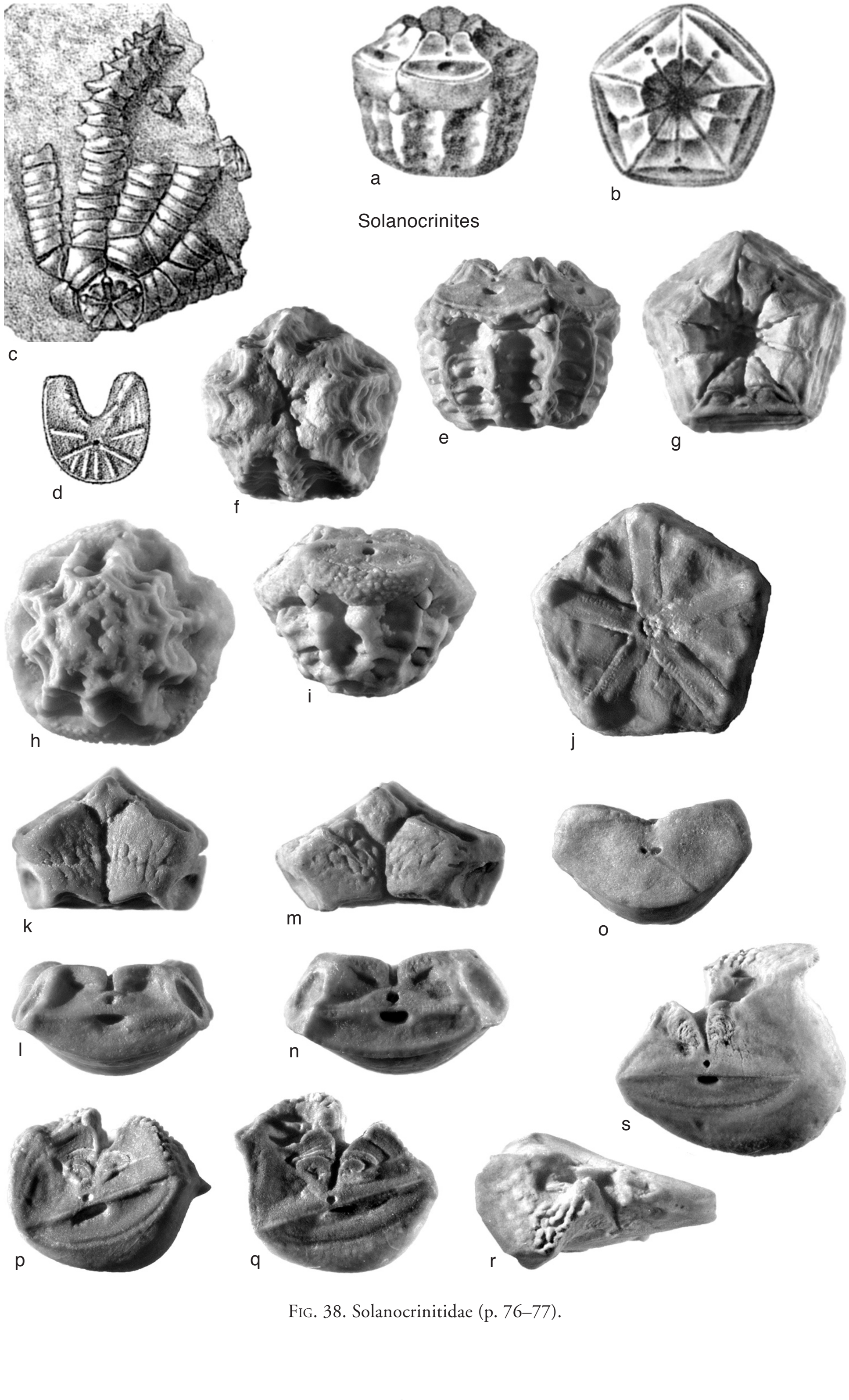

FIG. 38. Solanocrinitidae (p. 76–77).

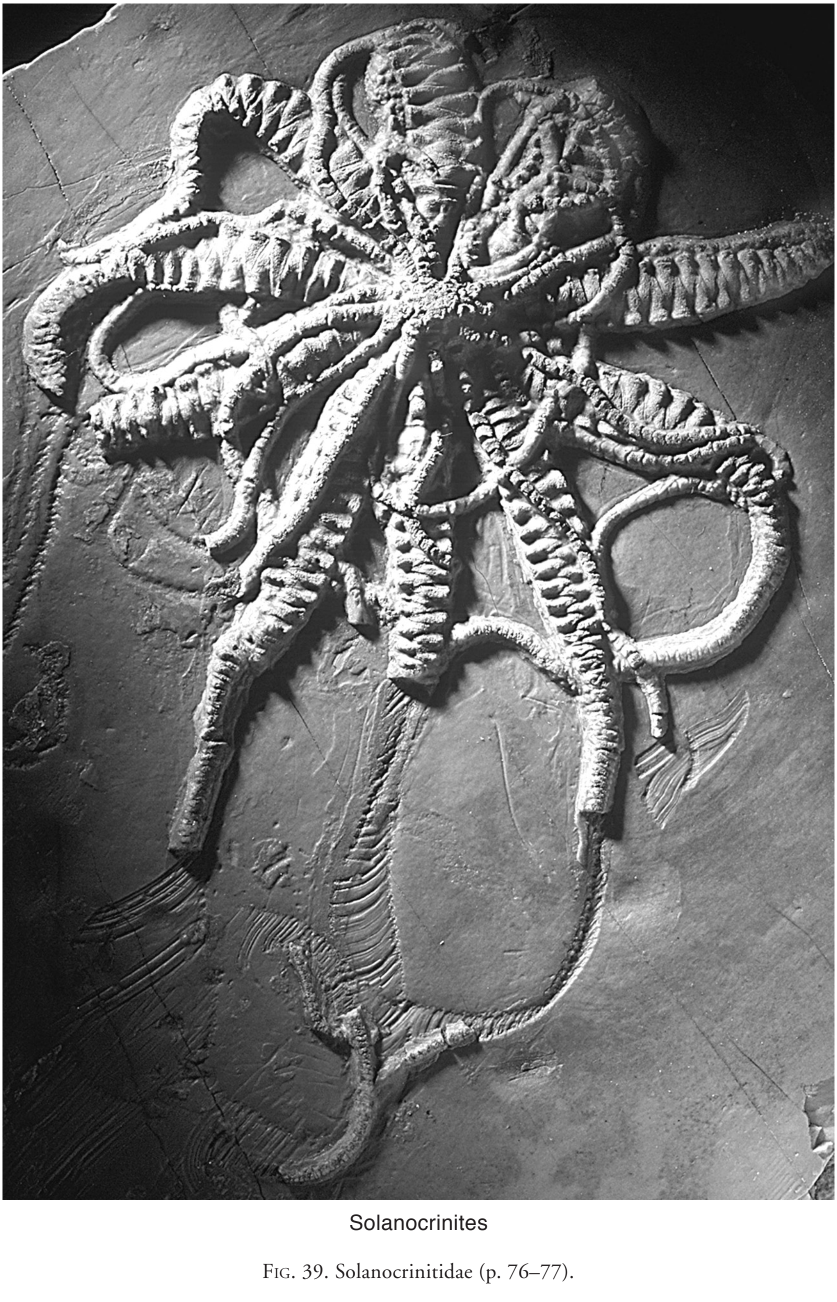

FIG. 39. Solanocrinitidae (p. 76–77).

along adoral edge. Radial cavity wide. Arms of *P.*? *calloviensis* (CARPENTER) from the Middle Jurassic (Callovian) of England have synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2, an axillary primibrachial 2, and the syzygy with few ridges between secundibrachials 3 and 4. [*Palaeocomaster styriacus* KRISTAN-TOLLMANN (1988a) from the Lower Jurassic (Hettangian) is the oldest comatulid with a centrodorsal composed of a single element, followed by the Pliensbachian *Palaeocomaster morierei* (DE LORIOL, 1888 in 1882–1889), known from a centrodorsal from France and a centrodorsal with basal circlet from Switzerland.] *Lower Jurassic*

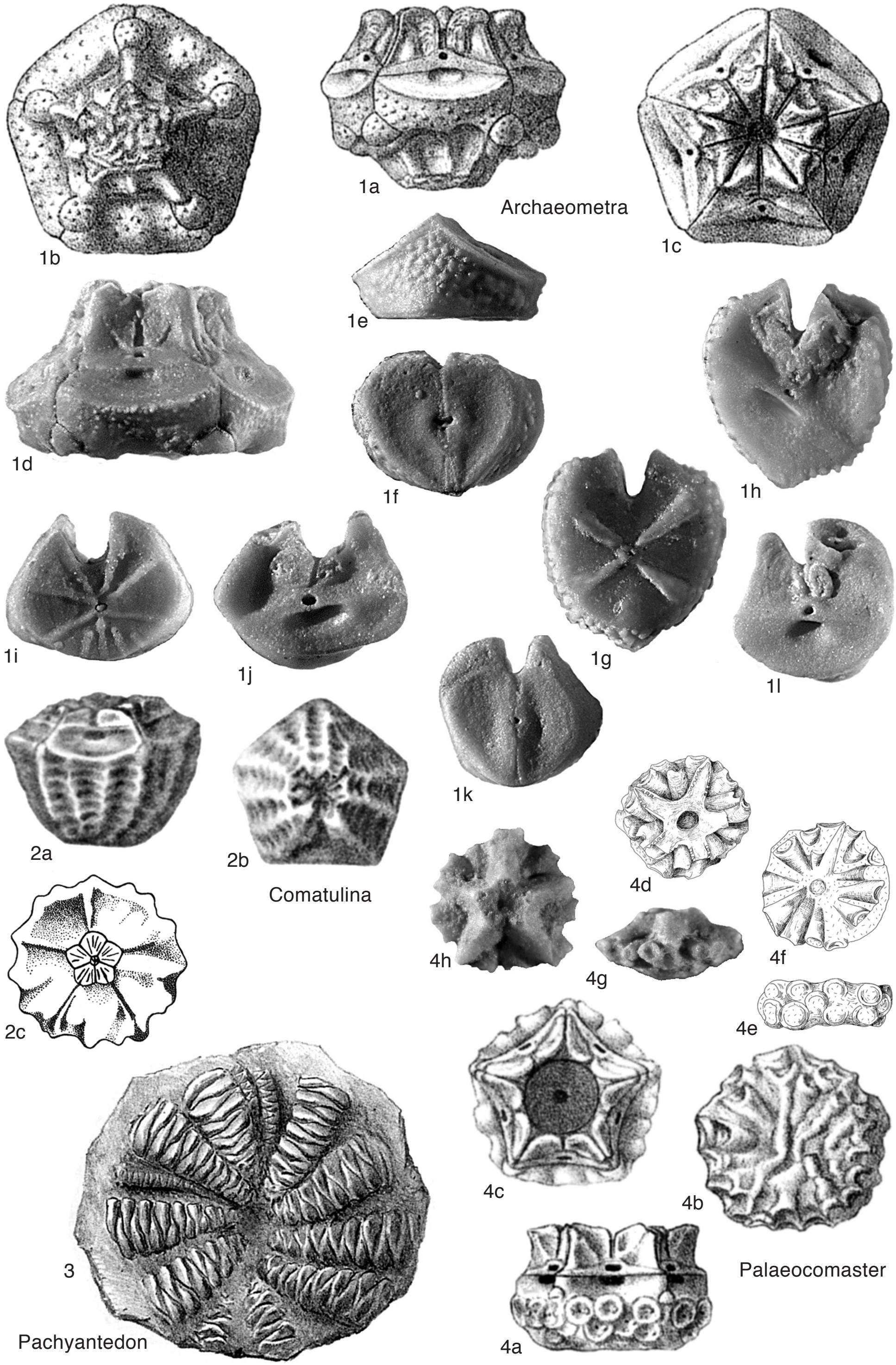

FIG. 40. Solanocrinitidae (p. 77–81).

(Hettangian)–Upper Jurassic (Tithonian): Austria, France, Switzerland, *Hettangian, Pliensbachian*; England, *Bathonian–Callovian*; England, France, Poland, *Oxfordian–Portlandian.*——Fig. 40,*4a–c*. **P. guirandi* (de Loriol); cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, Oxfordian, France, holotype, MHNL 20012857, ×7 (de Loriol, 1889 in 1882–1889).——Fig. 40,*4d–f. P. styriacus* Kristan-Tollmann (1988a), Hettangian, Austria, Kr-To collection; *d,* adoral view of centrodorsal with basal circlet, ×10 (Kristan-Tollmann, 1988a); *e–f*, centrodorsal, *e*, lateral, *f*, aboral, ×10 (Kristan-Tollmann, 1988a).——Fig. 40,*4g–h. P. morierei* (de Loriol, 1888 in 1882–1889); centrodorsal with basal circlet, *g*, lateral, *h*, adoral, Pliensbachian, Switzerland, NMB M10358, ×10 (Hess, 2006).

Family DECAMERIDAE Rasmussen, 1978

[Decameridae Rasmussen, 1978, p. 877]

Centrodorsal with 1 or 2 irregular circles of large cirrus sockets. Aboral apex flat or convex, with coelomic furrows or depressions. Basals centrally united, with or without rod-shaped interradial prolongations forming basal rays. Exposed surface of radials large, commonly overhanging, low or concealed. Radial articular facet steep, low and wide. Interarticular ligament fossae wide, rather low. Adoral muscle fossae very low, forming narrow band. Radial cavity large. [The coelomic impressions may indicate affinity to Mariametroidea.] *Lower Cretaceous (Valanginian–Albian).*

Decameros d'Orbigny, 1850 in 1850–1852, p. 121 [**D. ricordeanus*; SD Rasmussen, 1961, p. 253]. Centrodorsal large, discoidal; aboral apex flat or slightly arched, adoral side with feeble, radiating and meandering furrows. Large, stout, rhombic basals surrounded by radial circlet and forming large pentagon in bottom of wide, shallow, radial cavity; no interradial basal rays. Radials with low exposed surface or concealed in midradial area. Brachial articulations all muscular; no synarthry or syzygy. [*Decameros* Linck, 1733, is a *nom. van.* for *Decacnemos* Linck, 1733, first quoted by Agassiz (1836, p. 193) as a synonym of *Comatula* (without nomenclatorial status, ICZN, 1999, Art. 11d). It was used by d'Orbigny, 1850 in 1850–1852, in combination with 2 species described and maintained in 1852 as a genus different from *Decacnemos* Bronn, 1825, p. 6–7, *ex* Linck, 1733, which is a synonym of *Antedon* de Fréminville, 1811, *nom. conserv*. Specimens of *D. wertheimi* Peck & Watkins (1972) from the Albian of Texas indicate that juvenile specimens have a truncated, conical centrodorsal and overhanging radials as in *Pseudoantedon*; cirrals are rounded in section, length not exceeding width; rays undivided with the first pinnule on the first brachial.] *Lower Cretaceous (Valanginian–Albian):* France, Spain, Switzerland, Yugoslavia, *Valanginian–Aptian*; USA (Texas), Albian.——Fig. 41,*1a–d*. **D. ricordeanus*, Aptian, France; *a,* adoral view of centrodorsal, lectotype, MNHN B14288, ×2.5 (Rasmussen, 1961; also figured by Valette, 1921); *b–c*, cup with centrodorsal, *b*, lateral, *c*, aboral, lectotype, MNHN B14288, ×2.5 (Rasmussen, 1961; also figured by Valette, 1921); *d*, distal view of cup with basals, one radial missing, MGUH 8980, ×2.5 (Rasmussen, 1961).

Coelometra Rasmussen, 1978, p. 877 [**Antedon campichei* de Loriol, 1879 in 1877–1879, p. 269; OD]. Centrodorsal rather high, truncated subconical to almost hemispherical, aborally circular to subcircular; sides incompletely covered by large cirrus sockets; adoral surface with large, V-shaped, coelomic impression in radial areas as in modern *Zygometra* and Himerometridae. Stout, rod-shaped basals exposed interradially or concealed. Radials greatly overhanging centrodorsal, with large exposed surface tumid to swollen. Radial cavity large, deep, funnel shaped. Primibrachial 1 axillary; articulation between secundibrachials 1 and 2 oblique muscular. *Lower Cretaceous (Valanginian):* France, Switzerland.——Fig. 41,*2a–d*. **C. campichei* (de Loriol), Switzerland; *a–c,* cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, holotype, MGL 17039-21, ×2 (Rasmussen, 1961; also figured by de Loriol, 1879 in 1877–1879); *d*, adoral view of centrodorsal, MGL 17039-23, ×2.5 (Rasmussen, 1961; also figured by de Loriol, 1879 in 1877–1879).

Pseudoantedon Valette, 1933, p. 217 [**P. icauensis*; M; ?=*Comatula (Ophiocrinus) hiselyi* de Loriol in de Loriol & Gilliéron, 1869, p. 57]. Centrodorsal small, discoidal with steep or sloping sides; aboral apex flattened; adoral side with indistinct coelomic furrows. Basals united centrally, forming small pentagon in bottom of large, shallow, radial cavity, with interradial prolongations not exposed. Radials greatly overhanging centrodorsal, with exposed surface almost flat, more or less turned downward. Rays undivided, with apparently complete pinnulation, and the first pinnule on the first brachial. No indication of synarthry or syzygy. Pinnulars not carinate. Cirrals rounded, without aboral spines. *Lower Cretaceous (Valanginian–Barremian):* France, Switzerland.——Fig. 41,*3a–e*. **P. hiselyi* (de Loriol), Hauterivian; *a,* 3 specimens on slab, Switzerland, holotype, MHNG 28659, ×1 (de Loriol & Gilliéron, 1869); *b–c*, cup with centrodorsal, *b*, lateral, *c*, distal, Switzerland, MHNG 28661, ×2.5 (Rasmussen, 1961); *d–e*, cup with centrodorsal, *d*, lateral, *e*, aboral, also figured by Valette, 1933, as type of *Pseudoantedon icaunensis*, France, Auxerre Coll. 83-366, ×2.5 (Rasmussen, 1961).

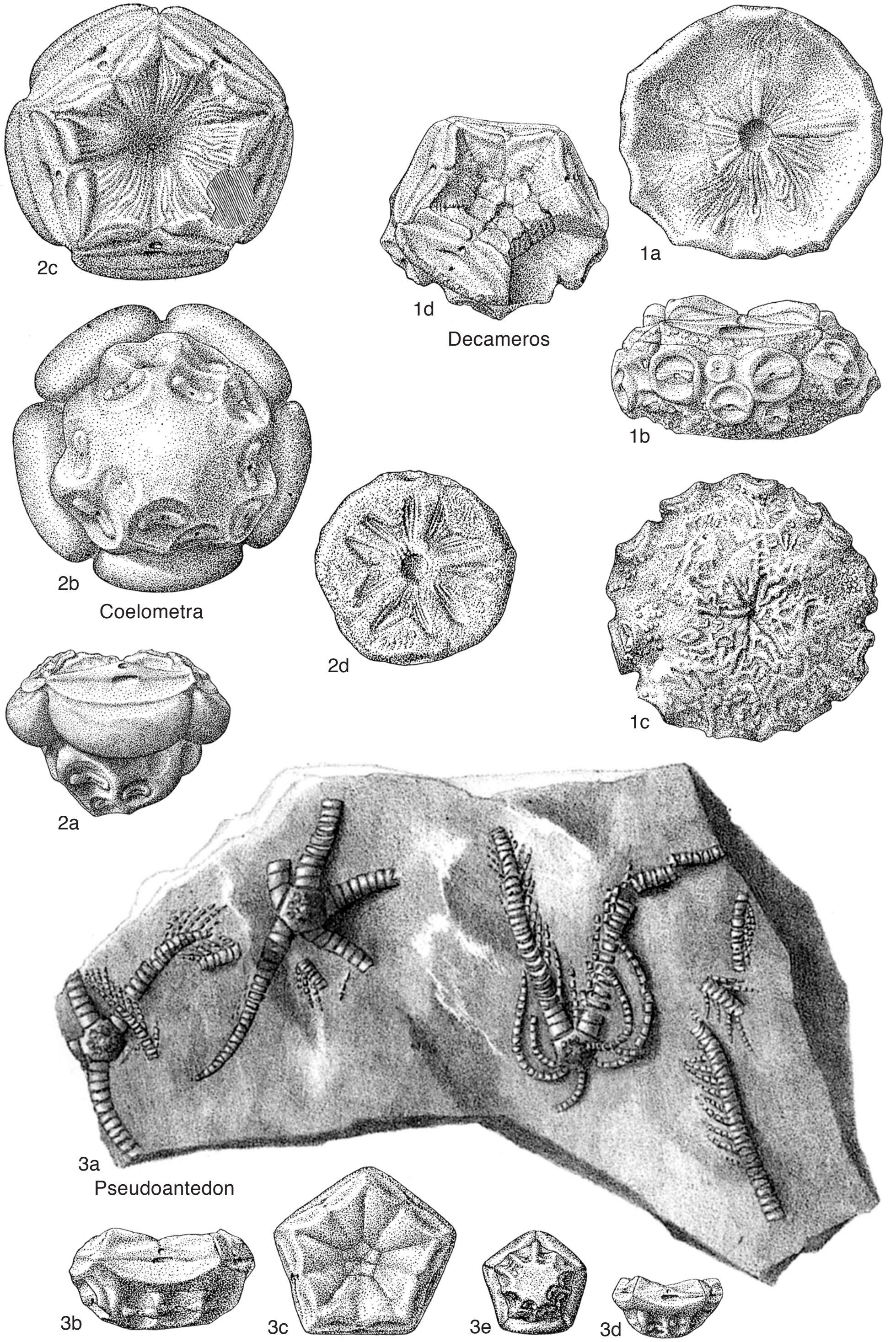

FIG. 41. Decameridae (p. 81).

Family THIOLLIERICRINIDAE A. H. Clark, 1908

[Thiolliericrinidae A. H. Clark, 1908b, p. 209]

Articulation of centrodorsal with column a large, circular to elliptical synarthry with narrow axial canal. Column presumably short; columnals large, barrel shaped or subcylindrical to hourglass shaped with synarthries at opposite ends oriented differently. Attachment by expanded terminal disk with synarthrial articulation commonly tilted obliquely relative to substrate. Cup with 5 basals that may be hidden. First primibrachial axillary. No ligamentary articulation in arms. Secundi- and tertibrachials commonly asymmetrical, suggesting that crown may have been able to close. [Thiolliericrinids appear to have developed from *Solanocrinites*-like forms through paedomorphosis during the Jurassic. Their further development up to the Early Cretaceous includes reduction of basals and loss of cirri resulting in permanent fixation to hardgrounds. They reached their highest diversity shortly before their demise, during the Lower Cretaceous of the Crimea, where they occur in different reefal settings (Klikushin, 1987b). Recognized genera differ in overall shape, development of basals (may be hidden or developed unequally in the same individual), and presence or absence of cirrus sockets. Thiolliericrinids share high intraspecific variability with cyrtocrinids that occur in similar settings.] *Upper Jurassic (Oxfordian)–Lower Cretaceous (Hauterivian).*

Thiolliericrinus Étallon, 1859, p. 445 [**T. flexuosus*; M; *non Apiocrinites flexuosus* Goldfuss, 1831 in 1826–1844, p. 186, which is incorrectly recorded by several authors]. Centrodorsal truncated conical with few cirrus sockets forming a single circle. In the type species, sockets very small, widely separated, elliptical or circular in outline, with or without articular ridge. Other species referred to this genus may have large, well-developed cirrus sockets or small, vestigial sockets, or both. Radials with large, vertical or slightly recumbent exposed surface, at least in type species. Basals may be concealed (in type species) or exposed. [Although Étallon (1859) considered the species described by him most probably identical with *Apiocrinites flexuosus* Goldfuss (1831 in 1826–1844), based on isolated columnals, he established *T. flexuosus* as a new species in his own name (Étallon) as shown in his text (p. 445–446) and in the number of new species recorded (p. 413). Étallon (1859) described and de Loriol (1877–1879) figured the genus and type species. To avoid secondary homonymy with *Apiocrinites flexuosus* Goldfuss, which, although indeterminable, most probably belongs to a genus of this family, Gislén (1924, p. 187) introduced the name *T. favieri* (Gislén, 1924) as a *nom. subst. pro T. flexuosus* Étallon, taken from the informal label name *Humberticrinus favieri* used in the collection by Étallon and quoted by de Loriol (1879 in 1877–1879, p. 195). This name was also considered valid by Klikushin (1987b, p. 635). Gislén (1924), at variance with the type species, restricted the genus to species with large cirrus sockets. Remeš (1905) referred axillary brachials with a strongly swollen aboral surface and with proximal muscular articulation, probably the first primibrachial, to this genus.] *Upper Jurassic (Oxfordian)–Lower Cretaceous (Hauterivian):* Czech Republic, France, Germany, Portugal, Switzerland.——Fig. 42,*1a–b*. **T. flexuosus*, Oxfordian, France; *a,* cup with centrodorsal, lectotype, ×3 (Klikushin, 1987b); *b*, proximal view of cup with basals, ×3 (de Loriol, 1889 in 1882–1889).——Fig. 42,*1c–e*. *T. ribeiroi* de Loriol, 1891; centrodorsal, *c*, lateral, *d*, aboral, *e*, adoral, Oxfordian, Portugal, ×3 (de Loriol, 1891).——Fig. 42,*1f–g*. *T. arzierensis* de Loriol (1879 in 1877–1879); centrodorsal, *f*, lateral, *g*, aboral, Valanginian, Switzerland, holotype, MHNG 58010, ×2 (Klikushin, 1987b).——Fig. 42,*1h*. indet. thiolliericrinid; attachment disk, Oxfordian, Switzerland, NMB M10601, ×8 (Hess, 1975).

Argoviacrinus Hess & Spichiger, 2001, p. 492 [**A. rarissimus*; M]. Uppermost columnal or centrodorsal high, distally cylindrical and tapered, with 3 cirri in each radius. Articular facet to column a cryptosymplexy with rim and secondary deposit of granules on a shallow areola superimposed on a cryptosynarthry. Cup composed of circlet of 5 radials with basals exposed interradially. Radial articular facet well developed, outward sloping; radial cavity moderately deep. [This monotypic genus is based on one specimen.] *Upper Jurassic (Oxfordian):* Switzerland.——Fig. 42,*2a–d*. **A. rarissimus*; cup with centrodorsal, *a*, lateral, ×7.7, *b*, proximal part of centrodorsal and cup, ×8, *c*, facet to column, *d*, facet to column moistened, holotype, NMB M9995, ×11 (Hess & Spichiger, 2001).

Burdigalocrinus Jaekel, 1918, p. 71 [**B. lorioli; M; nom. nov. ex Thiolliericrinus ribeiroi partim* de Loriol, 1891, pl. 29,*17*]. Centrodorsal rather high, truncated conical, with several small, rounded cirrus sockets without distinct articular ridge. Sockets widely separated, irregularly arranged, not restricted to a single circle on centrodorsal, may be vestigial. *Upper Jurassic (Oxfordian)–Lower Cretaceous (Berriasian):* Portugal, *Oxfordian;* Crimea, *Berriasian.*——Fig. 42,*3a–c*. **B. lorioli*; centrodorsal, *a*, lateral, *b*, aboral, *c*, adoral, Oxfordian, Portugal, ×2.4

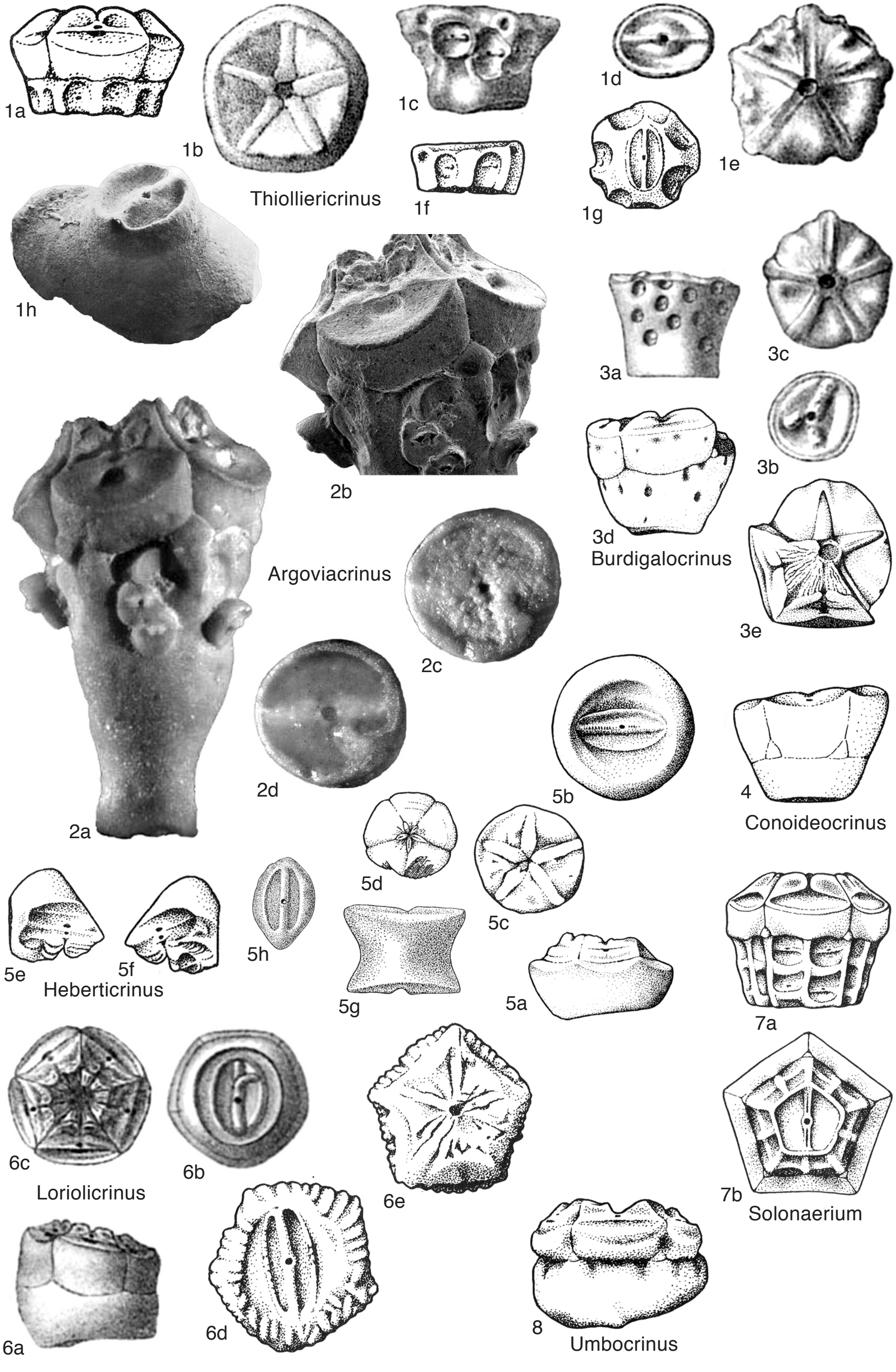

FIG. 42. Thiolliericrinidae (p. 83–85).

(de Loriol, 1891).——FIG. 42,*3d–e*. *B. maximus* KLIKUSHIN, 1987b; cup with centrodorsal (3 radials lost), *d*, lateral, *e*, distal, Berriasian, Crimea, holotype, LGI CK-81-1, ×1.5 (Klikushin, 1987b).

Conoideocrinus KLIKUSHIN, 1987b, p. 644 [**C. conoideus*; M]. Centrodorsal moderately high, conical, base flat with pronounced fulcral ridge; cirrus sockets absent. Cup high, conical. Radial articular facet narrow. Radial cavity broad and deep. Basals visible externally. [This monotypic genus is based on one specimen.] *Lower Cretaceous (Berriasian):* Crimea.——FIG. 42,*4*. **C. conoideus*; lateral view of cup with centrodorsal, holotype, LGI CK-97-1, ×2 (Klikushin, 1987b).

Hebericrinus KLIKUSHIN, 1987b, p. 646 [**Eugeniacrinus heberti* DE LORIOL in PICTET, 1868, p. 281; OD]. Centrodorsal mostly large, convex, without cirrus sockets or fossae; aboral facet concave or flat, rarely convex. Radials of variable height, but mostly low. Basals not visible externally. *Upper Jurassic (Tithonian)–Lower Cretaceous (Berriasian):* Portugal, France, Czech Republic, Romania, Crimea, Caucasus.——FIG. 42,*5a–f*. **H. heberti* (DE LORIOL), Berriasian, Crimea; *a–b,* cup with centrodorsal, *a*, lateral, *b*, aboral, LGI CK-51-2, ×1.5; *c*, proximal view of cup with large basals, LGI CK-51-70, ×1.5; *d*, proximal view of cup with small basals, LGI CK-30-1, ×1.5; *e–f*, secundibrachial, *e*, oblique proximal, *f*, oblique distal, LGI CK-51-206, ×2 (Klikushin, 1987b).——FIG. 42,*5g–h*. *H. algarbiensis* (DE LORIOL, 1888); columnal, *g*, lateral, *h*, facet, Hauterivian, Portugal, ×2 (Rasmussen, 1961).

Loriolicrinus JAEKEL, 1918, p. 72 [**Thiolliericrinus insuetus* DE LORIOL, 1891, p. 167; M]. Centrodorsal low, cylindrical or conical, without cirrus sockets, but small fossae may occur near radial-centrodorsal suture. Radials with high exposed surface. Basals typically not visible externally. *Upper Jurassic (Oxfordian)–Lower Cretaceous (Valanginian):* Portugal, France, Germany, Crimea.——FIG. 42,*6a–c*. **L. insuetus* (DE LORIOL); cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, Oxfordian, Portugal, holotype, ×2 (de Loriol, 1891).——FIG. 42,*6d–e*. *L. asper* KLIKUSHIN, 1987b; centrodorsal, *d*, aboral, *e*, adoral, Berriasian, Crimea, LGI CK-82-5, ×2 (Klikushin, 1987b).

Solonaerium ÉTALLON in THURMANN & ÉTALLON, 1861, p. 341 [**Solanocrinites costatus* GOLDFUSS, 1831 in 1826–1844, *partim*, pl. 51,*2;* M; =*S. sigillatum* QUENSTEDT, 1876, p. 176]. Centrodorsal rather high, truncated conical, with large, closely touching cirrus sockets arranged in 10 columns of 2 or 3 sockets. Radials with large exposed surface, somewhat recumbent or overhanging. [ÉTALLON (1862, p. 222) recorded the specimen figured by GOLDFUSS, 1831 in 1826–1844, pl. 51,*2* (*non* pl. 50,*7*) as a species probably belonging to *Thiolliericrinus*; and THURMANN and ÉTALLON (1861, p. 341) recorded the same specimen as *Solonaerium costatus*. QUENSTEDT (1876, p. 176) included the same specimen in his new species *Comatula sigillata*. KLIKUSHIN (1987b) refigured GOLDFUSS's and QUENSTEDT's specimens under *S. sigillatum*.] *Upper Jurassic (Kimmeridgian):* Germany.——FIG. 42,*7a–b*. **S. sigillatum* (QUENSTEDT); cup with centrodorsal, *a*, lateral, *b*, aboral, lectotype, ×1.5 (Klikushin, 1987b).

Umbocrinus KLIKUSHIN, 1987b, p. 646 [**U. umbonatus*; M]. Centrodorsal rather small, convex; cirrus sockets absent. Cup low. Basals visible externally. Row of fossae on suture between radials and centrodorsal. *Lower Cretaceous (upper Berriasian):* Crimea.——FIG. 42,*8*. **U. umbonatus*; cup with centrodorsal, syntype, LGI CK-83-2, ×2 (Klikushin, 1987b).

Superfamily COMASTEROIDEA A. H. Clark, 1908

[*nom. correct.* HESS & MESSING, herein, *pro* Comasteracea RASMUSSEN, 1978, p. 881, *nom. correct. pro* Comasterida GISLÉN, 1924, p. 229 (established as a superfamily although named a tribe), *nom. transl. ex* family Comasteridae A. H. CLARK, 1908h, p. 135]

Centrodorsal thick to thin discoidal or pentagonal, rarely stellate; aboral apex broad, cirrus-free, flat or slightly convex or concave, sometimes with narrow, radiating, interradial impressions (also in fossil Notocrinoidea); dorsal star absent, but center of aboral apex sometimes depressed; centrodorsal cavity less than 30 percent of centrodorsal diameter, larger in very small specimens; adoral surface with interradial furrows for basals, but no radial pits or coelomic impressions. Cirrus sockets generally rather large, without distinct ornament, crowded around centrodorsal margin in 1 to 3 irregular tiers, never forming vertical columns. Some species of *Comatula*, *Comanthus*, *Comaster*, *Phanogenia,* and *Capillaster* with centrodorsal thin, reduced, commonly not projecting below radials and bearing few or no cirri. Basal rosette; basals rod shaped, commonly exposed interradially. Subradial clefts may be present, especially in large specimens. Radials typically with low exposed surface, commonly concealed midradially or barely exposed interradially; rarely completely concealed; well exposed and trapezoidal in species with reduced centrodorsal; well exposed with tongue-like extensions separating bases of adjacent rays in paedomorphic *Comatilia*. Radial articular facet parallel to oral-aboral axis or nearly so and with shallow fossae. Interarticular ligament fossae large, high and wide, generally higher than aboral ligament fossa and separated by broad and shallow midradial furrow, which is commonly constricted between muscle fossae. Adoral border of interarticular fossae straight or slightly curved, horizontal or slightly sloping. Adoral muscle fossae low, always smaller than interarticular ligament fossae, forming narrow bands along horizontal adoral edge. Radial cavity large, with a spongy calcareous filling in living specimens. Rays divided at least at primibrachial 2, commonly up to several times more and producing as many as 180 undivided arms. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2, or modified synarthry either relatively featureless or resembling syzygies. True syzygies present only in *Comatula*. First pinnule on secundibrachial 2 (when series composed of 4 ossicles). Pinnulation incomplete only in *Comatilia*, which lacks several pinnules after the first pair. Oral pinnules slender, flagellate, of numerous short pinnulars. Distal pinnulars of at least some oral pinnules bearing a comb formed by peg- or bladelike teeth, 1 or 2 per pinnular. Similar combs present elsewhere only in some Heliometrinae (Antedonoidea). Middle and distal pinnules commonly extremely spiny. Arms arising farthest away from the eccentrically placed mouth (=posterior) commonly shorter than those arising closest to mouth, sometimes lacking ambulacral groove but with better developed gonads. Mouth typically displaced off center or marginal, and anal papilla central or subcentral on disk (commonly less so in juveniles); mouth central or subcentral in *Phanogenia*, *Palaeocomatella*, *Aphanocomaster*, *Comissia*, *Rowemissia,* and *Comatilia*. [The more or less marginal mouth and the modified posterior arms and specialized pinnules indicate that this is a specialized group among comatulids. Comasteridae resemble Solanocrinitoidea in their discoidal centrodorsals, large, cirrus-free, aboral apex, distinct cirrus sockets, rod-shaped basals, steep radial articular facet with low muscle fossae, and large radial cavity. RASMUSSEN (1978) transferred several Jurassic and Cretaceous species recorded under the genera *Actinometra* (=*Comatula*) and *Palaeocomaster* to Solanocrinitoidea.] *Paleogene (Eocene)–Holocene.*

Family COMASTERIDAE
A. H. Clark, 1908

[Comasteridae A. H. CLARK, 1908h, p. 135] [=Actinometridae BATHER, 1899, p. 923]

Characters as for superfamily. [The family name Comatuladae FLEMING, 1828, p. 494 (=Comatulidae D'ORBIGNY, 1852 in 1850–1852, p. 138), based on *Comatula,* was used for all comatulids as in the order Comatulida A. H. CLARK, 1908h. A. H. CLARK (1908h) erected the family Comasteridae to accommodate species in the genus *Actinometra* MÜLLER. During the following 2 decades, he established 3 subfamilies and 20 genera and subgenera, an output that culminated in a massive monograph (A. H. CLARK, 1931 in 1915–1950) still critical to any taxonomic study of the family. A. M. CLARK and ROWE's (1971) key to shallow Indo-western Pacific members of the family is based chiefly on A. H. CLARK (1931 in 1915–1950). In 1986, ROWE and others (1986) and HOGGETT and ROWE (1986) revised the Comasteridae, emphasizing different diagnostic features than recognized by A. H. CLARK (1931 in 1915–1950); notably the pinnule comb form. Their results have proven to be a very useful guide to the identification of Indo-western Pacific reef-dwelling species (MESSING, 1994, 1998). MESSING (1995a, 1995b, 1998) described 1 new species and 2 new genera, discovered new diagnostic characters for 2 other genera, and reassigned several species to different genera. This new information altered the characteristics of several abundant and widespread genera and led MESSING (2001) to prepare a new dichotomous, artificial (nonphylogenetic) key that remains chiefly based on HOGGETT and ROWE (1986). Morphological characteristics have not yet been examined in detail using phylogenetic techniques. For example, HOGGETT and ROWE (1986) placed *Comaster* (now *Phanogenia*) and *Comanthus* in separate subfamilies based on different distributions of syzygies, although both share uniquely similar modified oral pinnule combs that occur at intervals to near the arm tip, a combination of features unknown in any other comasterid. In addition, recent classifications (HOGGETT & ROWE, 1986; MESSING, 2001) rest on characters that occur only in taxa with more than 10 arms, so that a quarter of the genera cannot be assigned to a subfamily. Several genera listed under Comasteridae in RASMUSSEN (1978, p. 883) have been removed from the family (*Comatonia* and *Microcomatula* to Antedonidae) (MESSING, 1981; HOGGETT & ROWE, 1986) or synonymized (*Comanthoides* under *Cenolia*) (ROWE & others, 1986). RASMUSSEN (1978) also incorrectly included the antedonid *Ctenantedon* in the Comasteridae. The molecular phylogenetic reconstruction of WHITE and others (2001) of the family based on 30 species in 15 genera returned most but not all morphologically defined genera examined; support for subfamilies was less clear. Of the 19 extant families of comatulids, the Comasteridae ranks second only to Antedonidae in numbers of species and breadth of distribution. Of the 95 species currently recognized, approximately 65 occur on Indo-western Pacific coral reefs and adjacent deeper waters; 11 are endemic to southern China–Japan, 10 to southern temperate Australia–New Zealand, 8 to the tropical western Atlantic, and 1 to the northeastern Atlantic. Approximately 20 species are restricted to depths below 100 m, and 10 of these occur only below 200 m (MESSING, 2001). Comasterids dominate the modern coral reef crinoid fauna and typically account for more than half the crinoid species (and most of the individuals) present in tropical shallow-water surveys in both the Indo-western Pacific and western Atlantic (MEYER, 1973; MESSING, 1994, 1998, 2001).] *Paleogene (Eocene)–Holocene.*

Subfamily COMASTERINAE
A. H. Clark, 1908

[*nom. transl.* A. H. CLARK, 1909h, p. 175, *ex* Comasteridae A. H. CLARK, 1908h, p. 135] [=Actinometridae BATHER, 1899, p. 923, *sensu* JAEKEL, 1918, p. 74; =Comanthinae HOGGETT & ROWE, 1986, p. 124, *partim*]

Synarthry or cryptosynarthry between primibrachials 1 and 2. Arms divided at primibrachial 2 and either secundibrachial 2 or secundibrachial 4; further brachitaxis of 2 or 4 ossicles. Almost all species have more than 20 arms; many may exceed 40, and a few have more than 100 (up to approximately 180, the most of any comatulid). First syzygy always between secundibrachials 3 and 4. [MESSING's (1998) recognition that *Alecto multifidus* MÜLLER, 1841, the type species of *Comaster*, is synonymous with *Comanthina variabilis* (BELL, 1882a) makes *Comanthina* a junior synonym of *Comaster*. As a result, *Comaster* and its family-level derivatives are the senior names among the genera formerly placed in the Comanthinae. The subfamily Comanthinae was renamed Comasterinae accordingly by MESSING (2001). WHITE and others (2001) erected the new subfamily name Phanogeniinae for the remaining genera formerly in Comasterinae after *Comanthina* was synonymized with *Comaster*. Their molecular phylogenetic reconstruction included 13 species in 4 current comasterine genera. The subfamily approaches monophyly except for the inclusion of *Capillaster multiradiatus* (the only capillasterine analyzed) and the exclusion of *Oxycomanthus bennetti*.] *Neogene (Miocene)–Holocene.*

Comaster AGASSIZ, 1836, p. 193 [**Alecto multifida* MÜLLER, 1841, p. 188; OD; =*Comatula multiradiata* LAMARCK, 1816, p. 534, *partim*] [=*Comanthina* A. H. CLARK, 1909i, p. 142 (type, *Actinometra nobilis* CARPENTER, 1888, p. 336, OD)]. Typically 4 secundibrachials; tertibrachials typically 2 ossicles exteriorly and 4 interiorly. Pinnule combs present at least to third pinnule, sometimes at intervals to pinnule 14. On pinnules arising from arms (except sometimes the first), comb teeth paired, straight or gently curved, confluent with sides of pinnulars; each tooth of a pair the same size or nearly so; paired teeth sometimes joined to form a transverse bar or filled arch; teeth on adjacent segments not in contact basally; terminal tooth discrete or last few pinnulars tapering to a sharp point. Interradial surface of disk paved with irregular plates, especially in larger specimens. Mouth eccentric. [For a detailed history of the genus, see MESSING, 1998.] *Neogene (Miocene)–Holocene:* Italy, *Miocene;* tropical western and southern Pacific Ocean, tropical Indian Ocean (littoral to sublittoral), *Holocene.*——FIG. 43,*1a.* **C. multifidus* (MÜLLER); cryptosynarthry on distal facet of primibrachial 1, Holocene, AM J16467, ×8 (Hoggett & Rowe, 1986).——FIG.

43,*1b–d. C. formae* (Noelli, 1900); radial circlet, *b*, lateral, *c*, aboral, *d*, adoral, Miocene, Italy, holotype, ×4 (Noelli, 1900).——Fig. 43,*1e–f. C. schlegelii* (Carpenter, 1881d), Holocene; *e,* aboral view of specimen lacking cirri, Philippines, ×1 (Carpenter, 1888, as *Actinometra nobilis,* pl. 65,*1; Actinometra nobilis* is the type of *Comanthina,* which is a synonym of *Comaster*); *f,* aboral side of cup with reduced centrodorsal, ×3.5 (Carpenter, 1888, pl. 65,*2*).

Cenolia A. H. Clark, 1916c, p. 48, *nom. nov. pro Bennettia* A. H. Clark, 1909i, p. 142, *non* Fowler, 1904, p. 524 [**Comatula trichoptera* Müller, 1846, p. 178; SD A. H. Clark, 1916c, p. 48] [=*Comanthoides* A. H. Clark, 1931 in 1915–1950, p. 240 (type, *Comanthus spanoschistum* H. L. Clark, 1916, p. 17, OD)]. Brachitaxes beyond primibrachials typically of 4 ossicles, any series of 2 ossicles occurring irregularly. Pinnule combs extend to pinnule 4; teeth paired, straight, of more or less equal size, each confluent with the pinnular margin; teeth of a pair sometimes joined to form a transverse bar. Surface of disk not heavily plated. Mouth eccentric. *Holocene:* southern Pacific Ocean (littoral to upper bathyal).——Fig. 43,*2.* **C. trichoptera* (Müller); oblique aboral view of oral pinnule comb, enlarged (Messing, 2001, p. 287, fig. 5d, courtesy of the *Bulletin of the Biological Society of Washington*).

Clarkcomanthus Rowe & others, 1986, p. 232 [**Comanthus luteofuscum* H. L. Clark, 1915, p. 102; OD]. Brachitaxes beyond primibrachials typically of 4 ossicles, sometimes of 2. Pinnule comb no further than pinnule 2. Primary teeth slightly curved, accompanied by smaller tooth on opposite side. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* western and northern Pacific Ocean, Indian Ocean (littoral to sublittoral).——Fig. 43,*3. C. littoralis* (Carpenter, 1888); disk with marginal mouth and central papilla with anal opening, USNM, enlarged (Messing, 2001, p. 285, fig. 4b, courtesy of the *Bulletin of the Biological Society of Washington*).

Comanthus A. H. Clark, 1908l, p. 203 (A. H. Clark, 1908k, p. 220, *nom. nud.*) [**C. intricata* A. H. Clark, 1908k, p. 220; SD A. H. Clark, 1909f, p. 507; =*Alecto parvicirrus* Müller, 1841, p. 185] [=*Goldfussia* Norman, 1891, p. 387 (type, *G. multiradiata*; M; *nom. nov. pro Comatula multiradiata* as figured in Goldfuss, 1831 in 1826–1844, p. 202, *non* Lamarck), *non* Castelnau, 1843; =*Bennettia* A. H. Clark, 1909i, p. 142 (type, *Alecto bennetti* Müller, 1841, p. 187, OD); =*Comanthus* (*Comantheria)* A. H. Clark, 1909i, p. 142 (type, *Antedon briareus* Bell, 1882a, p. 534, OD); =*Comantheria* A. H. Clark, 1912d, p. 22 (type, *Antedon briareus* Bell, 1882a, p. 534, OD)] [For a discussion on the confused history of this genus, see Rowe and others, 1986, p. 209–211]. Brachitaxes beyond primibrachials typically of 2 or 4 ossicles. Pinnule combs commonly present at intervals to near arm tips. Proximal comb tooth oriented transversely and typically saucer shaped; remaining teeth curved and confluent with pinnular margin; smaller secondary tooth may be present; terminal tooth always discrete. *Holocene:* western, southern, and central Pacific Ocean (littoral to sublittoral).——Fig. 43,*4.* **C. parvicirrus* (Müller); oral pinnule comb with transverse, spoonlike, proximal tooth, NSU, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*).

Oxycomanthus Rowe & others, 1986, p. 248 [**Comanthus (Vania) parvicirra* beta *comanthipinna* Gislén, 1922, p. 51; OD; =*Comanthus comanthipinna* (Gislén), *comb. nov.*, Rowe & others, 1986, p. 249]. Brachitaxes beyond primibrachials of 2 or 4 ossicles. Combs not extending beyond fifth pinnule; teeth straight and bladelike, in center of pinnular (not confluent with margin), widely separated from each other; combs terminating in a sharp point, formed by fusion of progressively shorter distal teeth. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* tropical Indian Ocean, northern, western, and central Pacific Ocean (littoral to upper bathyal).——Fig. 44,*1a. O. bennetti* (Müller, 1841); base of crown with cirri attached to sponge, off Sulawesi at 20 m (Hess & others, 1999).——Fig. 44,*1b. O. mirus* Rowe & others, 1986; transverse view of comb segment with nonconfluent primary and secondary teeth from first pinnule, holotype, AM J17202, ×50 (Hoggett & Rowe, 1986).

Subfamily COMATULINAE Fleming, 1828

[*nom. transl. et correct.* Hoggett & Rowe, 1986, p. 112, *ex* Comatuladae Fleming, 1828, p. 494]

Cirri present or absent. First and second primibrachials, secundibrachials (when present), and first and second brachials united by syzygy. Rays divided at second secundibrachials only in *Comatula rotalaria*; all other species with 10 arms only (with rare exceptions). [Hoggett and Rowe (1986) distinguished this subfamily on the unique presence within the Comasteridae of a syzygy uniting the primibrachial ossicles. In an initial phylogenetic reconstruction using a portion of the mitochondrial 16S rDNA gene, White and others (2001) demonstrated weak support for nesting the Comatulinae (represented by *Comatula pectinata* and *C. rotalaria*) within a clade composed of *Comatella*, *Phanogenia*, *Alloeocomatella*, and *Comactinia.*] *Holocene.*

Comatula Lamarck, 1816, p. 530 [**C. solaris*; OD] [=*Actinometra* Müller, 1841, p. 181 (type, *A.*

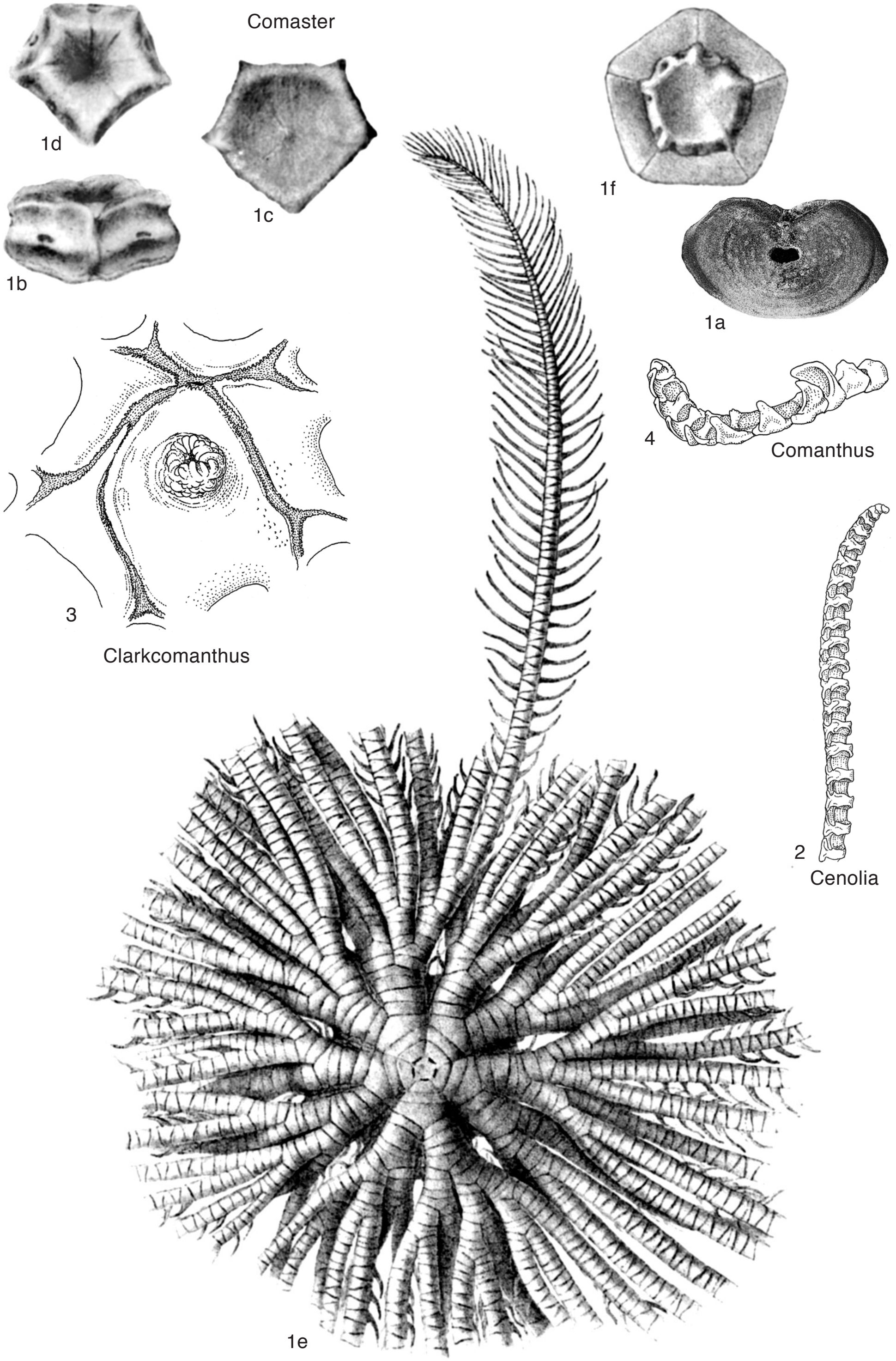

FIG. 43. Comasteridae (p. 87–88).

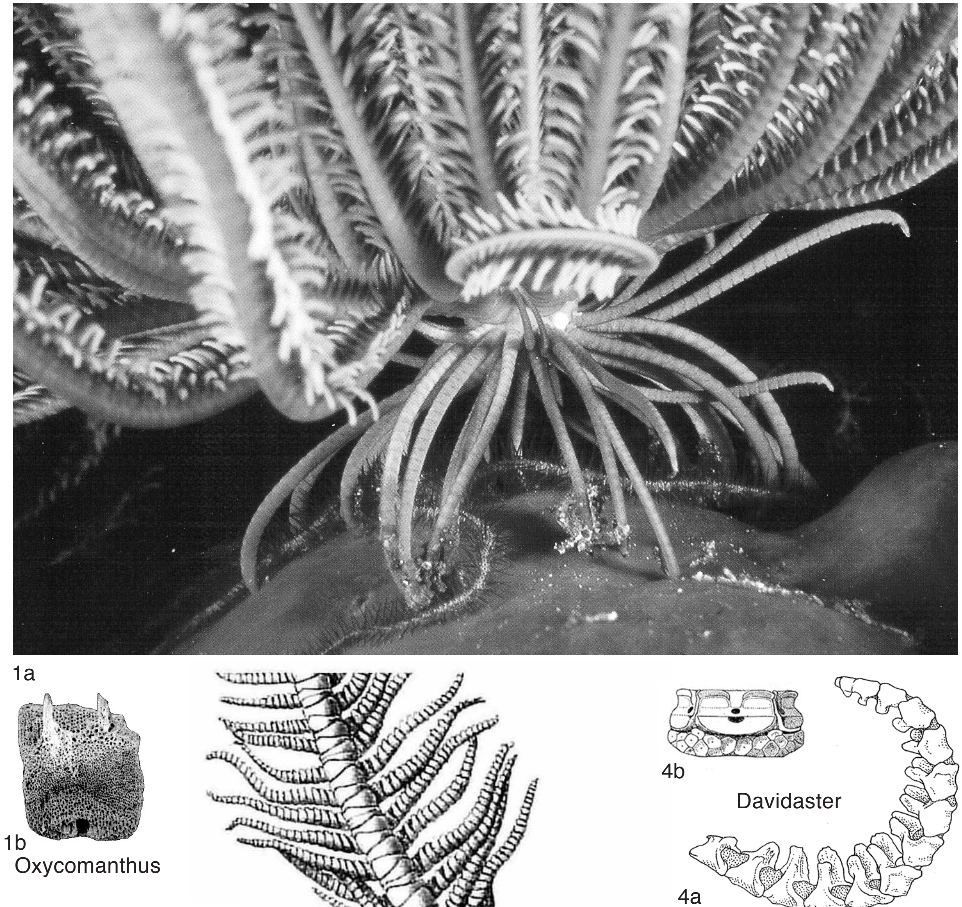

FIG. 44. Comasteridae (p. 88–94).

imperialis, OD), =*Aetinometra* CARPENTER, 1881d, p. 204, *nom. null.;* =*Actinomedra* VON GRAFF, 1883, p. 132, *nom. null.;* =*Actynometra* FILHOL, 1885, p. 213, *nom. null.;* =*Actrinometra* HARTLAUB, 1891, p. 97, *nom. null.;* =*Actinometer* SPRINGER, 1903, p. 220, *nom. null.;* =*Actinomerta* CLARK, 1912c, p. 91, *nom. null.;* all *errores pro Actinometra* MÜLLER, 1841]. Characters as for subfamily. *Holocene:* Pacific and Indian Ocean (littoral to sublittoral).——FIG. 44,*2a–b*. **C. solaris*; *a,* transverse view of comb segment with confluent tooth from first pinnule, AM J12150, ×50 (Hoggett & Rowe, 1986); *b*, aboral view of base of crown with centrodorsal and cirri, Torres Strait at 11 m, ×1.5 (Carpenter, 1888, pl. 53,*2*).——FIG. 44,*2c*. *C. purpurea* (MÜLLER); syzygy on distal facet of primibrachial 1, Holocene, AM J15333, ×10 (Hoggett & Rowe, 1986).

Subfamily CAPILLASTERINAE A. H. Clark, 1909

[Capillasterinae A. H. CLARK, 1909h, p. 175]

Synarthry between primibrachials 1 and 2. Secundibrachials of 4 ossicles (rarely 2 or 3) with syzygy between 3 and 4. Subsequent brachitaxes when of 3 brachials, the second and third united by syzygy. Arms arising from primibrachial 2 with first syzygy between secundibrachials 3 and 4 and first pinnule on secundibrachial 2; arms arising from secundibrachials and subsequent brachitaxes with first syzygy between brachials 2 and 3; first pinnule on brachial 1. Arms typically at least 20; as many as 40 in some species and exceeding 60 in 2 species. *Paleogene (Eocene)–Holocene.*

Capillaster A. H. CLARK, 1909c, p. 87 [**Actinometra sentosa* CARPENTER, 1888, p. 325; OD]. Cirri present or absent. Brachials beyond the basal few almost oblong, much wider than high and usually strongly spinose. Comb teeth single, curved, confluent with side of pinnular away from arm. Distalmost comb-bearing pinnule widely variable. *Holocene:* Indian Ocean, western Pacific Ocean (littoral to upper bathyal).——FIG. 44,*3*. **C. sentosus* (CARPENTER); middle brachials, enlarged (Messing, 2001, p. 283, fig. 3b, courtesy of the *Bulletin of the Biological Society of Washington*).

Davidaster HOGGETT & ROWE, 1986, p. 116 [**Actinometra rubiginosa* POURTALÈS, 1869, p. 356; OD]. Fewer than 20 cirrals. Brachials wedge shaped beyond the basal few. Comb teeth paired, more or less straight, decreasing in height toward pinnule tip, occurring no further than third pinnule. *Holocene:* tropical western Atlantic Ocean (littoral to sublittoral).——FIG. 44,*4a*. **D. rubiginosus* (POURTALÈS); oral pinnule comb with paired teeth, NSU, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*).——FIG. 44,*4b*. *D. discoideus* (CARPENTER); cup with centrodorsal, ×5 (A. H. Clark, 1921 in 1915–1950).

Nemaster A. H. CLARK, 1909f, p. 503 [**N. grandis*; OD]. Cirri with 30 to 35 short segments. Brachials wedge shaped beyond the basal few, commonly higher than broad. Comb teeth single, curved, confluent with side of pinnular closest to arm, occurring no further than sixth pinnule. [Unlike triangular confluent comb teeth in most other comasterids (e.g., *Alloeocomatella*, *Capillaster*, *Clarkcomanthus*, *Comanthus*), those of *N. grandis* arise from the side of the pinnule closest to the arm. *Comatella* (subfamily Phanogeniinae) is the only other comasterid genus known to share this feature. It remains unclear if this character is homoplasious in the 2 genera or a synapomorphy.] *Paleogene (Eocene)–Holocene:* North America (according to HOWE, 1942, p. 1192), *Eocene*; western Atlantic Ocean, Caribbean (littoral to sublittoral), *Holocene*.——FIG. 45,*1*. **N. grandis*; Holocene, Colon at 26 m, holotype, USNM 25459, ×1 (A. H. Clark, 1931 in 1915–1950).

Subfamily PHANOGENIINAE White & others, 2001

[Phanogeniinae WHITE & others, 2001, p. 136] [=Comasterinae HOGGETT & ROWE, 1986, p. 124, *partim*]

Synarthry or cryptosynarthry between primibrachials 1 and 2. Secundibrachitaxis and following brachitaxes of 2 ossicles united by synarthry except in *Phanogenia* (2 brachials united by syzygy or 4 with syzygy between brachials 3 and 4) and in *Aphanocomaster* (brachitaxes of 2 or 4 brachials variously united by synarthry or syzygy, sometimes with 2 pairs of each). [Corresponds to the Comasterinae of HOGGETT and ROWE (1986). WHITE and others (2001) erected the new name Phanogeniinae for the subfamily Comasterinae following MESSING's (1998) recognition that the type species of *Comaster* (*Alecto multifidus* MÜLLER, 1841) is a senior synonym of *Comanthina variabilis* (BELL, 1882a), a member of Comanthinae (renamed Comasterinae). The new subfamily name derives from *Phanogenia,* the most senior genus remaining after removal of *Comaster*. MESSING, AMÉZIANE, and ELÉAUME (2000) reinstated *Palaeocomatella* as a genus distinct from *Comissia*. Because all species left in *Comissia* have only 10 arms and cannot be assigned to the subfamily under the current organization of the family, the genus was removed from the Phanogeniinae and placed

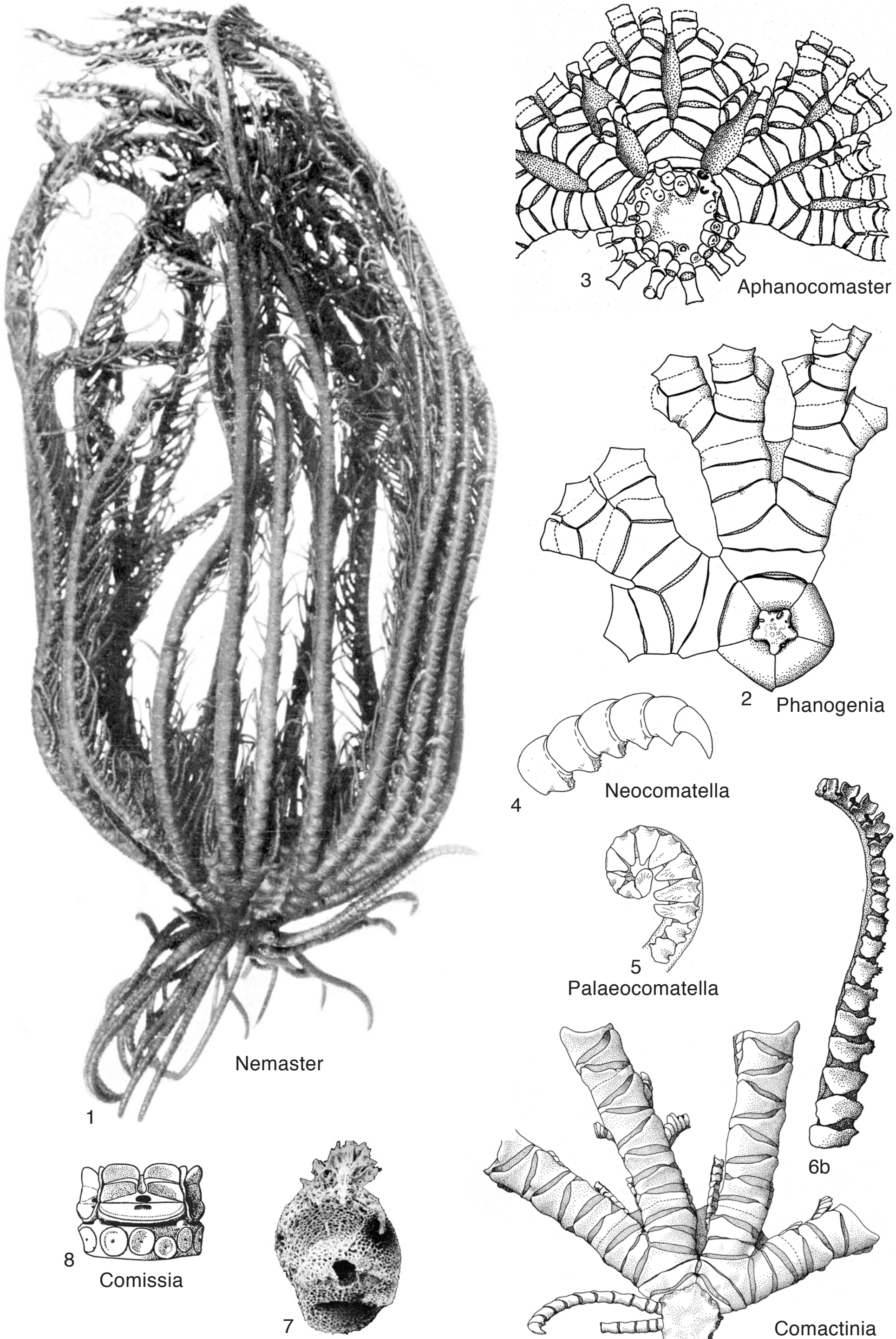

FIG. 45. Comasteridae (p. 91–95).

in *incertae sedis* at the subfamilial level by MESSING, AMÉZIANE, and ELÉAUME (2000). MESSING (1995a) did not place *Alloeocomatella* in a subfamily because 1 of 2 included species, *A. polycladia*, exhibits a comanthine pattern of syzygies in specimens with less than 20 arms, and a comasterine (=phanogeniine) pattern in those with more than 20 arms. The genus is included in the latter subfamily, herein, because fully developed individuals (20 to 30 arms) exhibit a phanogeniine pattern and because WHITE (2000, unpublished in MESSING, 2001) and WHITE and others (2001) demonstrated strong molecular support for a sister-clade relationship between *Comatella* and *Alloeocomatella*. The other species included in the genus, *A. pectinifera*, has only 10 arms, but both morphological and molecular evidence place it extremely close to *A. polycladia* (MESSING, 1995a; WHITE & others, 2001). *Aphanocomaster* was tentatively assigned by MESSING (2001) to the Phanogeniinae for the following reasons: primibrachials united by cryptosynarthry; tetrabrachials (and sometimes tertibrachials) of 2 ossicles typically joined by syzygy (although this might be a cryptosynarthry in some cases); and arms arising from tertibrachials bear the first and second and the third and fourth brachials united by syzygy (rarely syzygy between only one pair). The assignment is tentative because of the combination of unusual brachitaxes and because arms arising from secundibrachials almost always bear 4 brachials (syzygy between brachials 3 and 4) rather than 2 (united by syzygy), although a similar arrangement also occurs in *Alloeocomatella polycladia*. According to WHITE (2000, unpublished in MESSING, 2001), the Phanogeniinae appears to be at best a paraphyletic group.] *Holocene.*

Phanogenia LOVÉN, 1866, p. 231 [**P. typica*; M]. Secundibrachials and following brachitaxes with 2 (united by syzygy) or 4 brachials (syzygy between brachials 3 and 4); tertibrachials and following axillaries commonly bearing one brachitaxis and one free arm, alternating on successive axillaries. Syzygy between brachials 1 and 2 on all undivided arms arising from secundibrachials and subsequent brachitaxes. Arms 30 to approximately 150. Combs on proximal pinnules and at intervals to near arm tip; comb teeth single, curved, confluent with exterior side of pinnulars; terminal comb tooth discrete; proximal comb tooth transversely oriented and saucerlike. Mouth central or subcentral (see Fig. 3,*3*). [MESSING (1998) identified the holotype of *Comaster multifidus* MÜLLER as synonymous with and senior to *Comanthina variabilis* BELL. As a result, he removed all other species from *Comaster* and assigned them to the next most senior generic name, *Phanogenia* LOVÉN. He considered 3 species placed in *Comaster* by HOGGETT and ROWE (1986) (*decora*, *brachycirra*, and *africana*) as genera *incertae sedis* without subfamilial assignment, but subsequently moved *decora* to *Palaeocomatella* (MESSING, 2001).] *Holocene:* Indian and Pacific Ocean (sublittoral to upper bathyal).——FIG. 45,*2*. **P. typica*; aboral view of centrodorsal, radial circlet, and proximal part of 2 rays, Singapore, holotype, RM 60, ×3.5 (Messing, 1998).

Alloeocomatella MESSING, 1995a, p. 437 [**A. polycladia*; OD]. All brachitaxes of 2 ossicles joined by synarthry; tertibrachials developed exteriorly. Arms 10 to 30. Specimens with fewer than 20 arms have syzygies between brachials 3 and 4 on arms arising from secundibrachials; those with 20 arms or more have syzygies between brachials 1 and 2 and 3 and 4, or only brachials 3 and 4, on arms arising from secundibrachials; on arms arising from tertibrachials, syzygies occur chiefly between brachials 1 and 2 and 3 and 4 (interior arms) and brachials 3 and 4 (exterior arms); syzygy between brachials 1 and 2 sometimes present alone. Pinnule combs as far as pinnules 4 to 8; comb teeth 20 to 39 per comb, high (middle teeth at least twice as high as greatest width), triangular, confluent with exterior side of pinnulars and remaining high to pinnule tip. Mouth eccentric; anal papilla close to mouth. [MESSING (2001) placed *Alloeocomatella* in the Phanogeniinae because fully developed individuals of species with more than 10 arms (*A. polycladia*) exhibit the phanogeniine pattern of syzygy placement and because WHITE and others (2001) demonstrated strong molecular support for a sister-clade relationship between *Comatella* and *Alloeocomatella*.] *Holocene:* tropical Indian Ocean, western and central Pacific Ocean (littoral to sublittoral).——FIG. 44,*5*. **A. polycladia*; second pinnule with confluent comb teeth arising from exterior margin of pinnulars, NSU, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*).

Aphanocomaster MESSING, 1995b, p. 657 [**Comaster pulcher* A. H. CLARK, 1912d, p. 22; OD]. Cryptosynarthry between primibrachials 1 and 2. Two or 4 secundibrachials consisting of 1 or 2 synarthrial pairs, rarely 4 brachials with syzygy between brachials 3 and 4. Two or 4 tertibrachials joined by synarthry, syzygy, 2 synarthrial or syzygial pairs, or a synarthry followed by a syzygy. Arms up to 39, arising from secundibrachials typically with syzygy between brachials 3 and 4; arms arising from tertibrachials with syzygy between brachials 1 and 2 and 3 and 4 (rarely only one syzygy). Comb teeth single, triangular or spade shaped, confluent with exterior side of pinnulars; initial tooth sometimes slightly twisted but not oriented transversely. Mouth central. [MESSING (1995b) erected this genus to accommodate the holotype of *Comaster pulcher,* because the unique and variable arrangement of brachitaxes (including tertibrachials composed of 2 successive synarthrial or syzygial pairs) is unknown elsewhere in the Comasteridae, and because pinnule combs do not resemble those diagnostic of *Comaster* (now *Phanogenia*).] *Holocene:* tropical western Pacific Ocean (littoral to sublittoral).——FIG. 45,*3. *A. pulcher* (CLARK); aboral view of centrodorsal and proximal part of 3 rays, Indonesia, holotype, UA U.Cri.-2114, ×3.5 (Messing, 1995b, courtesy of the *Bulletin of the Biological Society of Washington*).

Comatella A. H. CLARK, 1908l, p. 207, *non* D'ORBIGNY, 1852, table p. 46, as *Comatella wagneri*, *error pro Comaturella wagneri* MÜNSTER, 1839, p. 85, *nom. nud., nec* BUCCHICH, 1886, p. 223, *nom. nud.*, *error pro Cometella* SCHMIDT, 1870, p. 49 (type, *C. gracilior*, SCHMIDT, 1870, p. 49, OD) [**Actinometra nigra* CARPENTER, 1888, p. 304; OD]. All brachitaxes of 2 ossicles united by synarthry; arms arising from secundibrachials and following brachitaxes with syzygy either between brachials 1 and 2, or 1 and 2 and 3 and 4. Arms approximately 20 to 80. Pinnule combs present as far as pinnule 5; comb teeth 14 to 18 per comb, single, curved, triangular, confluent with side of pinnulars closest to arm, decreasing in size near tip so that distal 1 or 2 teeth are reduced; proximal comb tooth not transverse. Mouth eccentric. [Comb teeth arising from the side of the pinnulars closest to the arm are unique within the subfamily Phanogeniinae and occur elsewhere only in *Nemaster*.] *Holocene:* tropical Indian Ocean, western and central Pacific Ocean (littoral to sublittoral).——FIG. 44,*6a. *C. nigra* (CARPENTER); synarthry on distal facet of primibrachial 1, AM J9930, ×8 (Hoggett & Rowe, 1986).——FIG. 44,*6b. C. stelligera* CARPENTER; second pinnule with confluent comb teeth arising from inner margin of pinnulars and rounded keels on first 2 pinnulars, NSU, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*).

Neocomatella A. H. CLARK, 1909h, p. 177 [**Antedon alata* POURTALÈS, 1878, p. 215; OD] [=*Neomatella* A. H. CLARK, 1909h, *nom. null.*]. All brachitaxes of 2 ossicles united by synarthry; arms arising from secundibrachials and the following brachitaxes with syzygy usually between brachials 1 and 2 and 3 and 4 (sometimes 1 and 2 alone, or 1 and 2 and 4 and 5). Arms rarely more than 20. Pinnule combs present as far as pinnule 6; comb teeth up to 20 per comb, single, curved, triangular, confluent with side of pinnulars away from arm. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* northeastern and western Atlantic Ocean, Mediterranean (littoral to bathyal).——FIG. 45,*4. N. pulchella* (POURTALÈS); distal portion of cirrus in oblique lateral view showing aboral processes, triangular in section, NSU, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*).

Palaeocomatella A. H. CLARK, 1912d, p. 18 [**Actinometra difficilis* CARPENTER, 1888, p. 93; OD]. Brachitaxes of 2 ossicles united by synarthry; exterior arms arising from secundibrachials and following brachitaxes with syzygy between brachials 1 and 2 or 3 and 4 or both, and interior arms with syzygy between only brachials 1 and 2 or between both 1 and 2 and 3 and 4 brachials (rarely also between brachials 1 and 2 and 4 and 5). At least the antepenultimate cirral has aboral spine or ridge compressed along longitudinal axis of the cirral. Pinnule combs present as far as pinnules 3 to 6; comb teeth triangular, curved, confluent with exterior side of pinnulars; proximal tooth oriented transversely or not; terminal tooth fan shaped. Mouth central. [HOGGETT and ROWE (1986) placed *Palaeocomatella* in synonymy under *Comissia* A. H. CLARK because both retain a central mouth as adults and share the same pinnule comb form. MESSING, AMÉZIANE, and ELÉAUME (2000) reinstated *Palaeocomatella* for 3 plesiomorphic reasons: The central mouth also occurs in juvenile comasterids (and almost all noncomasterid comatulids) and adult *Phanogenia*, *Aphanocomaster*, and *Comatilia* (though the latter is paedomorphic; MESSING, 1984). The shared comb form is the most generalized and widespread in the family, occurring also in *Neocomatella*, *Alloeocomatella*, *Capillaster*, and some *Comatula*. The mouth in the type specimen of *Comissia luetkeni* A. H. CLARK is subcentral, a feature also present in *Comissia (Leptonemaster) venustus* and juvenile *Neocomatella*. Thus, *Comissia* and *Palaeocomatella* share no uniquely derived features, only generalized apparent plesiomorphies. It remains unknown whether central versus subcentral mouths represent real anatomical differences or simply reflect within-taxon variations or preservational effects. *Palaeocomatella decora* was originally placed in *Comatella* by A. H. CLARK (1912d) but was transferred to *Comaster* (now *Phanogenia*) by HOGGETT and ROWE (1986) on the basis of its transverse first comb tooth and central mouth. HOGGETT and ROWE (1986) acknowledged that inclusion of *decora* (as well as *brachycirra* GISLÉN and *africana* GISLÉN) substantially broadened the diagnosis of *Comaster* and that the 3 species might warrant separate generic status. The species *decora* was placed in *Palaeocomatella* by MESSING (2001), because all 3 currently recognized species (*difficilis*, *hiwia,* and *decora*) share the unique combination of a fan-shaped terminal comb tooth; a longitudinally compressed aboral spine or ridge on at least the antepenultimate cirral; a central mouth; and a phanogeniine pattern of syzygies. The species *brachycirra* and *africana* are retained as "*Comissia*" *sensu lato*. The placement of proximal syzygies on arms arising from secundibrachials is similarly variable in all 3 included species. Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* tropical Indian and western Pacific Ocean, Caribbean (sublittoral to bathyal).——FIG. 45,*5. P. hiwia* MCKNIGHT, 1977; oral pinnule comb with terminal, fan-shaped tooth, MNHN EcCH 26, enlarged (Messing, 2001, courtesy of *Bulletin of the Biological Society of Washington*).

Subfamily UNCERTAIN

Comactinia A. H. CLARK, 1909f, p. 498 [**Alecto echinoptera* MÜLLER, 1841, p. 183; OD]. Centrodorsal flat disk or pentagon. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Arms 10; first syzygy between secundibrachials 3 and 4; combs present as far as pinnules 2 to 6; comb teeth single, either confluent with exterior side of pinnulars, with tall, narrow, terminal tooth and with tips of middle teeth flat or notched, or nonconfluent but off center, rounded or spade shaped, with the terminal 1 to 3 pinnulars bearing successively smaller teeth or tapering to a sharp tip. Mouth eccentric, but central in juveniles. *Holocene:* tropical western Atlantic Ocean and western Pacific Ocean (littoral to upper bathyal).——FIG. 45,*6a–b*. **C. echinoptera* (MÜLLER); *a,* aboral view of centrodorsal with cirrus and base of 2 rays, western Atlantic, USNM E18997, ×3 (Messing & Dearborn, 1990, p. 14, fig. 10a); *b*, third pinnule with comb, western Atlantic, USNM E18997, ×8 (Messing & Dearborn, 1990, p. 14, fig. 10g).

Comatilia A. H. CLARK, 1909d, p. 365 [**C. iridometriformis*; OD]. Small; ray length no more than approximately 30 mm. Longest cirrus segments 3.3 to 5 times longer than wide. Exposed surface of radials with lateral, tongue-like processes separating bases of adjacent rays. Arms 10. Synarthry between primibrachials and secundibrachials 1 and 2; first syzygy between brachials 3 and 4. Third exterior and second and third interior pinnules always absent; second and fourth exterior and fourth interior pinnules commonly absent; comb on first and (when present) second exterior pinnules and first interior pinnule; comb teeth single, triangular, confluent with exterior side of pinnulars; saccules present; terminal pinnular with a discrete tooth. Mouth central. [*C. iridometriformis* matures at a small size and bears gonads containing embryos at advanced developmental stages. It releases progeny as stalked postlarvae (MESSING, 1984).] *Holocene:* western Atlantic Ocean (sublittoral to upper bathyal).——FIG. 46,*1*. **C. iridometriformis*; aboral view of centrodorsal with bases of cirri and 2 rays, western Atlantic, USNM E18948, ×15 (Messing & Dearborn, 1990, p. 12, fig. 8a).

Comatulella A. H. CLARK, 1911f, p. 129 [**Comatula brachiolata* LAMARCK, 1816, p. 535; M; =*Alecto rosea* MÜLLER, 1841, p. 182]. 10 arms. Cryptosynarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Stout, curled pinnules with reduced food grooves interspersed among slender, grooved pinnules. *Holocene:* southwestern Pacific Ocean (littoral).——FIG. 46,*2*. **C. brachiolata* (LAMARCK); middle part of arm with 3 modified pinnules (curled, stout, with reduced food groove) and 2 complete, unmodified pinnules, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*).

Comatulides A. H. CLARK, 1918, p. 24, *nom. nov. pro Cominia* A. H. CLARK, 1909f, p. 497, *non* BROWN, 1844, p. 22 [**Comanthus decameros* A. H. CLARK, 1908k, p. 221; OD]. Arms 10. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2; syzygy between secundibrachials 3 and 4. Pinnule combs as far as pinnule 3; combs weakly developed, comb teeth atypical, not confluent with the edge of the segment, loosely constructed of numerous irregular spinules joined basally and flaring outward. Mouth eccentric. *Holocene:* northern and western Pacific Ocean (bathyal).——FIG. 45,*7*. **C. decameros* (CLARK); transverse view of pinnule comb segment, holotype, CM ZMUC-CRI-11, ×50 (Hoggett & Rowe, 1986, fig. 2-G).

Comissia A. H. CLARK, 1909f, p. 501 [**C. luetkeni*; OD] [=*Leptonemaster* A. H. CLARK, 1909f, p. 498 (type, *L. venustus,* OD)]. Arms 10. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2; first syzygy between secundibrachials 3 and 4. Pinnules with combs as far as pinnules 2 to 5; combs consisting of single, curved teeth confluent with exterior side of pinnulars; terminal pinnular with a discrete tooth; proximal tooth not transversely oriented. Mouth central or subcentral. [Because MESSING, AMÉZIANE, and ELÉAUME (2000) restored *Palaeocomatella* to separate generic status, *Comissia* reverts to a heterogeneous assemblage of species with a central or subcentral mouth; the genus cannot be assigned to a subfamily under the current organization of the family.] *Holocene:* tropical Indian and western Pacific Ocean, western tropical Atlantic Ocean (sublittoral to bathyal).——FIG. 45,*8*. **C. venusta* (CLARK); cup with centrodorsal, ×6 (A. H. Clark, 1921 in 1915–1950).

Rowemissia MESSING, 2001, p. 295 [**Comaster* (?) *scitulus* A. H. CLARK, 1911b, p. 534; OD]. Arms 10. Primibrachials closely articulated, possibly by cryptosynarthry. First syzygy between secundibrachials 3 and 4. Pinnules with combs to pinnule 5; proximal 1 or 2 comb teeth single, knob- or transverse bar shaped and nonconfluent; middle comb teeth paired, narrow and well separated; following 1 or 2 pinnulars with weaker, single, nonconfluent teeth, and tapering to a sharp terminal point. Disk covered orally and aborally with delicate, calcareous plates (not forming solid pavement); mouth almost central. [*Rowemissia* differs from *Comissia* in pinnule comb morphology and in having the disk covered with delicate, calcareous plates (although details of disk morphology have not been recorded for all species of *Comissia*). The 2 genera otherwise share only generalized, apparently plesiomorphic features: 10 arms, first syzygy between secundibrachials 3 and 4, and central (or subcentral) mouth.] *Holocene:* tropical western Pacific Ocean (sublittoral).——FIG. 46,*3*. **R. scitulus* (CLARK); centrodorsal with bases of cirri and base of one ray with bases of pinnules, Philippines, holotype, USNM 027488, ×10 (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*).

Sievertsella RADWAŃSKA, 2003, p. 321 [**Palaeocomaster seranensis* SIEVERTS, 1933a, p. 148; OD] [=*Sievertsia* RADWAŃSKA, 1987, p. 117 (type, *Palaeocomaster seranensis* SIEVERTS, 1933a, p. 148, OD), *non* SMITH & PAUL, 1982]. Centrodorsal low, subpentagonal, with large, cirrus-free, slightly convex or flat aboral apex. Cirrus sockets in 2 or 3 irregular circles, moderately large, deep, with a slightly elevated margin around lumen. Adoral side of centrodorsal with a rather

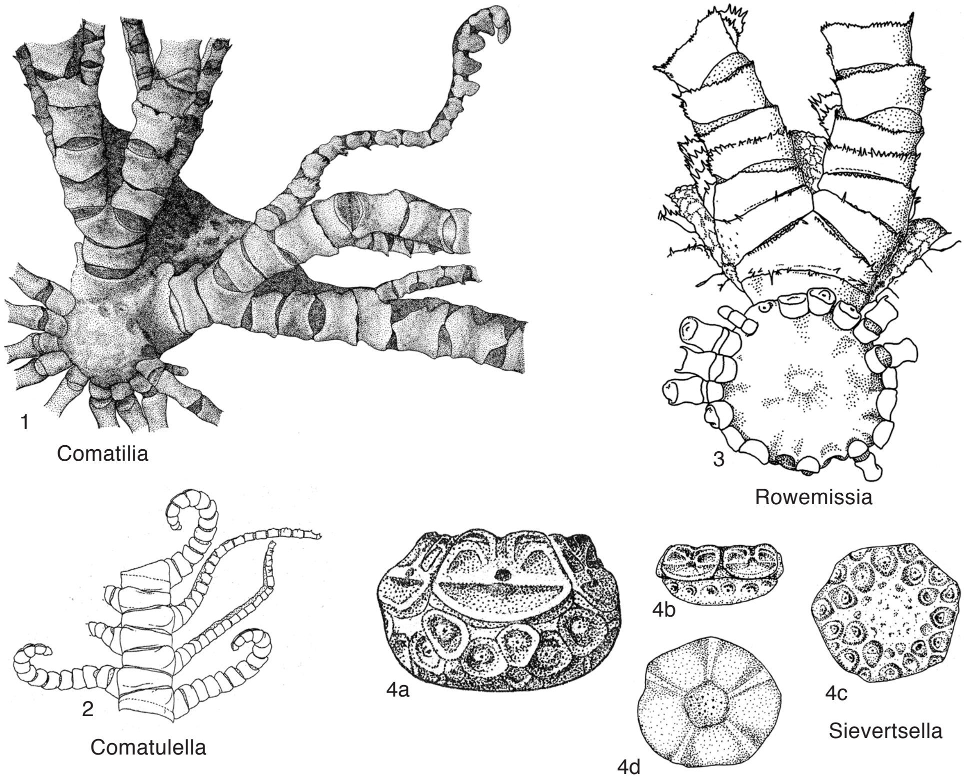

Fig. 46. Comasteridae (p. 95–96).

deep, moderately large depression. Basals exposed interradially. Radials trapezoidal with low exposed surface. Radial articular facet moderately large; interarticular ligament fossae subtriangular, rather deep, slightly higher than aboral ligament fossa; adoral muscle fossae deep, forming narrow triangular bands along edge. Radial cavity large, shallow, passing aborally into round, steep, central depression. Arms unknown. *Neogene (Miocene–Pliocene):* Poland, Indonesia.——Fig. 46,*4a*. **S. seranensis* (Sieverts); cup with centrodorsal, Pliocene, Indonesia, holotype, ×9 (Sieverts, 1933a).——Fig. 46,*4b–d*. *S. polonica* Radwańska, 1987, Miocene, Poland; *b,* cup with centrodorsal, holotype, ZPAL/UW-C/001, ×10; *c–d*, centrodorsal, *c*, aboral, *d*, adoral, paratype, ZPAL/UW-C/002, ×10 (Radwańska, 1987).

Superfamily UINTACRINOIDEA Zittel, 1879

[*nom. transl.* Hess & Messing, herein, *pro* Uintacrinidae Zittel, 1879 in 1876–1880, p. 345, 375] [=Uintacrinida Broili in Zittel, 1921, p. 186, *nom. transl.* Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952, p. 614; =suborder Innatantes A. H. Clark, 1909h, p. 174]

Large, subspheroidal calyx of thin, polygonal plates without column or cirriferous centrodorsal. Second primibrachials axillary, no further division. Arms composed of low, disk-shaped brachials, semicircular to almost circular in section. Syzygy between primibrachials 1 and 2 and secundibrachials 1 and 2, generally between secundibrachials 3 and 4, with intervals increasing from 3 to more than 6 in succeeding brachials; other arm articulations muscular, with adoral muscle fossae smaller than interarticular ligament fossae. Complete pinnulation beginning on abaxial side of secundibrachial 2. [Based on a cladistic analysis, Milsom, Simms, and Gale (1994) considered *Uintacrinus* and *Marsupites* to be closely related to the Comasteridae, and, thus, classified in the superfamily Comasteroidea. However, comasterids and *Uintacrinus* share no uniquely apomorphic features, with the exception of an eccentric mouth and a more or less central anus (the tegmen is unknown in *Marsupites*). Most comasterids have a synarthry (flat in some forms; e.g., *Phanogenia*) between primibrachials 1 and 2 and secundibrachials 1 and 2. The globose calyx of *Uintacrinus* and *Marsupites* appears to be an autapomorphy and an adaptation to an exceptional environment, the soupy sediment of the American Niobrara Chalk and the English Chalk. No other crinoid is adapted to a similar situation. Milsom, Simms, and Gale (1994) assigned both genera to a single family, Marsupitidae. However, the only synapomorphies linking the 2 genera are the size of the calyx and the arm structure. *Uintacrinus* and *Marsupites* differ in their calyces and do not overlap stratigraphically. Therefore, they are placed in separate families, although *Marsupites* probably evolved from *Uintacrinus*. According to Gale and others (2008, p. 143), the successive species and subspecies of the superfamily spanning the Santonian–Campanian interval were short ranged (mean duration of 200 kyr) and occur synchronously in precisely the same order on a global scale.] *Upper Cretaceous (Santonian–lower Campanian).*

Family UINTACRINIDAE Zittel, 1879

[Uintacrinidae Zittel, 1879 in 1876–1880, p. 345, 375]

Calyx composed of numerous, rather small, thin plates, including fixed interradials, fixed pinnulars, and fixed brachials. Both 2-circlet and 3-circlet forms are known, and both types have a centrale at the base of the calyx. Free part of arms may exceed one meter. Tegmen with large, conical, anal cone located centrally and marginal mouth. *Upper Cretaceous (upper Santonian–lower Campanian).*

Uintacrinus Grinnell, 1876, p. 81 [**U. socialis;* M; =*U. westfalicus* Schlüter, 1878, p. 55]. Characters as for family. [*Uintacrinus* is now considered to have been benthic (Milsom, Simms, & Gale, 1994; Hess, 1999d; Meyer & Milsom, 2001), see Fig. 48–49.] *Upper Cretaceous (upper Santonian–lower Campanian)*: North America (Western Interior, Gulf Coast, British Columbia), England, France, Germany, Italy, Sweden, Ukraine, Russia, Caucasus, Kazakhstan, Turkmenistan, Africa, western Australia, *upper Santonian (U. socialis);* USA (Texas), England, Kazakhstan, and western Australia, *upper Campanian* (*U. anglicus* Rasmussen; Gale & others, 2008).——Fig. 47*a–g*. **U. socialis*; *a,* calyces with proximal arms, upper Santonian, Kansas, IGPT, ×1 (Hess, 1999d); *b*, oral side of calyx with tegmen, upper Santonian, Kansas, MCZ, ×1.5 (Springer, 1901); *c*, adoral view of radial, primibrachial 1, and primibrachial 2, upper Santonian, England, BMNH E 51066-51068, ×2.5 (Rasmussen, 1961); *d–e*, primibrachial 1, *d*, proximal, *e*, distal, Santonian, England, BMNH E50162, ×2.5 (Rasmussen, 1961); *f,* syzygies of proximal secundibrachial (left) and distal secundibrachial (right), Santonian, Colorado, NMB M10632, ×5 (Hess, new); *g*, distal muscular facet of secundibrachial, Santonian, England, BMNH E50169, ×2.5 (Rasmussen, 1961).——Fig. 48. **U. socialis*; reconstruction in nonfeeding position prior to burial (R. Kindlimann, new).——Fig. 49. **U. socialis*; reconstruction in feeding position, modeled after living *Comatula rotalaria* Lamarck (Messing & others, 2004); calyx is shown partly embedded in soupy sediment, ×0.1 (Kindlimann, new).——Fig. 47*h–i*. *U. anglicus* Rasmussen, 1961; radial, *h*, adoral, *i*, aboral, Campanian, Texas, BMNH EE 13330, ×4 (Gale & others, 2008).

Family MARSUPITIDAE d'Orbigny, 1852

[Marsupitidae d'Orbigny, 1852 in 1850–1852, p. 138; *emend.*, Simms, 1988a, p. 284]

Calyx composed of 3 circlets of large, slightly convex plates of similar size, interpreted as the radials, basals, and infrabasals, with a centrale at the base. Typically ornamented with radiating ridges corresponding to courses of axial nerve canals inside the plates. Interradial plates rarely developed. Arm length and tegmen unknown. *Upper Cretaceous (Santonian).*

Marsupites Mantell in Miller, 1821, p. 135 [**M. ornatus;* M; =*Encrinites testudinarius* von Schlotheim, 1820, p. 339; =*M. milleri* Mantell, 1822, p. 184; =*Sitularia triangulariformis* Cumberland, 1826, p. 21; =*M. mantelli* Bronn, 1848 in 1848–1849, p. 705; =*M. laevigatus* Forbes in Dixon, 1850, p. 343; =*M. americanus* Springer, 1911, p. 158; =*M. lamberti* Besairie, 1936, p. 203] [=*Sitularia* Cumberland, 1826, p. 21 (type, *S. triangulariformis*, M); =*Marsupiocrinites* de Blainville, 1830, p. 244, *nom. van.*, *non* Phillips in Murchison, 1839, p. 672]. Characters as for family. [The name *Marsupites* was taken by Miller (1821) from a manuscript by Mantell published in 1822. The name *Marsupium* Koena, recorded by Agassiz (1836, p. 194) is presumably a *nomen vanum*, origin untraced.] *Upper Cretaceous (Santonian):* England, France, Germany, Poland, Kazakhstan, Turkmenistan, Crimea, Algeria, Gulf Coast, USA, Canada, Australia,

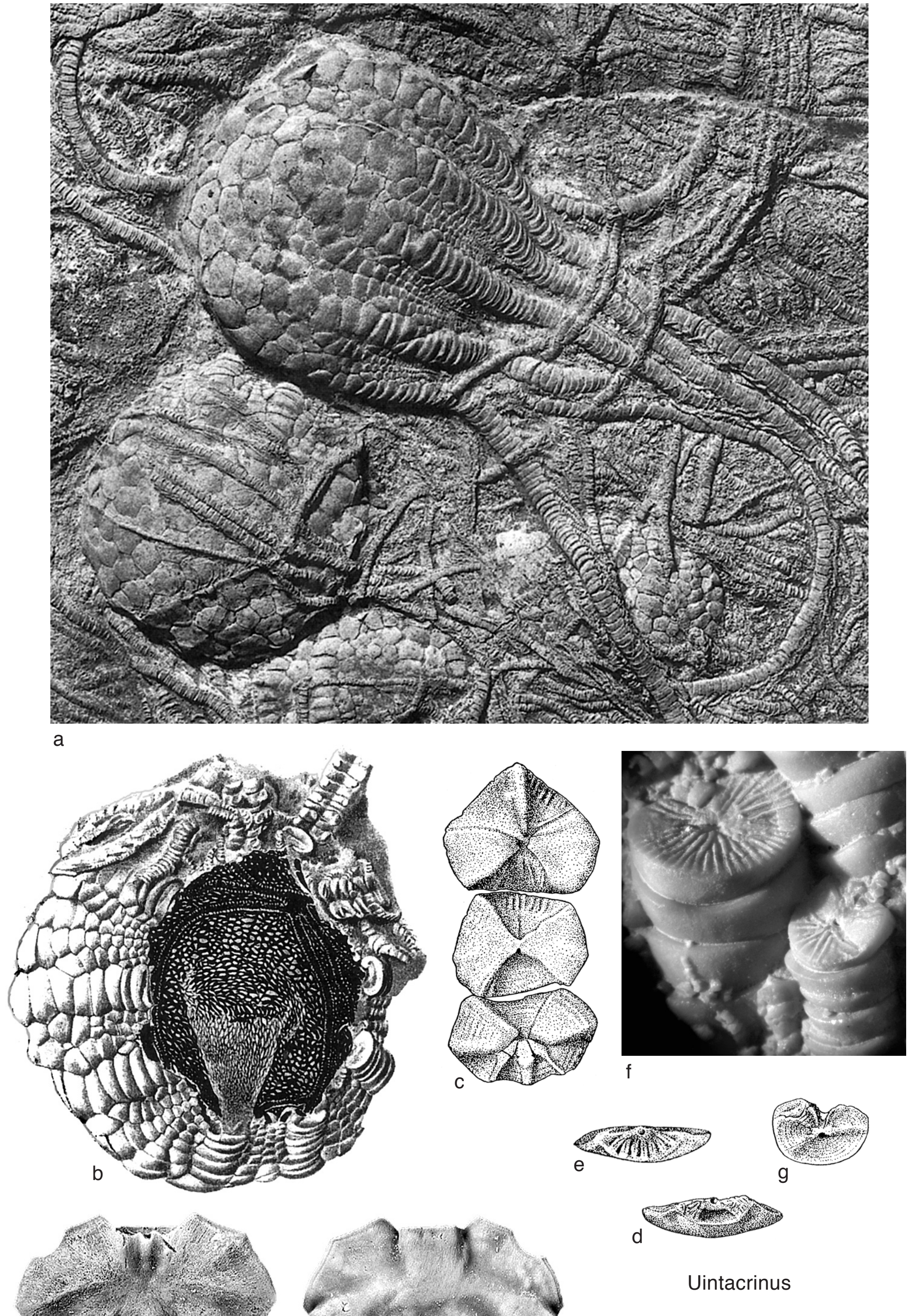

FIG. 47. Uintacrinidae (p. 97).

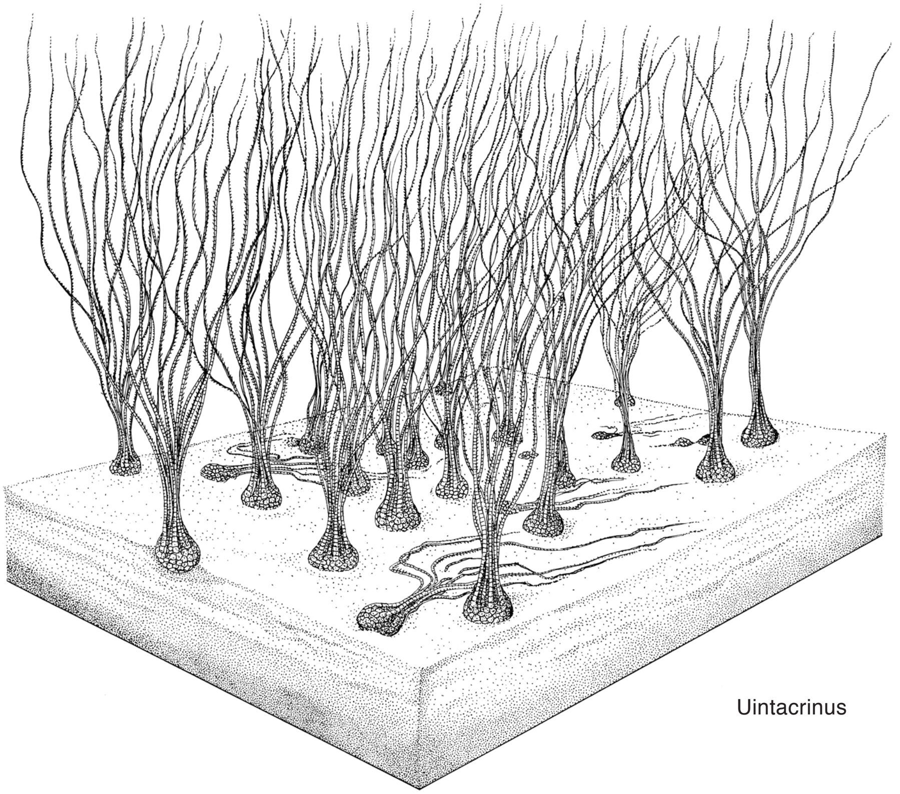

FIG. 48. Uintacrinidae (p. 97).

India, Madagascar, *Santonian* (*M. testudinarius*); USA (Texas), England, France, Germany, central Asia, Australia, *upper Santonian* (*M. laevigatus* FORBES).——FIG. 50,*1a–e*. **M. testudinarius* (VON SCHLOTHEIM); *a,* calyx, England, BMNH E14261, ×1.4 (Milsom, Simms, & Gale, 1994); *b*, distal view of radial, England, ×3 (Sieverts, 1927); *c*, distal facet of primibrachial 1, England, BMNH E46663, ×3 (Rasmussen, 1961); *d*, distal facet of secundibrachial 9, Germany, GZG 399/8, ×3 (Sieverts, 1927); *e*, distal facet of secundibrachial 11, Germany, GZG 399/10, ×3 (Sieverts, 1927).

Superfamily MARIAMETROIDEA A. H. Clark, 1909

[*nom. correct.* HESS & MESSING, herein, *pro* Mariametracea RASMUSSEN, 1978, p. 885, *nom. transl. ex* subfamily Mariametrinae A. H. CLARK, 1909h, p. 176] [=Mariametrida GISLÉN, 1924, p. 230, established as a superfamily-rank taxon although named tribe]

Centrodorsal low hemispherical to discoidal; aboral apex cirrus-free, flattened to concave, smooth or tuberculate, rarely rugose or with traces of obliterated cirrus sockets. No dorsal star. Cirrus sockets without distinct ornament or with slightly elevated rim around axial canal closely placed in 1 to 3, rarely 4, irregular marginal tiers. Marginal crenulae and distinct fulcral ridge or tubercles may be present in cirrus sockets of the fossil genus *Discometra*. Adoral side of centrodorsal with interradial ridges. Centrodorsal cavity less than 30 percent of centrodorsal diameter. Several genera with shallow, radial, coelomic depressions or radiating furrows in adoral side of centrodorsal and aboral side of radials. In fossil genus *Discometra,* coelomic canals near proximal surface of radials. Small radial pits around centrodorsal cavity present in *Cyllometra*. Aboral side of cirrals rounded or carinate, with or

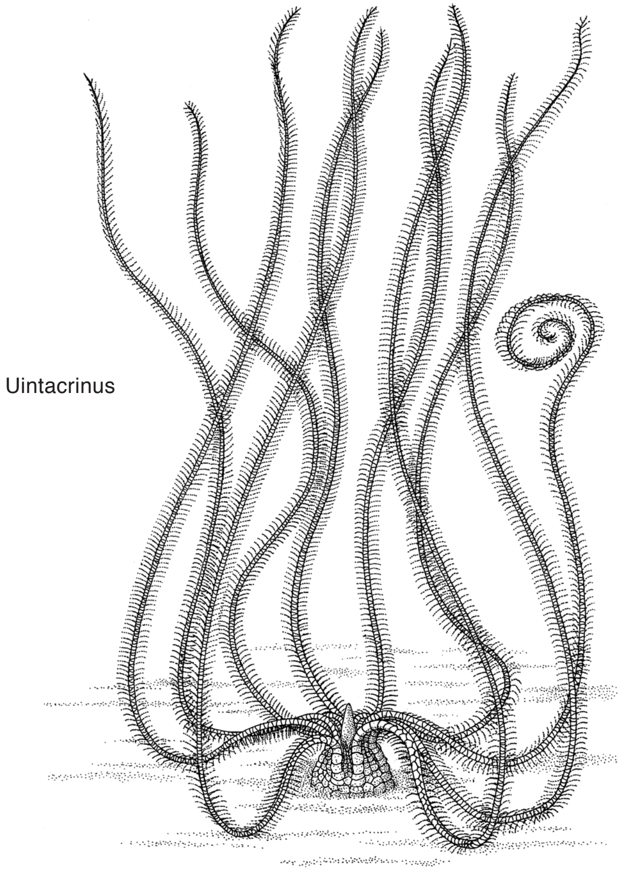

FIG. 49. Uintacrinidae (p. 97).

without aboral spines, in Colobometridae with transverse ridge or with transverse row of 2 to 4 spines. Basal rosette but no rod-shaped basals except in fossil specimens referred to *Himerometra*. Radials with low exposed surface, commonly concealed midradially, rarely moderate to high, as in *Amphimetra* and in juveniles. Radial articular facet commonly rather flat, moderately sloping to almost parallel to oral-aboral axis, and commonly separated by narrow, interradial margins. Interarticular ligament fossae large, high, and broad. Adoral muscle fossae generally small, commonly forming a narrow, crescentic band along adoral edge and midradial furrow. Muscle fossae triangular in *Colobometra*, large and high in *Cyllometra*. Wide midradial furrow with or without median ridge, except in *Cyllometra*, which has only a narrow midradial ridge. Radial cavity moderate to large with spongy calcareous filling; commonly very large in juveniles. Five rays undivided in *Eudiocrinus*; first pinnule on brachial 2 and second pinnule on brachial 4; no pinnule on brachial 3. Rays divided at least at primibrachial 2 in all other genera; additional brachitaxes of 2 to 4 ossicles commonly present, commonly different on inner and outer branches. First pair of ossicles of all brachitaxes and undivided arms joined by flat synarthry, except for a syzygy between the primibrachials in Zygometridae and Eudiocrinidae. Syzygy between brachials 3 and 4 of brachitaxes of 4 ossicles and undivided arms, and with variable,

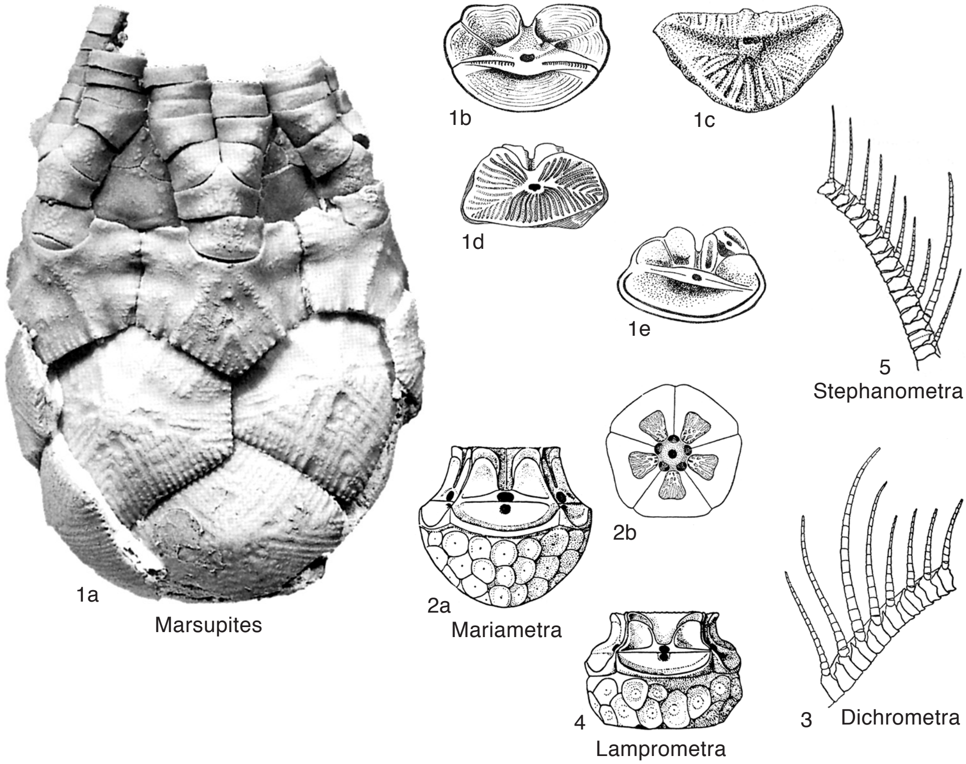

Fig. 50. Marsupitidae and Mariametridae (p. 97–102).

commonly large intervals in distal branches. Oral pinnules may be more or less carinate. One or more proximal pinnules, generally the first interior pinnule, absent in Colobometridae. Genital and distal pinnules not carinate, except for a trace on the proximalmost pinnulars. Ambulacral covering plates inconspicuous or absent. Mouth central. *Paleogene (Eocene)–Holocene.*

Family MARIAMETRIDAE A. H. Clark, 1909

[*nom. transl.* A. H. Clark, 1911e, p. 649, *ex* subfamily Mariametrinae A. H. Clark, 1909h, p. 176] [=Stephanometridae A. H. Clark, 1911e, p. 649, *nom. transl. ex* subfamily Stephanometrinae A. H. Clark, 1909h, p. 176]

Adoral side of centrodorsal described for species of *Mariametra* and *Lamprometra* with interradial ridges and with undivided coelomic impression in each radial area. Cirri of fewer than 40 ossicles, except in *Oxymetra* (up to 80). Radial articular facet steep, interarticular fossae large and high. Adoral muscle fossae low, curved along adoral edge and midradial furrow. Brachitaxes always of 2 ossicles joined by synarthry; usually fewer than 40 arms, except in *Oxymetra* (more than 40). Articular facets joining ossicles of proximal pinnules normally developed, except almost flat and featureless in *Stephanometra*. [Several genera are imperfectly distinguished on the basis of relative lengths of proximal 3 pinnules and require revision.] *Holocene.*

Mariametra A. H. Clark, 1909g, p. 144 [**Himerometra subcarinata* A. H. Clark, 1908b, p. 237; OD]. Brachitaxes in close lateral contact, laterally ornamented with small tubercles or spinules. Third pinnule longest and largest. *Holocene:* Indian Ocean, northern and western Pacific Ocean (sublittoral to upper bathyal).——Fig. 50,*2a–b*. **M. subcarinata* (A. H. Clark); *a,* cup with centrodorsal, enlarged (A. H. Clark, 1921 in 1915–1950, p. 26, fig. 47); *b*, proximal view of radial circlet, enlarged (A. H. Clark, 1915a in 1915–1950, p. 361, fig. 476).

Dichrometra A. H. Clark, 1909a, p. 12 [**Alecto flagellata* Müller, 1841, p. 186; OD; =*Alecto elongata* Müller, 1841, p. 187]. Brachitaxes separated laterally and smooth. Third pinnule longest and largest. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* Indian and western Pacific Ocean (littoral to sublittoral).——Fig. 50,*3. D. doederleini* (de Loriol, 1900); proximal pinnules, enlarged (A. H. Clark, 1921 in 1915–1950, p. 223, fig. 313).

Lamprometra A. H. Clark, 1913c, p. 143 [**Antedon imparipinna* Carpenter, 1882b, p. 505; OD; =*Alecto palmata* Müller, 1841, p. 185]. Cirri aborally carinate. Brachitaxes commonly in close lateral contact, unornamented laterally. Second pinnule longest and distinctly most robust. *Holocene:* Indian Ocean, western, central and southern tropical Pacific Ocean (littoral to sublittoral).——Fig. 50,*4. *L. palmata* (Müller); cup with centrodorsal, ×6 (A. H. Clark, 1921 in 1915–1950).

Liparometra A. H. Clark, 1913c, p. 143 [**Himerometra grandis* A. H. Clark, 1908k, p. 222; OD]. Cirri with aboral spine or carinate. Brachitaxes separated laterally and smooth. Second and third pinnules slender and of similar length. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (littoral to sublittoral).

Oxymetra A. H. Clark, 1909a, p. 13 [**Antedon erinacea* Hartlaub, 1890, p. 177; OD] [=*Selenemetra* A. H. Clark, 1911b, p. 541 (type, *Antedon finschii* Hartlaub, 1890, p. 176, OD)]. Cirri longer and with more ossicles than other mariametrids (usually at least 50); distal cirrals always with an aboral spine. [There is no suitable illustration available for the genus.] *Holocene:* northern Indian and western Pacific Ocean (littoral to sublittoral).

Pelometra A. H. Clark, 1941 in 1915–1950, p. 459 [**P. ambonensis;* OD]. Genital pinnules bearing prominent keel on some ossicles. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (sublittoral).

Stephanometra A. H. Clark, 1909a, p. 9 [**Antedon monacantha* Hartlaub, 1890, p. 179; OD; =*Comatula indica* Smith, 1876, p. 406; =*Antedon protectus* Lütken in Carpenter, 1879a, p. 19; =*Antedon marginata* Carpenter, 1888, p. 230; =*Antedon flavomaculata* Bell, 1894, p. 400; =*Himerometra heliaster* A. H. Clark, 1908g, p. 242; =*Himerometra acuta* A. H. Clark, 1908g, p. 242]. Cirri with aboral spine or carinate. Brachitaxes laterally separated, with brachials bearing rounded, adambulacral processes. Articular facets of proximal pinnules flat; one or more proximal pinnules enlarged, stiff and spikelike. [In their revision of the genus, Rankin and Messing (2008) recognized only 2 species, *S. tenuipinna* and *S. indica*.] *Holocene:* northern Indian and western Pacific Ocean (littoral to sublittoral).——Fig. 50,*5. *S. indica* (Smith); proximal pinnules, enlarged (A. H. Clark, 1921 in 1915–1950, p. 223, fig. 310).

Family COLOBOMETRIDAE
A. H. Clark, 1909

[Colobometridae A. H. Clark, 1909g, p. 145] [=Pontiometridae A. H. Clark, 1909h, p. 175]

Adoral side of centrodorsal in *Pontiometra* with several irregular, radiating, coelomic furrows, in *Cyllometra* with interradial ridges and a small radial pit. Some or all cirrals with aboral transverse ridge, commonly serrate or tuberculate, or transverse row of 2 or 3 tubercles or spines; distal (rarely all) spines single in many species. Radial articular facet steep, separated along interradial margin. Fulcral ridge in *Pontiometra* divided by narrow ligament. Interarticular ligament fossae moderate and triangular to large and high, separated by wide and shallow midradial furrow, except in *Cyllometra*, which has a narrow median ridge. Adoral muscle fossae small and vestigial to low, slightly curved along adoral margin; small and triangular in *Colobometra*; high in *Cyllometra*. Arms 10 to more than 80. Brachitaxes of 2 or 4 brachials (with syzygy between brachials 3 and 4); proximal brachials sometimes with lateral processes. One or more proximal pinnules, generally the first interior pinnule, may be absent. A few genera with pinnulars broadened over gonads on genital pinnules. *Holocene.*

Colobometra A. H. Clark, 1909a, p. 5 [**Antedon perspinosa* Carpenter, 1881d, p. 178; OD]. Proximal cirrals with distal aboral fringe of spines; middle and distal cirrals with paired spines. Arms 10. First interior pinnule present or absent. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* western Indian Ocean (littoral).——Fig. 51,*1. C. discolor* A. H. Clark; cup with centrodorsal, enlarged (A. H. Clark, 1921 in 1915–1950).

Alisometra A. H. Clark, 1947 in 1915–1950, p. 112 [**Colobometra* (*Prometra*) *owstoni* A. H. Clark, 1912a, p. 125] Cirrals as long as broad. Arms 10. Proximal, middle and distal pinnules similar, stiff and spinelike; pinnulars with everted and spinose distal ends. *Holocene:* Western Pacific Ocean (sublittoral).——Fig. 51,*2a–b. *A. owstoni* (A. H. Clark); holotype, Sagami Bay at 100 m, USNM 35631; *a,* proximal arm with pinnules; *b,* middle arm with pinnules, ×2 (A. H. Clark, 1921 in 1915–1950).

Analcidometra A. H. Clark, 1911g, p. 779 [**Oligometra caribbea* A. H. Clark, 1908b, p. 238; M]. Aboral spine flanked by pair of smaller spines on

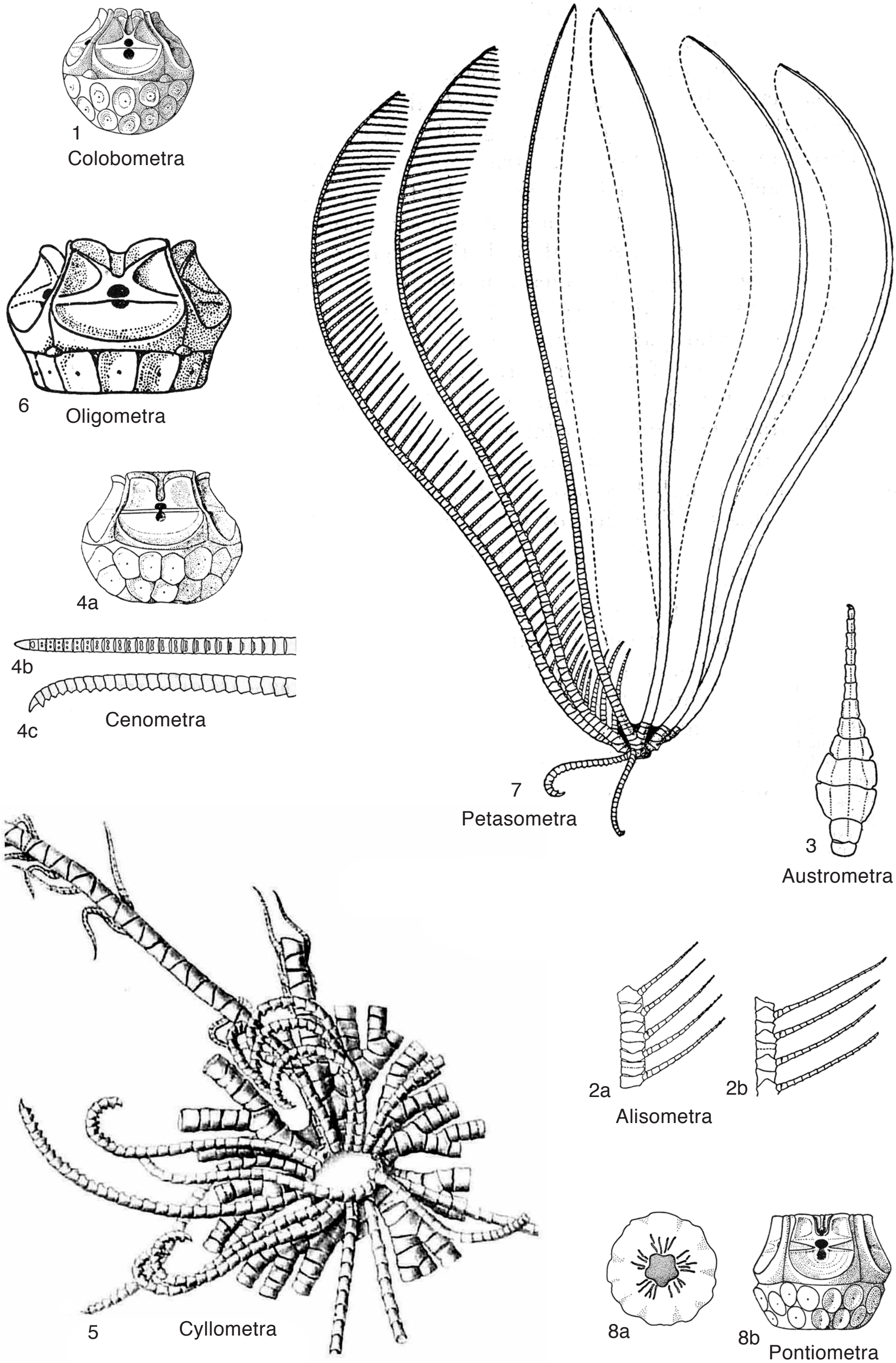

Fig. 51. Colobometridae (p. 102–105).

at least some distal cirrals. Arms 10. Pinnulars expanded over gonads. [There is no suitable illustration available for the genus.] *Holocene:* tropical western Atlantic Ocean (littoral to sublittoral).

Austrometra A. H. Clark, 1916a, p. 115 [**Oligometra thetidis* H. L. Clark, 1909, p. 522; OD]. Cirrals with aboral transverse ridge. Arms 10. Pinnulars expanded over gonads. *Holocene:* southern Pacific Ocean (sublittoral).——Fig. 51,*3.* **A. thetidis* (H. L. Clark); aboral view of genital pinnule, enlarged (A. H. Clark, 1921 in 1915–1950, p. 229, fig. 341).

Basilometra A. H. Clark, 1936b, p. 304 [**B. boschmai;* OD] [=*Rhadinometra* Gislén, 1936, p. 15 (type, *R. dawydovi* [=*B. boschmai*], OD)]. As many as 80 arms; first and third brachitaxes of 2 ossicles; second, fourth and more distal brachitaxes of 4 ossicles. At least first interior pinnule absent. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (littoral to sublittoral).

Cenometra A. H. Clark, 1909a, p. 8 [**Himerometra unicornis* A. H. Clark, 19081, p. 216; OD; =*Antedon bella* Hartlaub, 1890, p. 174; =*Antedon abotti* A. H. Clark, 1907d, p. 148; =*Cenometra delicata* A. H. Clark, 1909e, p. 398; =*Cenometra insueta* A. H. Clark, 1909g, p. 146]. As many as 40 arms; brachitaxes of 2 ossicles, with adambulacral flanges. Second pinnule large, stout, and curved. *Holocene:* Indian Ocean and western Pacific Ocean (littoral to sublittoral).——Fig. 51,*4a–c.* **C. bella* (Hartlaub); *a,* cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950); *b–c*, cirrus, *b,* aboral, *c,* lateral view, enlarged (A. H. Clark, 1915a in 1915–1950, p. 289, fig. 345).

Clarkometra Gislén, 1922, p. 142 [**C. elegans;* OD]. Cirri with aboral curved ridge becoming a single tubercle on distal segments. Arms 10. First exterior and interior pinnules absent. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (sublittoral).

Cotylometra A. H. Clark, 1916a, p. 116 [**Oligometra gracilicirra* A. H. Clark, 1908l, p. 221; OD]. Distal margin of all cirrals smooth; middle and distal cirrals with single aboral spine. Arms 10. First interior pinnule present or absent; second pinnule largest. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (sublittoral).

Cyllometra A. H. Clark, 1907f, p. 359 [**Antedon manca* Carpenter, 1888, p. 226; OD]. Adoral side of centrodorsal may have small radial pits. As many as 30 arms; all brachitaxes of 2 ossicles. First interior (and sometimes exterior) pinnule absent. Second pinnule larger than first. *Holocene:* western Pacific Ocean (sublittoral to bathyal).——Fig. 51,*5.* **C. manca* (Carpenter); aboral view of base of crown with centrodorsal and cirri, holotype, Kai Islands, Indonesia, at 255 m, ×3 (Carpenter, 1888, pl. 44,*3*).

Decametra A. H. Clark, 1911c, p. 31 [**D. moebius*; SD A. H. Clark, 1911g, p. 774] [=*Prometra* A. H. Clark, 1912c, p. 321 (type, *Colobometra chadwicki* A. H. Clark, 1911c, p. 30, OD)]. Proximal cirrals with transverse aboral ridge, becoming paired spines or single spine distally. Arms 10. First interior pinnule absent. Second pinnule rounded or rounded triangular in cross section (prismatic); distal ends of pinnulars uniformly spinose or smooth. [There is no suitable illustration available for the genus.] *Holocene:* Indian Ocean (littoral to sublittoral).

Embryometra Gislén, 1938b, p, 12 [**E. mortenseni;* OD]. Cirrals with distal aboral edge finely spinose. Arms 10. First interior and usually one or more other proximal pinnules absent. Pinnulars expanded over gonads. [There is no suitable illustration available for the genus.] *Holocene:* southeastern Atlantic Ocean (upper bathyal).

Epimetra A. H. Clark, 1911b, p. 542 [**E. nympha;* OD]. Cirrals with 1 or 2 median keels; opposing spine forked. As many as 40 arms; all brachitaxes of 2 ossicles. First interior (and sometimes exterior) pinnule absent. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (upper bathyal).

Gislenometra A. H. Clark, 1947 in 1915–1950, p. 57 [**G. perplexa*; OD]. Distal aboral border of distal cirrals finely serrate. Arms 10. First pinnule stout and stiff; pinnulars expanded over gonads. [There is no suitable illustration available for the genus.] *Holocene:* southwestern Indian Ocean (upper bathyal).

Iconometra A. H. Clark, 1929, p. 643 [**I. speciosa*; OD]. Aboral transverse ridge near proximal end of cirrals. Arms 10 to 21; all brachitaxes of 2 ossicles. All pinnules present; proximal 3 pinnules similar, stiff and composed of much elongated pinnulars. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (littoral to upper bathyal).

Oligometra A. H. Clark, 1908h, p. 126 [**Antedon serripinna* Carpenter, 1881d, p. 182; OD; =*O. pulchella* A. H. Clark, 1908k, p. 226; =*O. concinna* A. H. Clark, 1912c, p. 172]. Cirrals with transverse aboral ridge. Arms 10. First interior pinnule present or absent; second pinnule enlarged, stiff, prismatic, with distal ends of pinnulars produced as broad spine, flange, or tuft of spines. *Holocene:* western Pacific Ocean (littoral to sublittoral).——Fig. 51,*6.* **O. serripinna* (Carpenter); cup with centrodorsal, ×8 (Carpenter, 1888 in 1884–1888).

Oligometrides A. H. Clark, 1913d, p. 37 [**Comatula adeonae* Lamarck, 1816, p. 535; M; =*Antedon bidens* Bell, 1884, p. 158]. Distal cirrals with paired, transverse, aboral ridges. Arms 10. First pinnule largest. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific and eastern Indian Oceans (littoral to sublittoral).

Petasometra A. H. Clark, 1912h, p. 25 [**Antedon clarae* Hartlaub, 1890, p. 174; OD]. Cirri with aboral transverse ridge on proximal segments, becoming median spine distally. Arms 10 to 22; brachitaxes distal to primibrachials of 4 ossicles. First interior pinnule absent; first and second exterior pinnules similar. *Holocene:* western Pacific Ocean (littoral to sublittoral).——FIG. 51,*7*. **P. clarae* (HARTLAUB); lateral view, ×1 (A. H. Clark, 1921 in 1915–1950).

Pontiometra A. H. CLARK, 1907f, p. 354 [**Antedon andersoni* CARPENTER, 1889, p. 306; OD; =*P. inspertatus* A. H. CLARK, 1909e, p. 397]. Adoral side of centrodorsal with irregular, radiating, coelomic furrows. Cirri with as many as 80 cirrals; proximal cirrals with distal aboral spinose edge; middle cirrals with paired spines; distal cirrals with single spine. As many as 120 arms; all brachitaxes of 2 ossicles. First pinnule on exterior arms of a ray much longer than succeeding pinnules. *Holocene:* western Pacific Ocean (littoral to sublittoral).——FIG. 51,*8a–b*. **P. andersoni* (CARPENTER); *a,* adoral view of centrodorsal, ×3 (A. H. Clark, 1915a in 1915–1950, p. 255, fig. 261); *b*, cup with centrodorsal, ×3 (A. H. Clark, 1921 in 1915–1950).

Family EUDIOCRINIDAE A. H. Clark, 1907

[Eudiocrinidae A. H. CLARK, 1907f, p. 344]

Centrodorsal discoidal, aboral side flat, smooth, or rugose; cirrus sockets marginal, in 1 or 2 tiers; adoral side of centrodorsal without coelomic impressions. Radial articular facet gently sloping with rather shallow fossae; adoral muscle fossae crescentic, forming narrow band along adoral edge and midradial furrow. Rays 5, undivided. Syzygy between brachials 1 and 2 and 5 and 6, synarthry between brachials 3 and 4. First pinnule on brachial 2 interpreted as suppressed arm, as next pinnule is on brachial 4, corresponding to a second secundibrachial after a synarthrial articulation and succeeded by a syzygy between secundibrachials 3 and 4. *Holocene.*

Eudiocrinus CARPENTER, 1882b, p. 493, *nom. nov. pro Ophiocrinus* SEMPER, 1868, p. 68, *non* SALTER, 1856, *nec* ANGELIN, 1878 [**Ophiocrinus indivisus* SEMPER, 1868, p. 68; M; =*E. granulatus* BELL, 1894, p. 397]. Characters as for family. [The Lower Cretaceous *Pseudoantedon hiselyi* (DE LORIOL in DE LORIOL & GILLIÉRON, 1869) was referred by DE LORIOL in DE LORIOL and GILLIÉRON (1869) and DE LORIOL (1879 in 1877–1879) to this genus under the synonym *Ophiocrinus*, but there is no agreement in size of radials, in articulation of brachials, or in distribution of pinnules.] *Holocene:* Indian and western Pacific Ocean (sublittoral).——FIG. 52,*1*. **E. indivisus* (SEMPER); intact specimen, figured by BELL (1894) as *E. granulatus*, BMNH, ×1 (Bell, 1894).

Family HIMEROMETRIDAE A. H. Clark, 1908

[Himerometridae A. H. CLARK, 1908h, p. 135]

Centrodorsal discoidal to hemispherical; cirrus-free aboral apex broad and flat, depressed or deeply concave, small in juveniles; cirrus sockets in 1 to 3, rarely 4, irregular tiers, without distinct sculpturing except in *Discometra*, which may have lateral tubercles and marginal crenulae; adoral side of centrodorsal in extant genera with interradial ridges and paired, Y-shaped, or radiating coelomic furrows. Cirrals with aboral tubercle or spine in *Heterometra*, *Amphimetra*, and some species of *Himerometra,* but not in *Craspedometra* and *Homalometra*. Basal rosette but no rod-shaped basals, except in *Discometra* and in a fossil species referred to *Himerometra*. Radials with aboral exposed surface typically low or concealed midradially, more exposed in small species of *Amphimetra*; coelomic furrows on proximal surface of radials in extant genera, internal near proximal surface in *Discometra*. Radial articular facet moderately sloping to very steep; interarticular ligament fossae large and high; adoral muscle fossae low, curved along adoral edge and more or less continued along part of midradial furrow. Radial cavity large. Primibrachials united by synarthry; following brachitaxes of either 2 or 4 ossicles; syzygy between brachials 3 and 4. Brachials of undivided arms typically extremely low and disklike. One or more proximal pinnules enlarged, unknown in fossil species. *Paleogene (Eocene)–Holocene.*

Himerometra A. H. CLARK, 1907f, p. 355 [**Antedon crassipinna* HARTLAUB, 1890, p. 185; OD; =*Actinometra robustipinna* CARPENTER, 1881d, p. 201]. Centrodorsal low hemispherical to discoidal with concave to deeply depressed aboral apex. Cirrals with or without aboral spines. Adoral side of centrodorsal with Y-shaped coelomic furrows. As many as approximately 60 arms; ray bases narrow and well separated laterally. Secundibrachials and following brachitaxes typically of 4 ossicles, except inner tertibrachials commonly of 2 ossicles. Proximal pinnules much larger and thicker than those succeeding and sometimes carinate, decreasing in size from the proximalmost on secundibrachial 2. [Eocene *H. bassleri* GISLÉN (1934) differs in absence of coelomic furrows and presence of rod-shaped

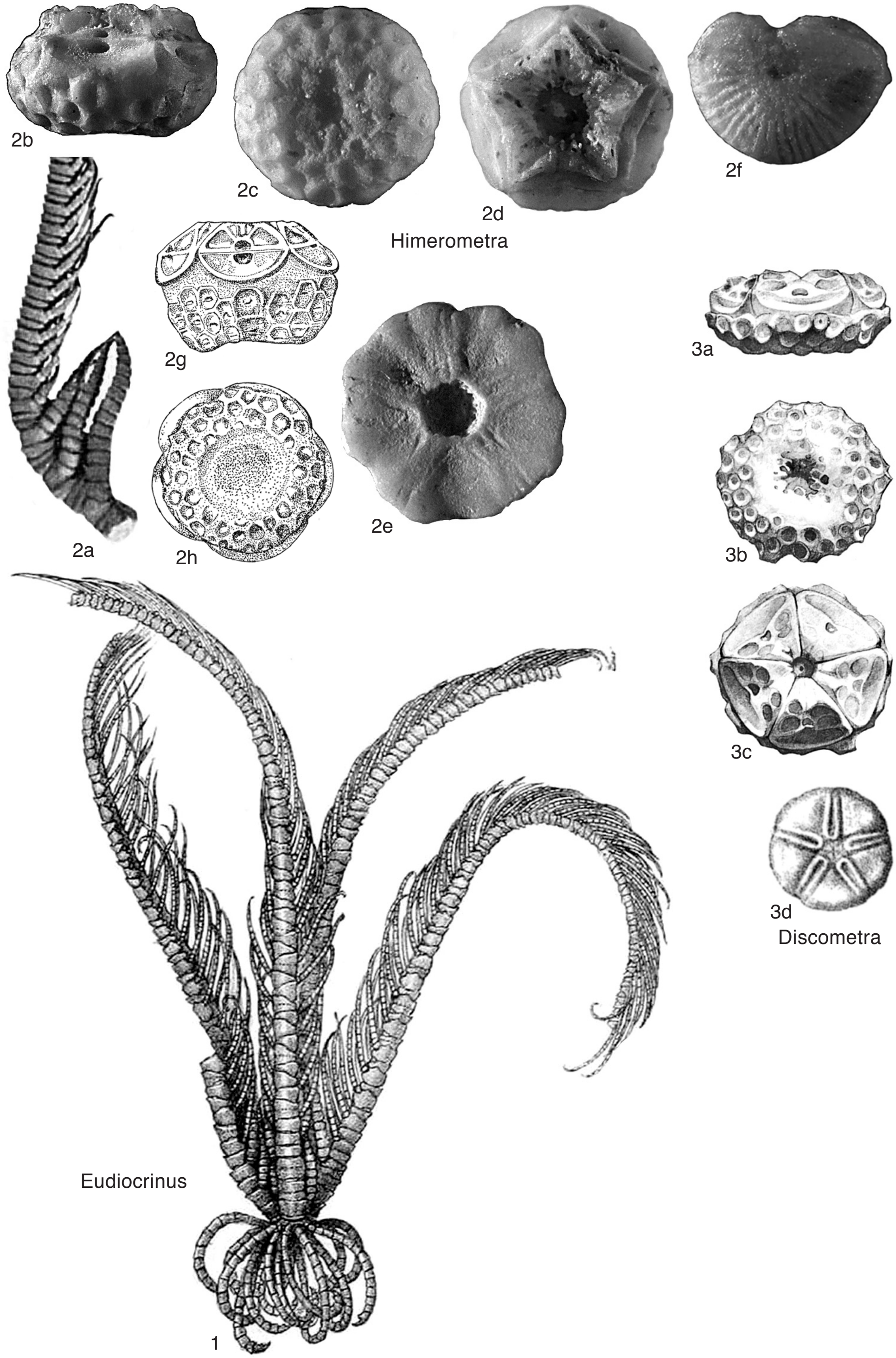

FIG. 52. Eudiocrinidae and Himerometridae (p. 105–107).

basals. In Oligocene *H. grippae,* basals and coelomic furrows are unknown.] *Paleogene (Eocene)–Holocene:* USA, Germany, *Eocene–Oligocene;* tropical western Pacific Ocean, Indian Ocean (littoral to sublittoral), *Holocene.*——Fig. 52,*2a.* **H. robustipinna* (Carpenter); arm with proximal pinnules; Sulu Archpelago at 16 m, holotype, USNM 25439, ×2 (A. H. Clark, 1941 in 1915–1950).——Fig. 52,*2b–f. H. bassleri* Gislén, 1934, Eocene, USA; *b–d,* cup with centrodorsal, *b*, lateral, *c*, aboral, *d*, distal, neotype herein, USNM 92074a, ×4.2 (Hess, new); *e*, adoral view of centrodorsal, paratype, USNM 92074b, ×4 (Hess, new); *f,* distal view of secundibrachial 3, paratype, USNM 92074c, ×10 (Hess, new).——Fig. 52,*2g–h. H. grippae* Anderson, 1967; cup with centrodorsal, *g*, lateral, *h*, aboral, Oligocene, Germany, holotype, GPI Kiel No. 2818, ×8 (Anderson, 1967).

Amphimetra A. H. Clark, 1909a, p. 6 [**Comatula (Alecto) milberti* Müller, 1846, p. 178; OD; =*Alecto tessellata* Müller, 1841, p. 184; =*Comatula jacquinoti* Müller, 1846, p. 178]. Centrodorsal low hemispherical to discoidal; adoral side with radiating coelomic furrows. Exposed surface of radials low, but higher in small species. Arms 10; rare individuals with more than 10 arms have secundibrachials of 2 ossicles. Proximal pinnules only slightly enlarged. *Holocene:* Indian and western Pacific Oceans (littoral to sublittoral).——Fig. 53,*1a.* **A. tessellata* (Müller); base of crown with cirri, Indonesia at 20 m, ×1.5 (Carpenter, 1888, as *Actinometra milberti,* pl. 35,*4*).——Fig. 53,*1b–c. A. ensifer* (A. H. Clark); *b,* cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950); *c*, proximal view of radial circlet, ×4 (A. H. Clark, 1915a in 1915–1950, p. 361).

Craspedometra A. H. Clark, 1909a, p. 8 [**Antedon acuticirra* Carpenter, 1882b, p. 509; OD; =*Antedon ludovici* Carpenter, 1882b, p. 510; =*Antedon australis* Carpenter, 1882b, p. 510; =*Antedon pinna* Carpenter, 1882b, p. 512]. Centrodorsal discoidal; adoral side with radiating coelomic furrows. Long stout cirri of as many as 60 cirrals tapering to sharp point. As many as 36 arms; secundibrachials of 4 ossicles; tertibrachials of 2 or 4 ossicles. *Holocene:* northern Indian and western Pacific Oceans (littoral to sublittoral).——Fig. 53,*2a–b.* **C. acuticirra* (Carpenter); *a,* cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950); *b*, adoral view of centrodorsal, ×4 (A. H. Clark, 1915a in 1915–1950, p. 253, fig. 255).

Discometra Gislén, 1924, p. 180 [**Eugeniacrinus*? *rhodanicus* Fontannes, 1877, p. 669; OD; ?=*Antedon meneghinianus* Fontannes, 1880, p. 415]. Centrodorsal low hemispherical with concave, cirrus-free aboral apex to discoidal and flattened or concave aborally; cirrus sockets with indistinct ridge or tubercles closely placed in 3 to 5 irregular tiers; adoral side with interradial ridges; central cavity less than 20 percent of centrodorsal diameter. Cirrals without aboral spines. No rod-shaped basal rays. Radial circlet lower and narrower than centrodorsal; radials with internal, Y-shaped coelomic canals close to proximal surface; interarticular ligament fossae rather large, separated by wide midradial area; radial cavity large. Syzygies present. *Neogene (Miocene):* Austria, France, Germany, Hungary, Italy, Algeria.——Fig. 52,*3a–d.* **D. rhodanica* (Fontannes); *a–c,* cup with centrodorsal, *a*, lateral, *b*, lower, *c*, distal, Hungary, ×6 (Vadász, 1915); *d*, proximal side of cup with coelomic canals, France, ×2.5 (de Loriol, 1897).

Heterometra A. H. Clark, 1909a, p. 11 [**Antedon quinduplicava* Carpenter, 1888, p. 262; OD; =*Antedon clemens* Carpenter, 1888, p. 229; =*Antedon anceps* Carpenter, 1888, p. 254] [=?*Alecto* Leach, 1815, p. 61 (type, *A. horrida,* SD A. H. Clark, 1908d, p. 449, =?*Comatula (Alecto) reynaudi* Müller, 1846, p. 178]. Centrodorsal hemispherical to discoidal with flat aboral apex; adoral side with radiating coelomic furrows in paired depressions. Arms 10 to 48; brachitaxes of 2 or 4 ossicles; ray bases separated or laterally apposed. Proximal pinnules increasing in length and stoutness to the third; pinnulars smooth, carinate or distally spinose or flanged. *Holocene:* Indian and western Pacific Oceans (littoral to sublittoral).——Fig. 53,*3a–b.* **H. quinduplicava* (Carpenter); *a,* aboral view of centrodorsal, ×5 (Carpenter, 1888); *b*, proximal view of radial circlet, ×5 (A. H. Clark, 1915a in 1915–1950, p. 359, fig. 470).

Homalometra A. H. Clark, 1918, p. 72 [**Antedon denticulata* Carpenter, 1888, p. 130; M]. Cirri small, slender, and tapering to a sharp point. Arms 10 or 11. *Holocene:* western Pacific Ocean (sublittoral).——Fig. 53,*4.* **H. denticulata* (Carpenter); base of crown with centrodorsal and 2 cirri, Caroline Islands, at 90 m, ×4 (Carpenter, 1888, pl. 22,*1*).

Family ZYGOMETRIDAE

A. H. Clark, 1908

[Zygometridae A. H. Clark, 1908h, p. 135]

Centrodorsal rather large, aboral side flattened or slightly concave, commonly with granulation, radiating furrows or obsolete cirrus sockets; adoral side smooth (*Catoptometra*) or with large, paired or V-shaped radial impressions (*Zygometra*); 1 to 4 marginal circles of sockets. Cirri smooth or with aboral spines; distal cirrals may be compressed or swollen at articulations. Radial articular facet rather flat, moderately sloping to almost vertical; adoral muscle fossae narrow, curved bands along adoral edge and midradial furrow. As many as 100 arms; primibrachials of 2 ossicles united by syzygy; secundibrachials and tertibrachials typically of 4 ossicles, syzygy between 3 and 4, tertibrachials commonly 2 in some species. *Holocene.*

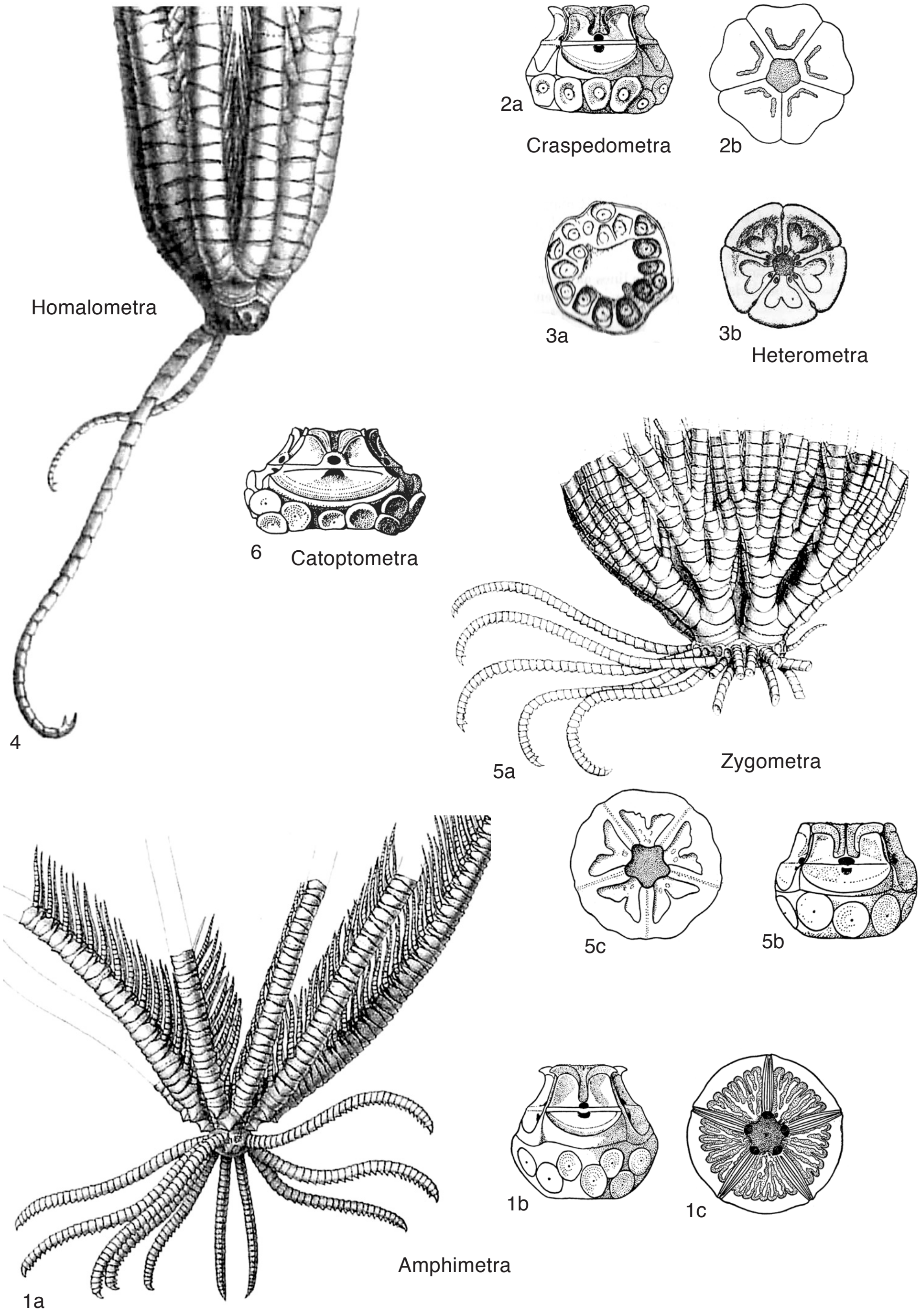

FIG. 53. Himerometridae and Zygometridae (p. 107–109).

Zygometra A. H. Clark, 1907f, p. 347 [**Antedon microdiscus* Bell, 1884, p. 163; OD] [=?*Hyponome* Lovén, 1869, p. 54 (type, *H. sarsi*, M), based on detached tegmen and visceral mass probably belonging to this species]. Distal cirrals short, with prominent aboral spine. *Holocene:* western Pacific Ocean, eastern Indian Ocean (littoral to sublittoral).——Fig. 53,*5a*. **Z. microdiscus* (Bell); base of crown with cirri, Torres Strait at 15 m, ×2 (Carpenter, 1888, pl. 37,*4*).——Fig. 53,*5b–c*. *Z. comata* A. H. Clark; *b,* cup with centrodorsal, ×6 (A. H. Clark, 1921 in 1915–1950); *c*, adoral view of centrodorsal, ×6 (A. H. Clark, 1915a in 1915–1950, p. 253, fig. 252).

Catoptometra A. H. Clark, 1908c, p. 317 [**Antedon hartlaubi* A. H. Clark, 1907c, p. 72; OD]. Distal cirrals little if at all shorter than proximal and without aboral spine; articulations swollen. *Holocene:* western Pacific Ocean (sublittoral to upper bathyal).——Fig. 53,*6*. **C. hartlaubi* (A. H. Clark); cup with centrodorsal, ×6 (A. H. Clark, 1921 in 1915–1950).

Superfamily TROPIOMETROIDEA A. H. Clark, 1908

[*nom. correct.* Hess & Messing, herein, *pro* Tropiometracea Rasmussen, 1978, p. 893, *nom. transl. ex* Tropiometridae A. H. Clark, 1908h, p. 135] [=Tropiometrida A. H. Clark, 1932b, p. 560, incl. Thalassometroida A. H. Clark, 1908j, p. 722; =Thalassometrida Gislén, 1924, p. 231, *nom. van.*]

Centrodorsal discoidal, pentagonal, hemispherical, conical, or columnar; centrodorsal cavity generally less than a third of centrodorsal diameter, except in very small specimens; aboral radial star, adoral radial pits, and subradial clefts present or absent; adoral surface typically with distinct, interradial grooves; aboral surface broad, flat, and cirrus-free to narrow and convex or conical; cirrus-free apex commonly rugose or tuberculate. Cirrus sockets large, without distinct ornament or with articular tubercles and in some genera with marginal crenulae; arranged in 10 or more (rarely 5) distinct columns or irregular and crowded. Cirrals with or without aboral spine. Rod-shaped basals present, with tips commonly exposed interradially. Radials with exposed aboral surface commonly low or concealed, but may be moderate to large and recumbent or overhanging; radial articular facet gently sloping to steep, almost vertical, high and almost triangular to low and wide, rarely broadly U-shaped; adoral muscle fossae low and wide to high and wide or narrow; radial cavity narrow to wide. Arms divided at primibrachial 2 and commonly at some or all secundibrachials 2 and tertibrachials 2, rarely at tetrabrachials 2, in some species at secundibrachials 4 and tertibrachials 4. Synarthry between brachials 1 and 2 may be flat or embayed, commonly narrow. Syzygy between brachials 3 and 4, rarely between brachials 1 and 2 of distal branches. Further syzygies with variable intervals through distal branches. Pinnulation complete. Pinnules distinctly prismatic, triangular in cross section with aboral keel (unknown in most fossil species). Distal pinnules extending beyond tip of arm. Ambulacral covering plates commonly distinct along pinnules. Mouth central. [Substantial variation in other features, plus the occurrence of similarly prismatic pinnules in several stalked taxa, suggest that this might be a polyphyletic group, a conclusion supported by recent preliminary molecular phylogenetic results (Rouse, Jermin, & Messing, 2006).] *Middle Jurassic (Callovian)–Holocene.*

Family TROPIOMETRIDAE A. H. Clark, 1908

[Tropiometridae A. H. Clark, 1908h, p. 135]

Centrodorsal large, thick discoidal to low columnar with large, flattened, cirrus-free aboral area. Cirrus sockets large, without distinct ornament, arranged irregularly around margin but tending to form 15 or 20 short columns. Cirri stout, rather short, without aboral spines. Cirrals 20 to 40, short, generally wider than long. Distal cirrals may be laterally compressed. No dorsal star. Shallow radial depressions at edge of centrodorsal cavity may be indicated. Rod-shaped basals not united around center, tapering outward and rarely exposed on surface. Exposed surface of radials low and outward sloping, or concealed. Radial articular facet steep and wide, meeting along interradial suture. Adoral muscle fossae large and wide, approximately twice as high as interarticular ligament fossae and separated from these by a ridge almost parallel to the fulcral ridge. Radial cavity wide; no central plug. Brachials wider than high. Primibrachial series of 2 ossicles, the first low and wide, and the second an axil; 10 arms only. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Syzygy between secundibrachials 3 and 4 and with intervals of generally 4 to 9 muscular articulations. Pinnules without distinct ambulacral covering plates. *Holocene.*

Tropiometra A. H. CLARK, 1907f, p. 349 [**Comatula carinata* LAMARCK, 1816, p. 535; OD; =?*Alecto carinata* LEACH, 1815, p. 63]. Characters as for family. *Holocene:* southern Atlantic Ocean, eastern Pacific Ocean, Indian Ocean (littoral to sublittoral).——FIG. 54,*1.* **T. carinata* (LAMARCK); cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950).

Family ASTEROMETRIDAE
Gislén, 1924

[Asterometridae GISLÉN, 1924, p. 231]

Centrodorsal small, 5-sided, low columnar to truncated subconical with cirrus-free, flattened, low conical to concave apex, commonly with 5 radial tubercles, which may have pits or canals that form a dorsal star. Large cirrus sockets without distinct ornament arranged in 10 vertical columns of 2 to 4 sockets, commonly separated by radial and interradial furrows or ridges. Adoral surface of centrodorsal similar to Notocrinidae with narrow but multiple, deep radial pits, which may form canals to dorsal star in juvenile specimens. Cirri long and slender; cirrals more than 50, sometimes laterally compressed with distal adoral projection or spine; some cirrals may be longer than wide; distal cirrals with aboral spine, except in *Sinometra*. Rod-shaped basals not united around centrodorsal cavity; tips exposed interradially. No subradial cleft. Radials exposed; articular facet moderately sloping, adoral muscle fossae steep, high, and narrow. Radial cavity narrow to moderate, with central plug. As many as 30 arms. Brachitaxes of 2 ossicles united by synarthry. Syzygies between brachials 3 and 4 and more distally at intervals of 5 to 12. Radials and proximal brachials commonly with a median ridge, distal brachials angular in section. Pinnules with distinct ambulacral covering plates. [Radials, brachials, and cirrals from the Pliocene of Indonesia have been referred to this family by SIEVERTS (1933b) without record of any genus or species. GISLÉN (1924) referred this family to Notocrinoidea, also having radial pits, but CLARK and CLARK (1967, p. 2) placed the family in Tropiometroidea.] *Holocene.*

Asterometra A. H. CLARK, 1907f, p. 358 [**Antedon macropoda* A. H. CLARK, 1907d, p. 136; OD]. Cirrals without constriction or distal projection. As many as 16 arms. Proximal pinnules shorter than distal pinnules. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* northwestern and western Pacific Ocean (sublittoral).——FIG. 54,*2. A. longicirra* (CARPENTER); centrodorsal, bases of several cirri and bases of 3 rays, Indonesia, MNHN EcCh 28, ×2 (Messing, Améziane, & Eléaume, 2000).

Pterometra A. H. CLARK, 1909h, p. 177 [**Ptilometra trichopoda* A. H. CLARK, 19081, p. 224; OD]. Proximal cirrals constricted with projecting distal margin commonly developed as adoral spine; proximal pinnules as long as or longer than distal pinnules. As many as 30 arms. [*Pterometra* may be congeneric with *Asterometra* (A. M. CLARK, 1972; YULIN, 1984).] *Holocene:* northwestern and western Pacific Ocean (littoral to sublittoral).——FIG. 54,*3a–b.* **P. trichopoda* (A. H. CLARK); *a*, adoral view of centrodorsal; *b*, aboral (proximal) view of radial circlet, ×6 (Gislén, 1924).——FIG. 54,*3c–e. P. pulcherrima* (A. H. CLARK); centrodorsal, *c*, adoral, *d*, aboral, *e*, lateral, ×4 (A. M. Clark, 1972).

Sinometra YULIN, 1984, p. 112 [**S. acuticirra;* OD]. Cirri exceedingly long, may be as long as arms; no opposing spines; terminal claw nearly straight or rudimentary; aboral surface of cirrals smooth. Arms 10. Proximal pinnules shorter than distal pinnules. *Holocene:* East China Sea (sublittoral).——FIG. 54,*4a–b.* **S. acuticirra*; *a,* cup with centrodorsal, holotype, IOAS-E00970, ×2; *b*, tip of cirrus, IOAS-E00969, ×5 (Yulin, 1984).

Family CALOMETRIDAE
A. H. Clark, 1911

[Calometridae A. H. CLARK, 1911e, p. 649]

Centrodorsal discoidal to low hemispherical with broad, flattened, cirrus-free aboral apex. No radial pits or subradial cleft. Dorsal star present only in *Kiimetra miocenica*. Large cirrus sockets without distinct sculpturing, crowded in 1 or 2 (rarely 3) irregular rows, commonly corresponding to 15 to 20 short, irregular columns. Cirrals short; distal cirrals with aboral ridge or spine. Tip

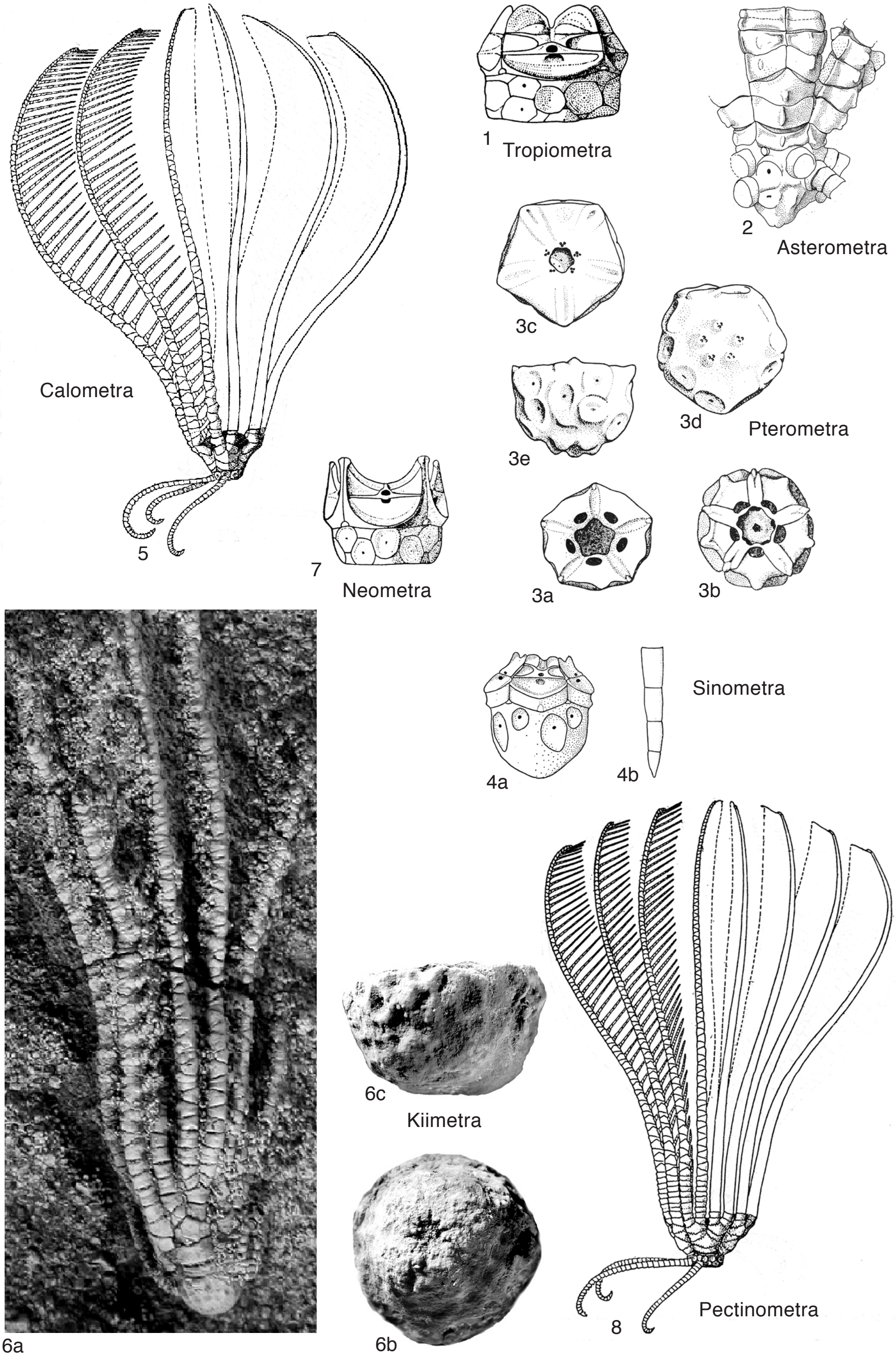

FIG. 54. Tropiometridae, Asterometridae, and Calometridae (p. 110–112).

of rod-shaped basals exposed interradially or concealed. Radials exposed or concealed, commonly with lateral margins visible and separating adjacent primibrachials. Radial articular facet crescent shaped, steep and wide, with muscle fossae reduced to thin, curved bands. Radial cavity very wide. Arms 10 to 40. Brachitaxes of 2 ossicles (except 4 in *Reometra*). Synarthry between brachials 1 and 2; syzygy between brachials 3 and 4 and more distally at intervals of 2 to 7. First pinnule delicate and weak but with first 2 segments enormously enlarged; following pinnules elongate, enlarged, stiffened, and composed of elongate pinnulars. Pinnules with distinct ambulacral covering plates. Disk globose, covered with a pavement of plates, and easily detached. *Neogene (Miocene)–Holocene.*

Calometra A. H. Clark, 1907f, p. 362 [**Antedon callista* A. H. Clark, 1907d, p. 135; OD]. Arms 10 to 15. Secundibrachials of 2 ossicles. Radials separating adjacent primibrachials narrowly or not at all. Second and following pinnules short, subequal. *Holocene:* northwestern and western Pacific Ocean (sublittoral to upper bathyal).——Fig. 54,*5.* **C. callista* (A. H. Clark); lateral view, ×1 (A. H. Clark, 1921 in 1915–1950).

Gephyrometra A. H. Clark, 1912c, p. 184 [**Antedon versicolor* A. H. Clark, 1907d, p. 132; OD]. Radials separating adjacent primibrachials very narrowly or not at all. As many as 20 arms. Secundibrachials of 2 ossicles. Brachitaxes distal to first primibrachial widely separated; ossicles without lateral extensions. Second and third pinnules longer than genital pinnules. [There is no suitable illustration available for the genus.] *Holocene:* northwestern Pacific Ocean (littoral to sublittoral).

Kiimetra Shibata & Oji, 2007, p. 397 [**K. miocenica;* OD]. Centrodorsal hemispherical with dorsal star; cirrus sockets arranged in 2 or 3 irregular rows. Cirri stout and as long as arms. Arms 10 to 20 (averaging 15). Aboral surface of brachials smooth. *Neogene (Miocene):* Japan.——Fig. 54,*6a–c.* **K. miocenica*; *a,* lateral view of holotype, NSM PA 15492-110, ×2.5; *b*, aboral view of centrodorsal, paratype, NSM PA 15488, ×6; *c*, lateral view of centrodorsal, paratype, NSM PA 15492-110, ×2.5 (Shibata & Oji, 2007).

Neometra A. H. Clark, 1912c, p. 181 [**Antedon multicolor* A. H. Clark, 1907d, p. 130; OD]. Radials separating adjacent primibrachials widely. As many as 40 arms. All brachitaxes of 2 ossicles. Brachitaxes distal to primibrachial 1 widely separated; ossicles without lateral extensions. Second and third pinnules longer than genital pinnules. [A. H. Clark (1947 in 1915–1950, p. 355) distinguished *Neometra* from *Gephyrometra* by broad, interradial extensions of the radials, separating the bases of adjacent first primibrachials. In contrast, in *Gephyrometra,* the extensions are undeveloped or narrow, and the bases of adjacent first primibrachials meet distal to them. However, several specimens of *N. multicolor*, including the holotype, have very narrow interradial extensions, and adjacent first primibrachials are barely separated (Messing, Améziane, & Eléaume, 2000, p. 647). Thus, the genus requires revision.] *Holocene:* eastern Indian Ocean, northwestern and western Pacific Ocean (sublittoral to upper bathyal).——Fig. 54,*7.* **N. multicolor* (A. H. Clark); cup with centrodorsal, ×5 (A. H. Clark, 1921 in 1915–1950).

Pectinometra A. H. Clark, 1912c, p. 185 [**Antedon flavopurpurea* A. H. Clark, 1907d, p. 134; OD] [=*Pectiometra* Gislén, 1924, p. 54, *nom. null.*]. Radials not separating adjacent brachitaxes. Arms 15 to 20. All brachitaxes of 2 ossicles. Adjacent brachitaxes apposed, either directly or via lateral extensions. Proximal pinnules longer than genital pinnules. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* eastern Indian Ocean, northwestern and western Pacific Ocean (sublittoral to upper bathyal).——Fig. 54,*8. P. carduum* (A. H. Clark); lateral view, ×1 (A. H. Clark, 1921 in 1915–1950).

Reometra A. H. Clark, 1934b, p. 14, *nom. nov. pro Oreometra* A. H. Clark, 1912c, p. 179, *non* Aurivillius, 1910 [**Oreometra mariae* A. H. Clark, 1912c, p. 179; OD]. As many as 17 arms. Primibrachials united by close synarthry. Secundibrachials of 4 ossicles with 3 and 4 united by syzygy (exceptionally secundibrachials of 3 ossicles with 2 and 3 united by syzygy). Cirrus sockets encroach on exposed surface of radials. [There is no suitable illustration available for the genus.] *Holocene:* southwestern Pacific Ocean (sublittoral).

Family CHARITOMETRIDAE
A. H. Clark, 1909

[*nom. transl.* A. H. Clark, 1911g, p. 728, *ex* subfamily Charitometrinae A. H. Clark, 1909a, p. 2]

Centrodorsal hemispherical, conical, or truncated conical to discoidal with rounded or flattened, cirrus-free, commonly rugose or tuberculate aboral apex; some species of *Monachometra* with a dorsal star. No adoral radial pits. Cirrus sockets commonly with distinct articular tubercles and, in some genera, with marginal crenulae; sockets large, irregularly crowded or in 10 to 15 distinct columns (5 or 10 in *Chondrometra*). Cirri short and stout. Cirrals commonly fewer than 25, cylindrical or laterally compressed, without aboral spines, but sometimes carinate or with low distal tubercle. Rod-shaped

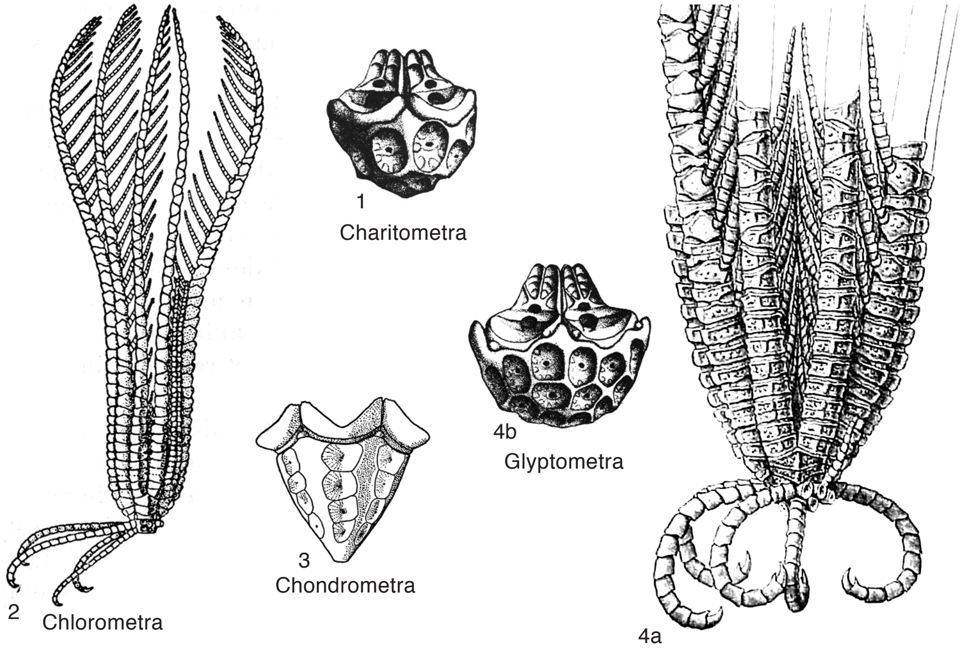

FIG. 55. Charitometridae (p. 113–115).

basals exposed interradially or concealed. Subradial cleft commonly present. Radials concealed or narrowly exposed. Radial articular facet moderately sloping, not angularly bent. Muscle fossae high and narrow. Radial cavity narrow. Arms 10 to 33. Synarthry between brachials 1 and 2, syzygy between brachials 3 and 4, or between 1 and 2 in distal branches, and at intervals of 2 to 26 (commonly 6 to 11) distally. Arms aborally rounded or laterally compressed and carinate, commonly with rugose or tuberculate surface. First and second pinnules slender, with numerous short pinnulars. Genital pinnules may have segments broadened and covering gonad. Pinnules with distinct ambulacral covering plates. [Examination of some type material suggests that generic boundaries may need to be reevaluated.] *Holocene.*

Charitometra A. H. CLARK, 1907f, p. 360 [**Antedon incisa* CARPENTER, 1888, p. 124; OD]. Centrodorsal hemispherical; cirrus sockets in irregular marginal rows; sockets with marginal crenulae. Arms 10. Brachitaxes and proximal brachials in close contact and flattened laterally. Genital pinnule segments greatly expanded over gonad. *Holocene:* southern Pacific Ocean (bathyal).——FIG. 55,*1*. **C. incisa* (CARPENTER); cup with centrodorsal, ×4 (Carpenter, 1888).

Chlorometra A. H. CLARK, 1909a, p. 21 [**Antedon garrettiana* A. H. CLARK, 1907d, p. 142; OD] [=*Diodontometra* GISLÉN, 1922, p. 121 (type, *D. bocki,* M)]. Centrodorsal sharply conical with cirri in 5 columns of 1 or 2 each. Opposing spine on cirri forked. Arms 14 to 20. Secundibrachials of 2 ossicles. Genital pinnule segments expanded over gonad. *Holocene:* northwestern Pacific Ocean (sublittoral).——FIG. 55,*2*. **C. garrettiana* (A. H. CLARK); lateral view, ×1 (A. H. Clark, 1921 in 1915–1950).

Chondrometra A. H. CLARK, 1916b, p. 608 [**Chlorometra robusta* A. H. CLARK, 1911b, p. 558; OD]. Centrodorsal conical or truncated with cirrus sockets in 5 to 10 columns. Arms 10. Distal brachials laterally compressed and carinate. Genital pinnule segments not expanded over gonad. *Holocene:* western Pacific Ocean, western Indian Ocean (bathyal).——FIG. 55,*3*. **C. robusta* (A. H. CLARK); cup with centrodorsal, ×3 (A. H. Clark, 1915a in 1915–1950).

Crinometra A. H. CLARK, 1909a, p. 22 [**Comatula brevipinna* POURTALÈS, 1868, p. 111; OD]. Centrodorsal hemispherical to discoidal, aboral apex generally tuberculate. Cirrus sockets irregularly arranged but tending to form 10 or 15 columns. As many as 32 arms. Secundibrachials and following brachitaxes of 2 or 4 ossicles. Brachials aborally

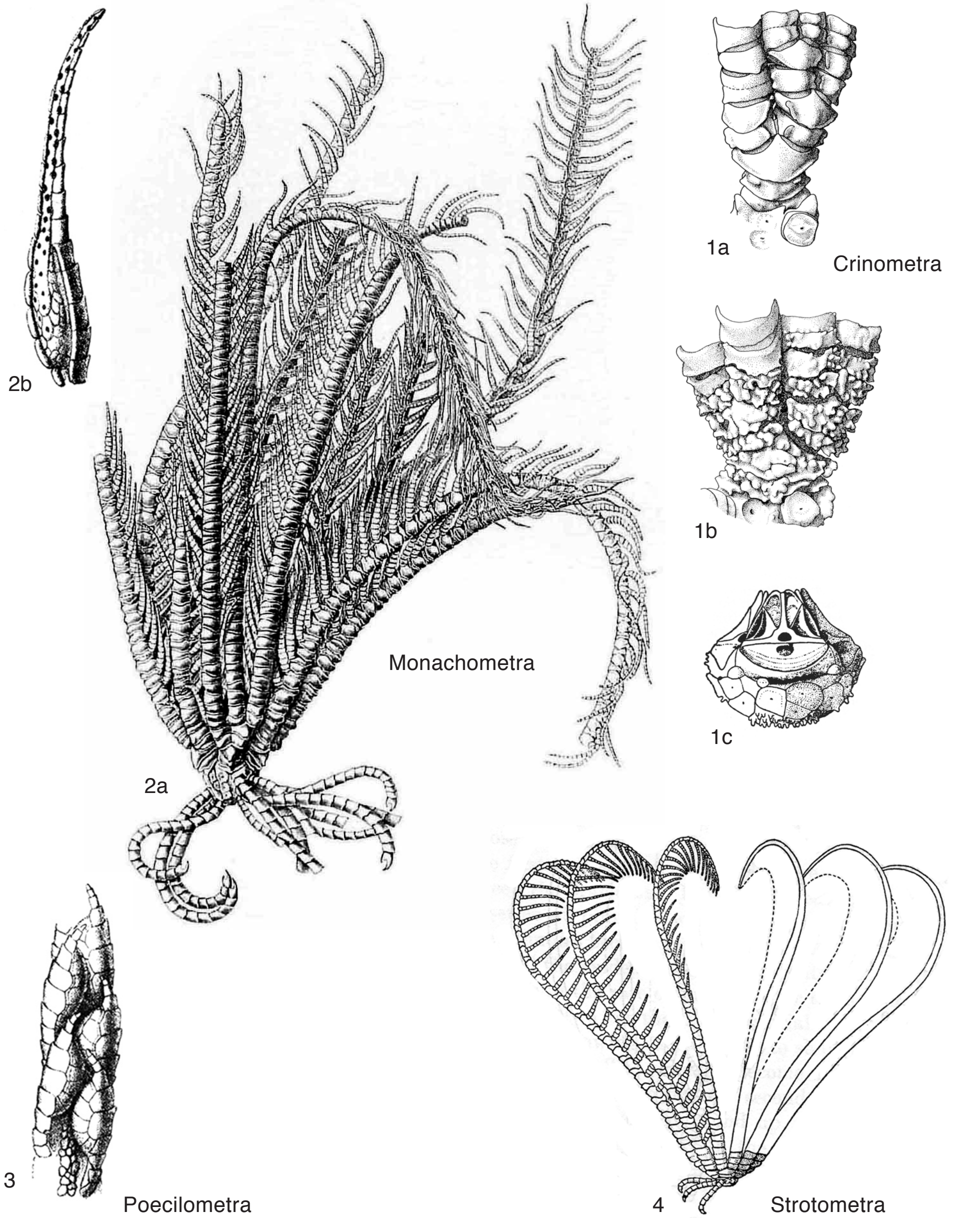

Fig. 56. Charitometridae (p. 113–115).

rounded. Oral pinnules markedly longer than following pinnules. Genital pinnules tapering from broadened proximal segments to slender tip. *Holocene:* western Atlantic Ocean (sublittoral to upper bathyal).——Fig. 56,*1a–c*. *_C. brevipinna_ (Pourtalès); *a,* arm base and proximal arms of weakly sculptured specimen, enlarged; *b*, part of centrodorsal and arm bases of heavily sculptured specimen, enlarged (Messing, 1997); *c*, cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950).

Glyptometra A. H. Clark, 1909a, p. 18 [*_Antedon tuberosa_ Carpenter, 1888, p. 126; OD] [=*Pachylometra* A. H. Clark, 1909a, p. 20 (type, *Antedon distincta* Carpenter, 1888, p. 247, OD); =*Crossometra* A. H. Clark, 1916b, p. 606 (type, *Pachy-*

lometra investigatoris A. H. CLARK, 1909b, p 82, OD); =*Calyptometra* A. H. CLARK, 1916b, p. 608 (type, *Charitometra lateralis* A. H. CLARK, 1908b, p. 226, OD)]. Centrodorsal hemispherical or truncated conical. Cirrus sockets irregularly arranged but tending to form 10 or 15 columns. Sockets commonly with marginal crenulae. As many as 33 arms. Secundibrachial and following brachitaxes of 2 or 4 ossicles. Brachials aborally rounded with ossicles ornamented or not. Oral pinnules little or not longer than following pinnules. Genital pinnules tapering from broadened proximal segments to slender tip. *Holocene:* Indian and western Pacific Oceans (littoral to sublittoral).——FIG. 55,*4a.* **G. tuberosa* (CARPENTER); proximal part of crown with cirri, Philippines at 686 m, holotype, ×2.5 (Carpenter, 1888, pl. 23,*2*).——FIG. 55,*4b. G. inaequalis* (CARPENTER); cup with centrodorsal, ×4 (Carpenter, 1888).

Monachometra A. H. CLARK, 1916b, p. 607 [**Pachylometra fragilis* A. H. CLARK, 1912g, p. 79; OD] [=*Perissometra* A. H. CLARK, 1916b, p. 606 (type, *Antedon flexilis* CARPENTER, 1888, p. 217, OD)]. Centrodorsal discoidal, conical, hemispherical or columnar. Cirrus sockets in 10 or 15 columns. As many as 21 arms. Secundibrachials all 2. Brachitaxis ossicles rise to prominent, narrow, synarthrial tubercles. Genital pinnules tapering from broadened proximal segments to slender tip. *Holocene:* western Pacific Ocean (sublittoral to bathyal).——FIG. 56,*2a.* **M. flexilis* (CARPENTER); complete specimen, Kai Islands Indonesia at 256 m, ×1.5 (CARPENTER, 1888, pl. 42).——FIG. 56,*2b. M. angusticalyx* (CARPENTER); genital pinnule, enlarged (A. H. Clark, 1921 in 1915–1950).

Poecilometra A. H. CLARK, 1907f, p. 361 [**Antedon acoela* CARPENTER, 1888, p. 132; OD]. Centrodorsal hemispherical or discoidal. Cirrus sockets in irregular marginal rows. Arms 10. Brachitaxes and proximal brachials narrow and well separated by gaps bridged by lateral flanges. Genital pinnule segments expanded over gonad. *Holocene:* western Pacific Ocean (bathyal).——FIG. 56,*3.* **P. acoela* (CARPENTER); genital pinnules, enlarged (A. H. Clark, 1921 in 1915–1950).

Strotometra A. H. CLARK, 1909a, p. 19 [**Antedon hepburniana* A. H. CLARK, 1907d, p. 139; OD]. Centrodorsal hemispherical or discoidal. Cirrus sockets in irregular marginal rows. Cirri with not more than 15 segments. Arms 10. Rays extend outward from oral-aboral axis. Genital pinnule segments expanded over gonad. *Holocene:* northwestern and western Pacific Ocean (sublittoral to upper bathyal).——FIG. 56,*4.* **S. hepburniana* (A. H. CLARK); lateral view, ×1 (A. H. Clark, 1921 in 1915–1950).

Family CONOMETRIDAE Gislén, 1924

[Conometridae GISLÉN, 1924, p. 159]

Centrodorsal conical or truncated conical to hemispherical with or without rounded or flattened aboral apex. No dorsal star or radial pits. Cirrus sockets without distinct ornament or with feeble articular tubercles. Sockets arranged in 10, exceptionally 15, distinct columns of 3 to 6 sockets, increasing in size toward the base, and commonly separated by radial or interradial spaces or ridges. Centrodorsal cavity narrow, 20 to 30 percent of centrodorsal diameter or larger in very small specimens. Rod-shaped basals exposed interradially or concealed. Radials generally exposed. Radial articular facet generally high, with high and narrow adoral muscle fossae surrounding narrow radial cavity but may be lower and wider with rather low and wide muscle fossae and with radial cavity funnel shaped, strongly widened at adoral edge. [This family includes fossil genera resembling modern Tropiometroidea in the form of centrodorsal and radials and in arrangement of cirrus sockets. Pinnules are unknown.] *Upper Cretaceous (Cenomanian)–Neogene (Miocene).*

Conometra GISLÉN, 1924, p. 166 [**Alecto alticeps* PHILIPPI, 1844, p. 540; OD]. Similar to *Amphorometra* but with 15 distinct columns of 4 or 5 cirrus sockets, or crowded, commonly 20 columns. Centrodorsal high conical. Basals not exposed. No subradial cleft. Adoral muscle fossae moderate to high. Radial cavity narrow. *Paleogene (Eocene)–Neogene (Miocene):* Italy, Hungary.——FIG. 57,*1a.* **C. alticeps* (PHILIPPI); cup with centrodorsal, Eocene, Italy, ×5 (Rasmussen, 1978).——FIG. 57,*1b–d. C. hungarica* (VADÁSZ, 1915); cup with centrodorsal, *b*, lateral, *c*, lower (aboral), *d*, distal, Miocene, Hungary, ×10 (Vadász, 1915).

Amphorometra GISLÉN, 1924, p. 159 [**Glenotremites conoideus* GOLDFUSS, 1840 in 1826–1844, p. 286; OD]. Centrodorsal conical or slightly truncated conical. Centrodorsal cavity 20 to 30 percent of centrodorsal diameter, as much as 50 percent in very small specimens, with overhanging edge. Cirrus sockets with narrow axial canal and indistinct fulcral ridge, but no marginal crenulae, in 10 distinct columns. Proximal cirrals short, smooth, wider than long, elliptical in section, not carinate. Rod-shaped basals exposed interradially or concealed. Subradial cleft usually present. Radials generally exposed. Radial articular facet high, rather flat and steep. Adoral muscle fossae high and narrow, separated from interarticular ligaments by oblique ridge. Radial cavity narrow. *Upper Cretaceous (Cenomanian)–Paleogene (Danian):* Czech Republic, Denmark, England, Germany, Netherlands, Tunisia.——FIG. 57,*2.* **A. conoidea* (GOLDFUSS); lateral view of cup with centrodorsal

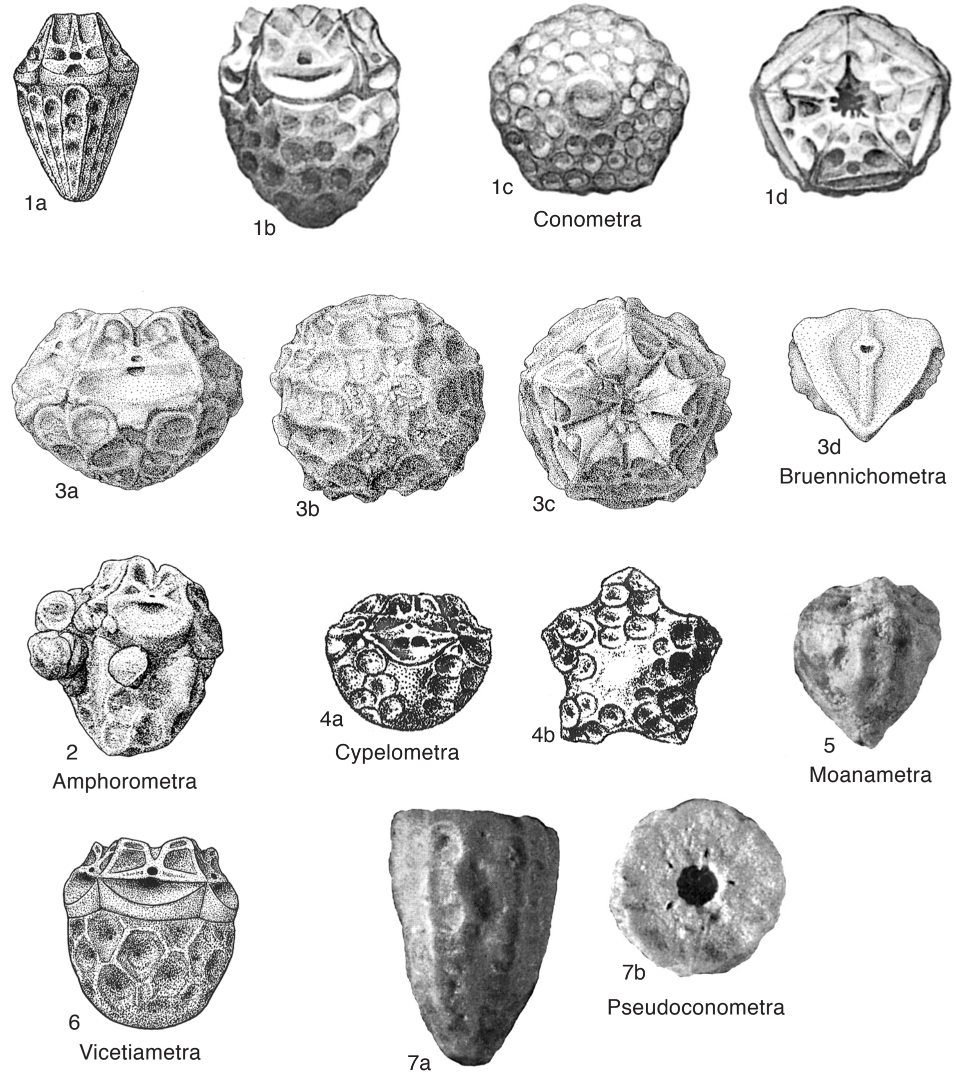

FIG. 57. Conometridae and Pseudoconometridae (p. 115–117).

and cirrals, Maastrichtian, Denmark, MGUH 8990, ×5.5 (Rasmussen, 1961).

Bruennichometra RASMUSSEN, 1961, p. 339 [**Antedon danica* NIELSEN, 1913, p. 100; OD]. Centrodorsal truncated conical to hemispherical with a flattened, cirrus-free, rugose or granulated aboral apex. Centrodorsal cavity narrow, 20 to 30 percent of centrodorsal diameter, relatively smaller in large specimens. Large cirrus sockets with fulcral ridge or tubercles but no marginal crenulae, in 10 columns of 1 to 3 sockets. Rod-shaped basals concealed, united around center. No subradial cleft. Radials with little or no exposed surface. Edge of radial may project aborally in midradial area between basal cirrus sockets. Radial articular facet flat, low, wide, steep, almost vertical. Adoral muscle fossae similar to interarticular ligament fossae or smaller, with adoral edge wide, slightly curved with a shallow median incision. Muscle fossae separated from ligament fossae by diagonal or almost horizontal ridge. Radial cavity funnel shaped, narrow, but greatly expanded at top. Proximal brachials smooth or granulated, commonly with median crest. Synarthry between primibrachials 1 and 2; primibrachial 2 an axil. Adjacent first primibrachials joined laterally. Distal brachials with muscular and syzygial articulations. *Paleocene (Danian):* Denmark.——FIG. 57,*3a–d*. **B. danica* (NIELSEN); *a–c,* cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, MGUH 8992, ×7; *d*, distal view of primibrachial 1, MGUH 8993, ×7 (Rasmussen, 1961).

Cypelometra Gislén, 1924, p. 159 [**Antedon iheringi* de Loriol, 1902 in 1902–1904, p. 22; OD]. Centrodorsal hemispherical to subconical, aborally rounded. Cirrus sockets with indistinct articular tubercles, in 10 columns of 3 or 4 sockets well separated by a slightly vermiculate radial area. Rod-shaped basal rays commonly concealed but may be exposed interradially. Centrodorsal cavity small. Radials with very low exposed surface or concealed. Radial articular facet gently sloping. Interarticular ligament fossae rather small to moderate. Adoral muscle fossae similar in size, separated by midradial ridge. Radial cavity moderate to rather small. *Neogene (Miocene):* Argentina.——Fig. 57,*4a–b*. **C. iheringi* (de Loriol); cup with centrodorsal, *a*, lateral, *b*, aboral, ×1.6 (Rasmussen, 1978).

Moanametra Eagle, 2001, p. 87 [**M. torehinaensis*; M]. Centrodorsal arched conical with cirrus-free aboral apex. Cirri in 15 columns of 2 to 4 sockets. Basals concealed. Radial circlet 25 percent height of centrodorsal. Radial articular facet low, wide. [Genus and species are based on a single specimen. It seems very similar to species of *Amphorometra*.] *Paleogene (Oligocene):* New Zealand.——Fig. 57,*5*. **M. torehinaensis*; cup with centrodorsal, holotype, AK 72848, ×3 (Eagle, 2001).

Vicetiametra Malaroda, 1950, p. 6 [**V. albertinii*; OD]. Centrodorsal hemispherical to truncated subconical; aborally rounded, cirrus-free, slightly rugose. Cirrus sockets large, without distinct ridge or ornament, irregularly arranged, more or less forming 15 columns of 1 or 2 sockets. Basals not exposed. Exposed surface of radials low. Radial articular facet low, wide, rather steep. Interarticular ligament fossae large. Adoral muscle fossae very low, forming narrow bands along adoral edge. Midradial furrow present. Radial cavity large. *Paleogene (Eocene):* Italy.——Fig. 57,*6*. **V. albertinii*; cup with centrodorsal, ×5 (Rasmussen, 1978).

Family PSEUDOCONOMETRIDAE Eagle, 2001

[Pseudoconometridae Eagle, 2001, p. 83]

Centrodorsal conical; adoral face circular with 5 radial pits and 5 indistinct basal furrows. Aboral apex with large, cirrus-free area; no dorsal star. Cirri in 15 columns of 7 to 10 circular sockets without ornament, with large circular axial canal; rows of sockets separated by smooth ridges. [The family was proposed by Eagle (2001) for a single genus based on a single centrodorsal. It is mainly based on the presence of 5 radial pits on the adoral surface of the centrodorsal.] *Paleogene (Oligocene).*

Pseudoconometra Eagle, 2001, p. 83 [**P. coromandelensis*; M]. Characters as for family. *Paleogene (Oligocene):* New Zealand.——Fig. 57,*7a–b*. **P. coromandelensis*; centrodorsal, *a*, lateral, *b*, adoral, holotype, AK 72847, ×5 (Eagle, 2001).

Family PTEROCOMIDAE Rasmussen, 1978

[Pterocomidae Rasmussen, 1978, p. 894]

Centrodorsal very small, conical, or truncated conical to low columnar or discoidal, commonly with a large, rounded or flattened, smooth aboral apex. No dorsal star; no radial pits in adoral surface of centrodorsal. Centrodorsal cavity narrow, 20 to 30 percent of centrodorsal diameter. Few large cirrus sockets, 1 to 3 in each radial area. Sockets without distinct ornament or with articular tubercles and marginal crenulae. Rod-shaped basals exposed interradially or concealed, united around central cavity. No subradial cleft. Radials with greatly overhanging, almost horizontal, smooth exposed surface. Radial articular facet wide and high, almost parallel to oral-aboral axis. Adoral muscle fossae large, separated from interarticular ligament by slightly oblique ridge. Adoral edge wide, concave, with or without a median incision. Radial cavity large and wide. Arms long, with slender brachials and long pinnules. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2; syzygy between secundibrachials 3 and 4. *Middle Jurassic (Callovian)–Paleogene (Danian).*

Comaturella Münster, 1839, p. 85 [**Ophiurites pennatus* von Schlotheim, 1820, p. 326; M; =*Comatula pinnata* Goldfuss, 1831 in 1826–1844, p. 203; =*Comaturella wagneri* Münster, 1839, p. 85] [=*Pterocoma* Agassiz, 1836, p. 193, obj., *non* Dejean, 1833–1836, p. 178, *nom. nud.*, *nec* Solier, 1836, p. 42; =*Comatulithes* von Schlotheim, 1823 in 1822–1823, p. 47, name not available (ICZN, 1999, *Code*, Art. 20), used in combination *C. mediterraneaeformis pro Ophiurites pennatus* von Schlotheim, 1820, p. 326, =*Asteriatites pennatus*, obj.]. Centrodorsal discoidal, less than 2 mm in diameter. Ten cirrus sockets in a single marginal row. Centrodorsal cavity approximately 30 percent of centrodorsal diameter. No radial pits. Cirri tapering to a point, up to 25 mm, slender, with approximately 25 long cirrals without aboral spines; no opposing spine. Distal cirrals very long, slender, and laterally compressed, 2 to 3 times longer than

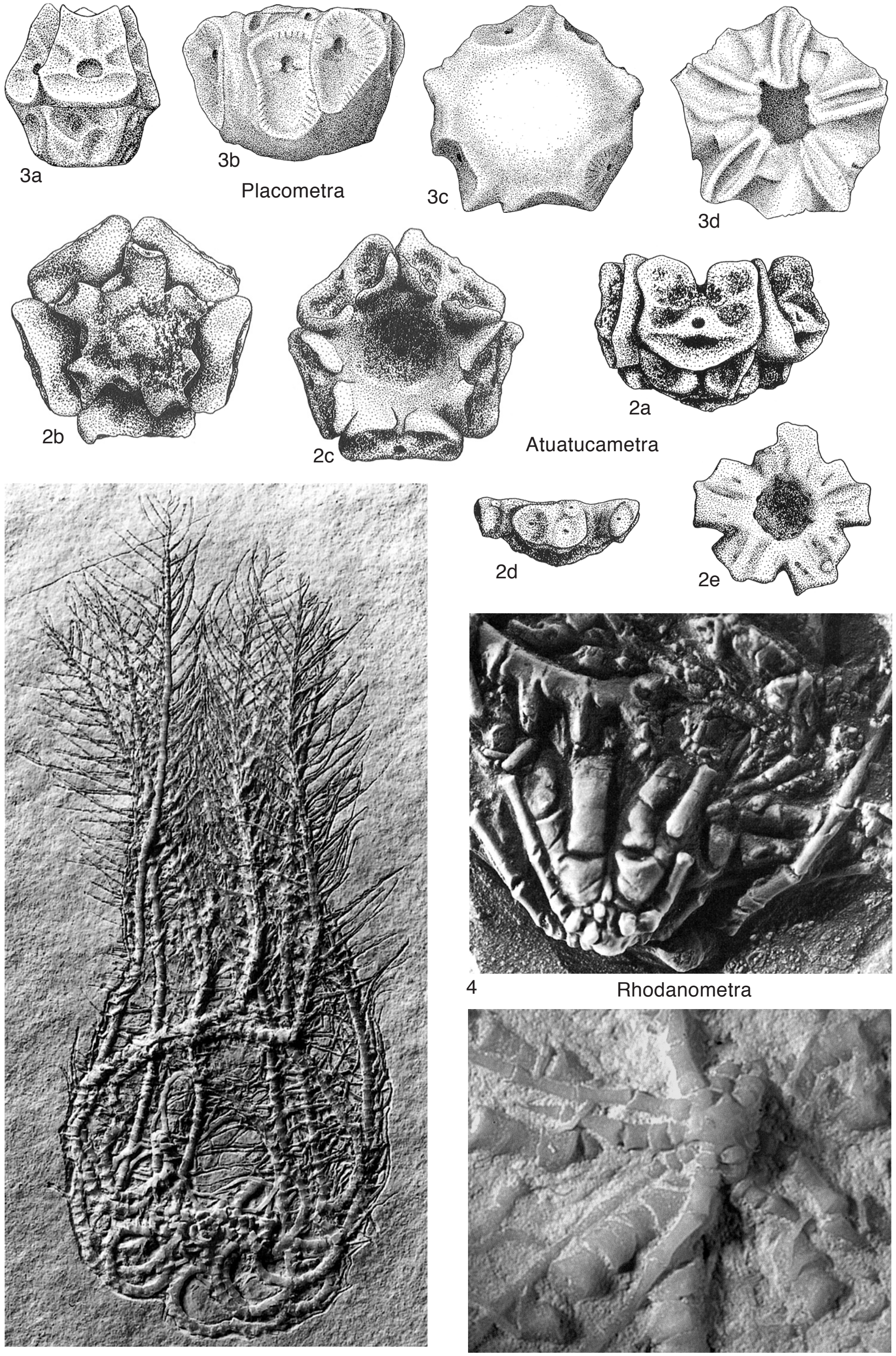

FIG. 58. Pterocomidae (p. 117–119).

wide. Rod-shaped basals exposed interradially and apparently united around central canal at base of radial cavity. Exposed surface of radial ring contiguous, almost horizontal, low midradially, but visible along interradial suture, separating neighboring primibrachials. Radial articular facet almost parallel to oral-aboral axis, wide, with distinct muscle fossae and wide upper margin divided by median notch. Arms 10; rays divided at primibrachial 2; first primibrachial low and wide. Syzygy between secundibrachials 3 and 4 and at subsequent intervals of 4 or 5 articulations. Arms as long as 130 mm. Secundibrachials rather high, slightly oblique; distal brachials more than twice as high as wide, slender, and with articulations almost perpendicular to arm. Pinnules long, up to 15 mm, with 15 to 20 pinnulars, extremely slender, swollen at articulations, apparently without terminal hooks or combs, but with a longitudinal ridge or crest, which may be serrate. First and second pinnulars short, succeeded by very long pinnulars, length 4 to 7 times greatest width, not differentiated in size or form. Distalmost pinnules, although extremely slender, appear as long as more proximal ones. Ambulacral groove distinct. Large covering plates have been recorded. Surface of cirri, brachials, and pinnulars with fine, reticulate to longitudinal sculpturing. [The names *Asteriatites* and *Ophiurites* have been used for *Pterocoma* and *Saccocoma*. The name *Geocoma* used by FRAAS (1878) for this species was established by D'ORBIGNY (1850 in 1850–1852, p. 381) for an ophiuroid. *Pterocoma* AGASSIZ is preoccupied by a genus of insects (DEJEAN, 1833–1836; SOLIER, 1836) and must be replaced by *Comaturella* MÜNSTER, the next youngest available name (FRICKHINGER, 1999, p. 68). *C. wagneri* is based on a specimen from the Solnhofen Limestone with only cirri attached to a centrodorsal; however, the very long cirrals are typical of *pennatus*, the only species of this type of comatulid known from the Solnhofen Limestone. As discussed by GISLÉN (1924, p. 122), the species was first given a binominal name by VON SCHLOTHEIM (1820) who also added some figures, although GOLDFUSS's (1831 in 1826–1844) description and figures of his *Comatula pinnata* are superior. The Upper Cretaceous species, *Geocoma pinnulata* FRAAS (1878), is insufficiently known. *Antedon formosus* WALTHER (1886) from the Solnhofen Limestone, based on the wrong assumption of fused primibrachials, is assumed to be conspecific with *C. pennata*.] *Upper Jurassic (Tithonian)–Upper Cretaceous (Turonian):* Germany, *Tithonian;* France, *Berriasian;* Lebanon, *Turonian.*——FIG. 58,*1a–b.* **C. pennata* (VON SCHLOTHEIM), Tithonian, Germany; *a,* intact specimen, JME SOS-3624, ×1.2 (Hess, 1999c); *b*, aboral view of cup with centrodorsal and arm base of juvenile specimen, NMB M10536, ×10 (Hess, new).

Atuatucametra JAGT, 1999a, p. 94 [**A. annae*; M]. Centrodorsal low to slightly conical, irregularly pentagonal with protruding, small, irrregularly arranged cirrus sockets; side view dominated by articular facets of radials, which are almost parallel to oral-aboral axis. Radial cavity wide. Basals exposed interradially as knobs. *Paleogene (Danian):* Belgium.——FIG. 58,*2a–e.* **A. annae*; *a–c,* cup with centrodorsal, *a*, lateral, *b*, lower (aboral), *c*, distal, holotype, NHMM 1997088, ×10; *d–e*, centrodorsal, *d*, lateral, *e*, adoral, paratype, NHMM 1997089, ×10 (Jagt, 1999a).

Placometra GISLÉN, 1924, p. 162 [**P. mortenseni*; OD]. Centrodorsal high conical or truncated conical to low columnar, generally with large, rounded or flattened, smooth aboral apex. No dorsal star, but central pit or feeble interradial impressions may be present. No radial pits in adoral side of centrodorsal. Centrodorsal cavity 20 to 30 percent of centrodorsal diameter and with overhanging edge. A few, very large, high, elliptical, cirrus sockets, 1 to 3 in each radial area (commonly only one large, and at the adoral margin one small juvenile socket). Sockets without distinct sculpturing or with articular tubercles and marginal crenulae. Rod-shaped basals not exposed. Radials, known only in type species, with narrow, overhanging, almost horizontal, and smooth exposed surface. Radial articular facet very high and wide, almost parallel to oral-aboral axis, meeting articular facet of neighboring radial along interradial suture. Adoral muscle fossae large, median ridge faint, adoral edge wide, concave, without median incision. Brachials, pinnules, and cirri unknown. *Upper Cretaceous (Turonian)–Paleogene (Danian):* Denmark, England, Germany.——FIG. 58,*3a.* **P. mortenseni*; cup with centrodorsal, Turonian, England, holotype, BMNH E25419, ×10 (Rasmussen, 1961).——FIG. 58,*3b–d. P. laticirra* (CARPENTER); centrodorsal, *b*, lateral, *c*, aboral, *d*, adoral, Turonian–Coniacian, England, holotype, BMNH E4675, ×7 (Rasmussen, 1961).

Rhodanometra MANNI, NICOSIA, & RIOU, 1985, p. 88 [**R. lorioli*; M]. Centrodorsal subpentagonal, convex, and smooth aborally. Cirrus sockets smooth, 2 or 3 in each radial area. Cirri of approximately 19 cirrals; proximal cirrals short; distal cirrals long and slender. Basals not exposed. Arms 10. Pinnules without longitudinal ridge or crest, no pinnules on proximal brachials. *Middle Jurassic (Callovian):* France.——FIG. 58,*4.* **R. lorioli*; proximal part of crown with centrodorsal, paratype, MNHN R.06566, ×2.2 (Manni, Nicosia, & Riou, 1985).

Family PTILOMETRIDAE
A. H. Clark, 1914

[*nom. transl.* GISLÉN, 1934, p. 18, *ex* subfamily Ptilometrinae A. H. CLARK, 1914b, p. 10; *emend.*, GISLÉN, 1924]

Centrodorsal large, rather high discoidal to low columnar with a flat, cirrus-free aboral apex. Cirrus sockets without distinct sculpturing, in 15 or 20 irregular columns of 2 to 4 sockets each. No dorsal star, radial pits, or

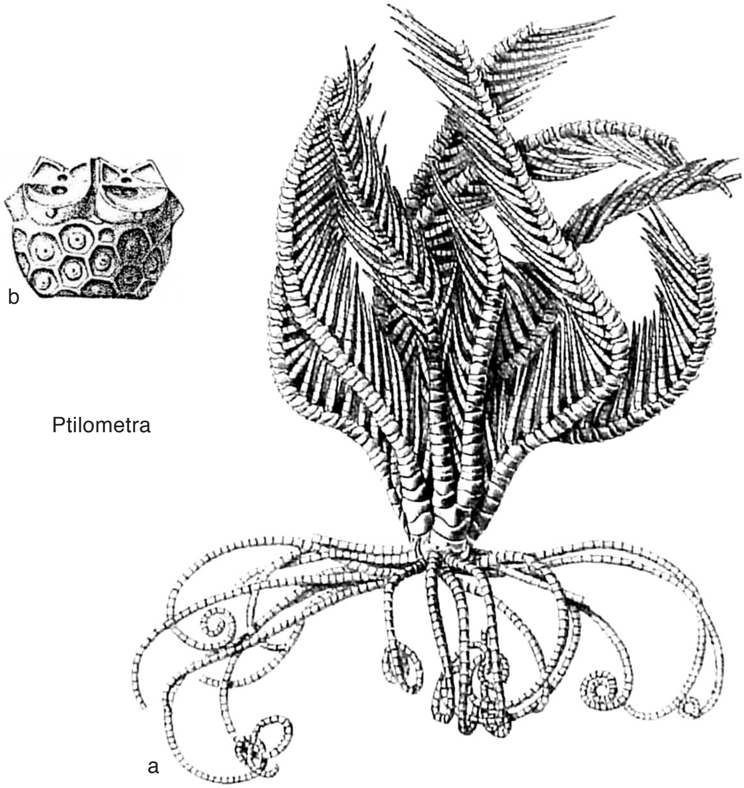

FIG. 59. Ptilometridae (p. 120).

subradial cleft. Cirri almost as long as arms, as many as 94 segments, cirrals at most twice as long as wide, distally with aboral ridge or spine. Rod-shaped basals exposed interradially. Radials with low exposed surface. Radial articular facet steep, low, and wide. Adoral muscle fossae forming a narrow band along adoral edge of radial. Radial cavity wide. As many as 23 arms. All brachitaxes with synarthry between brachials 1 and 2; syzygy between brachials 3 and 4 and more distally at intervals of 4 to 9. Pinnules with distinct ambulacral covering plates. *Holocene.*

Ptilometra A. H. CLARK, 1907f, p. 358 [**Alecto macronema* MÜLLER, 1841; OD; *error pro Comatula macronema* MÜLLER, 1846, p. 179]. Characters as for family. *Holocene:* southern Pacific Ocean (Australia), littoral to sublittoral.——FIG. 59*a–b*. **P. macronema* (MÜLLER); *a,* complete specimen, Port Jackson, Australia at 60 m, ×2 (Carpenter, 1888, pl. 38,*5*); *b,* cup with centrodorsal, ×4 (Carpenter, 1888, pl. 4,*3*).

Family THALASSOMETRIDAE A. H. Clark, 1908

[Thalassometridae A. H. CLARK, 1908h, p. 136]

Centrodorsal variable, conical, or hemispherical to truncated conical, columnar or discoidal, with rounded or flattened, cirrus-free, rugose to tuberculate or spiny aboral apex. No dorsal star or radial pits. Cirrus sockets large, without distinct ornament or with articular tubercles, in 10 distinct columns of 2 to 4 sockets on conical to columnar centrodorsals, or irregularly crowded and tending to form 10 or 15 columns of 1 to 3 sockets, mainly in larger, truncated or discoidal centrodorsals. Cirri long and slender with 30 to 90 cirrals (except 18 to 27 in *Parametra*). Distal cirrals short, with prominent aboral processes or spines (except in *Leilametra*). Rod-shaped basals exposed interradially or concealed.

Subradial cleft may be present. Radials with low exposed surface or concealed; articular facet moderately sloping, more or less angularly bent. Muscle fossae steep, high and narrow, separated from interarticular ligament by diagonal ridge. Radial cavity narrow. As many as 30 arms. Synarthry between primibrachials 1 and 2. Secundibrachials of 2 or 4 ossicles, the latter with a syzygy between brachials 3 and 4. Synarthry between brachials 1 and 2; syzygy between brachials 3 and 4 (between brachials 2 and 3 following distalmost axil in *Koehlermetra).* Further syzygies at interval of 2 to 17, generally 4 to 9. Brachials aborally rounded or laterally compressed and with aboral ridge or spines, commonly with marginal spines. First pinnule longer and stouter than second. Some proximal pinnulars may be enlarged; pinnule segments covering gonad broadened in *Horaeometra*. Pinnules with distinct ambulacral covering plates. *Neogene (Miocene)–Holocene.*

Thalassometra A. H. Clark, 1907f, p. 359 [**Antedon villosa* A. H. Clark, 1907d, p. 138; OD]. Arms 10 to 15, aborally rounded, with small spines or tubercles, at least marginally. Secundibrachials of 2 or 4 ossicles. First pinnule usually stout, large and basally broadened. *Holocene:* Pacific, Indian, and Atlantic Oceans (bathyal to abyssal).——Fig. 60,*1a.* **T. villosa* (A. H. Clark); cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950, p. 43, fig. 71).——Fig. 60,*1b. T. marginata* A. H. Clark; proximal part of crown with centrodorsal and cirrus, ×2 (A. H. Clark, 1915a in 1915–1950, p. 159, fig. 96).

Aglaometra A. H. Clark, 1913d, p. 47 [**Antedon valida* Carpenter, 1888, p. 104; SD A. H. Clark, 1950 in 1915–1950, p. 108]. Arms 10, aborally rounded. Proximal brachials rounded, without spines. First pinnule commonly stout, large, and basally broadened. *Holocene:* western Pacific Ocean (bathyal).——Fig. 60,*2.* **A. valida* (Carpenter); base of ray with centrodorsal margin, Indonesia, MNHN EcCh 43, ×4 (Messing, Améziane, & Eléaume, 2000).

Cosmiometra A. H. Clark, 1909a, p. 16 [**Thalassometra komachi* A. H. Clark, 1908i, p. 311; OD; =*Antedon aster* A. H. Clark, 1907d, p. 145]. Arms as many as 30, distally carinate. Brachitaxes all of 2 brachials. Proximal brachials aborally broad and commonly flattened, smooth or with fine marginal spines or tubercles. First pinnule larger than second, but not especially stout or basally broadened. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* Indian and central and western Pacific Oceans (sublittoral to upper bathyal).——Fig. 60,*3. C. iole* (A. H. Clark); base of ray with centrodorsal margin, Indonesia, MNHN EcCh 34, ×4 (Messing, Améziane, & Eléaume, 2000).

Crotalometra A. H. Clark, 1909e, p. 403 [**C. rustica*; M]. As many as 20 arms, rounded aborally, but distal brachials sometimes with distal spine. Secundibrachials 2 or 4. Proximal brachials smooth or with lateral edges everted and tuberculate or serrated. First pinnule usually stout, large, and basally broadened. *Holocene:* Indian and western Pacific Oceans (?sublittoral to bathyal).——Fig. 60,*4.* **C. rustica*; centrodorsal and bases of 2 rays, Indonesia, MNHN EcCh 42, ×2 (Messing, Améziane, & Eléaume, 2000).

Daidalometra A. H. Clark, 1916a, p. 116 [**Antedon hana* A. H. Clark, 1907d, p. 137; OD]. [Probably immature *Stenometra*. There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (sublittoral to upper bathyal).

Horaeometra A. H. Clark, 1918, p. 160 [**Antedon duplex* Carpenter, 1888, p. 212; M]. As many as 22 arms. Brachitaxes all of 2 brachials. Segments of genital pinnules expanded over gonads. *Holocene:* tropical western Atlantic Ocean (bathyal).——Fig. 60,*5.* **H. duplex* (Carpenter); cup with centrodorsal, enlarged (Messing, 1997).

Koehlermetra A. H. Clark, 1950 in 1915–1950, p. 100 [**Antedon porrecta* Carpenter, 1888, p. 250; OD]. Arms as many as 20, rounded aborally. Secundibrachials 2 or 4. Proximal brachials smooth. Tertibrachials following secundibrachials of 4 ossicles with syzygy between brachials 2 and 3. *Holocene:* southern and eastern Atlantic Ocean (bathyal).——Fig. 60,*6.* **K. porrecta* (Carpenter); syntype, arms broken at syzygy between tertibrachials 2 and 3, Ascension at 768 m, ×1.5 (Carpenter, 1888, pl. 52,*3*).

Leilametra A. H. Clark, 1932a, p, 379 [**L. necopinata*; OD]. Arms 10. Proximal brachials with spinose margins; more distal brachials spinose. Cirri nearly straight, without opposing spine. *Holocene:* Indonesia (bathyal).——Fig. 61,*1.* **L. necopinata*; Lombok at 1097 m, holotype, BMNH 1932.12.25.1, ×1 (A. H. Clark, 1950 in 1915–1950).

Lissometra A. H. Clark, 1918, p. 147 [**Antedon alboflava* A. H. Clark, 1907d, p. 145; M]. Arms 13 to 15, somewhat carinate distally. Proximal brachials with strong midaboral crest. Brachitaxes all with 2 brachials. Cirri relatively short, with as many as 34 segments, only approximately one-third arm length. *Holocene:* Japan (upper bathyal).——Fig. 61,*2.* **L. alboflava* (A. H. Clark); lateral view, ×1.2 (A. H. Clark, 1921 in 1915–1950, p. 161, fig. 216).

Oceanometra A. H. Clark, 1916b, p. 606 [**Thalassometra gigantea* A. H. Clark, 1908b, p. 222; OD]. Arms as many as 28, rounded aborally. Proximal brachials with midaboral keel and spinose at least along margins. First pinnule usually stout, large and basally broadened. [At least some species of *Oceanometra* and *Thalassometra* are congeneric (Messing, Améziane, & Eléaume, 2000, p. 671).

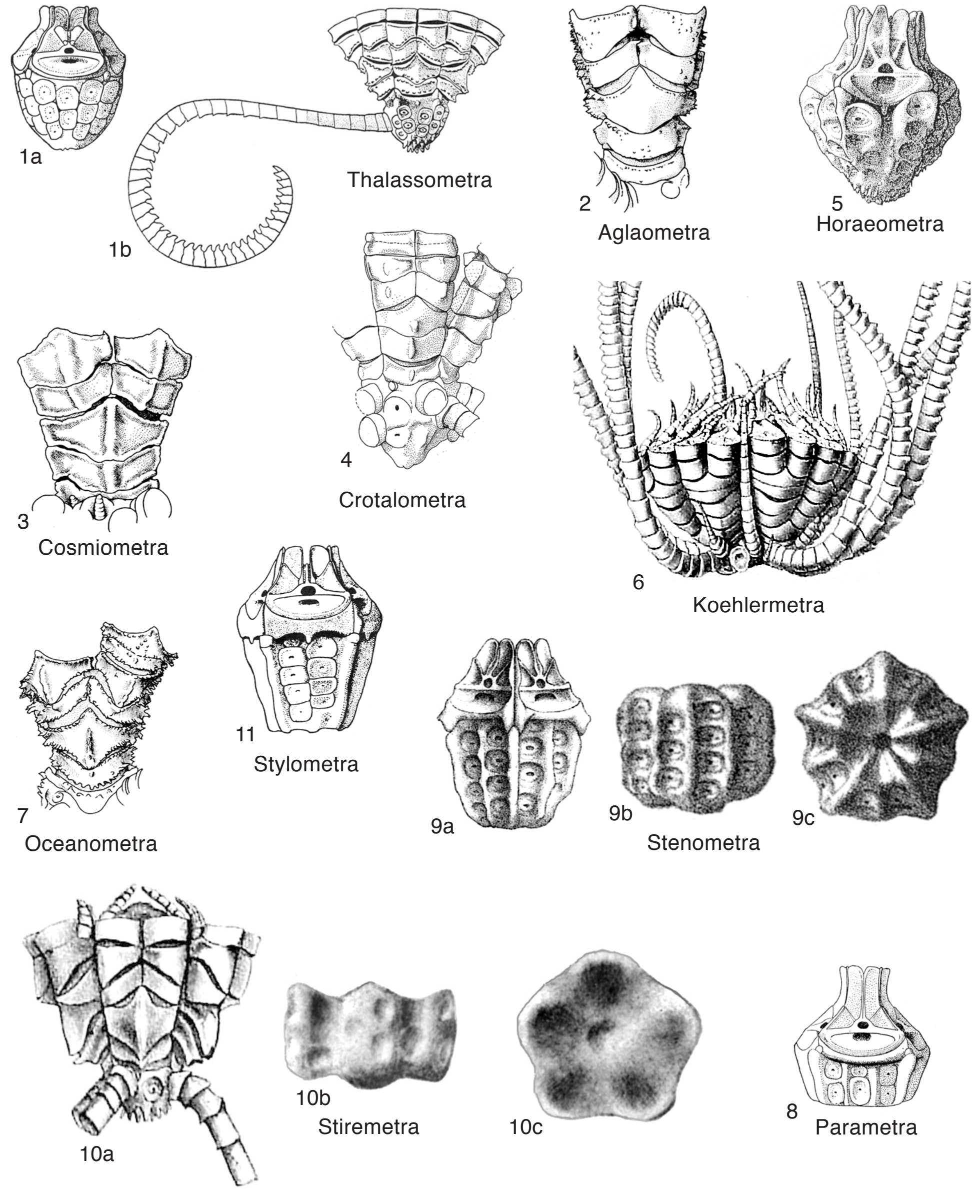

FIG. 60. Thalassometridae (p. 121–124).

Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* Indian and western Pacific Oceans (?sublittoral to upper bathyal).——FIG. 60,*7. O. annandelei* (A. H. CLARK); base of ray with centrodorsal margin, Indonesia, MNHN EcCh 51, ×3 (Messing, Améziane, & Eléaume, 2000).

Parametra A. H. CLARK, 1909a, p. 15 [**Antedon orion* A. H. CLARK, 1907d, p. 143; OD]. Arms 10 to 20, somewhat carinate distally. Brachitaxes all with 2 brachials. Proximal brachials aborally rounded, commonly with weak, midaboral carina. Cirri relatively short, with as many as 27 segments, less than one-third arm length. *Holocene:* central and western Pacific Oceans (sublittoral to bathyal).——FIG. 60,*8.* **P. orion* (A. H. CLARK); cup with centrodorsal, ×5 (A. H. Clark, 1921 in 1915–1950, p. 43, fig. 74).

Stenometra A. H. CLARK, 1909a, p. 14 [**Antedon quinquecostata* CARPENTER, 1888, p. 215; OD].

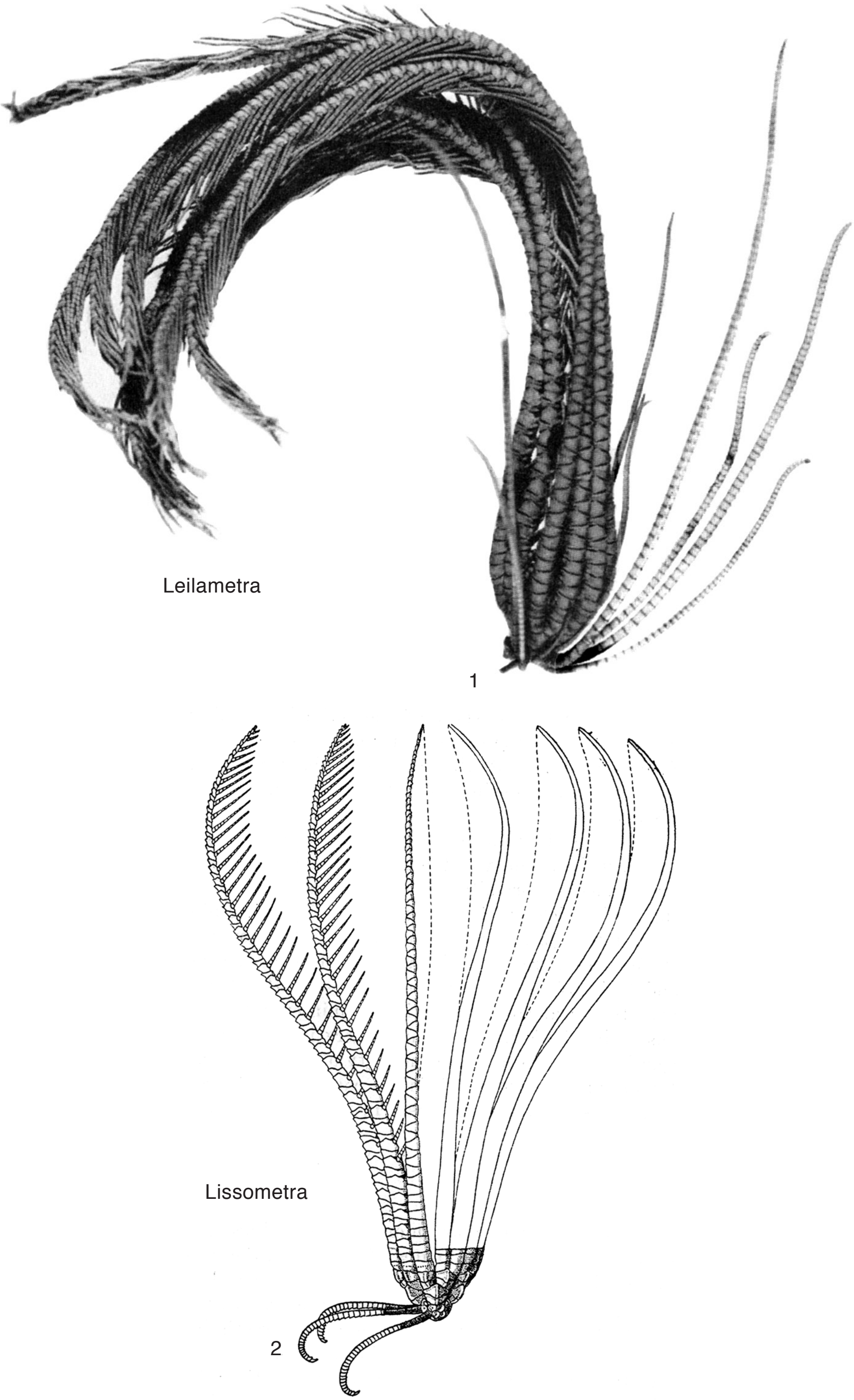

FIG. 61. Thalassometridae (p. 121).

Centrodorsal truncated conical to columnar with 10 columns of 2 to 4 cirrus sockets separated by interradial ridges and alternating along midradial line. Arms as many as 20, compressed and sharply carinate, sometimes with overlapping spine. Brachitaxes all with 2 brachials. Proximal brachials narrow, gable-like in cross section. First pinnule larger than second, but not especially stout or basally broadened. [*Antedon pellati* DE LORIOL, 1897, is referred to this genus.] *Neogene (Miocene)–Holocene:* France, *Miocene;* western Pacific Ocean (sublittoral to bathyal), *Holocene.*——FIG. 60,*9a*. **S. quinquecostata* (CARPENTER); cup with centrodorsal, Holocene, ×4 (Carpenter, 1888, pl. 3,*6d*).——FIG. 60,*9b–c*. *S. pellati* (DE LORIOL); centrodorsal, *b*, lateral, *c*, aboral, Miocene, France, holotype, ×3 (Rasmussen, 1978).

Stiremetra A. H. CLARK, 1909a, p. 15 [**Antedon acutiradia* CARPENTER, 1888, p. 113; OD]. Centrodorsal hemispherical or truncated conical to columnar, in some species 5-sided columnar with 10 columns of cirrus sockets separated by interradial ridges and wide radial furrows. Arms as many as 14 (typically 10), distal brachials aborally rounded. Secundibrachials 2 or 4. Proximal brachials carinate or subcarinate, smooth, with straight or everted margins. [Following RASMUSSEN (1978, p. 901), *Antedon stellatus* NOELLI (1900) is referred to this genus.] *Neogene (Miocene)–Holocene:* Italy, *Miocene;* Indian, central and western Pacific Ocean, central and eastern Atlantic Ocean (bathyal to abyssal), *Holocene.*——FIG. 60,*10a*. **S. acutiradia* (CARPENTER); base of crown with centrodorsal and base of 2 cirri, Fiji at 2470 m, ×4 (Carpenter, 1888, pl. 11,*3*).——FIG. 60,*10b–c*. *S. stellata* (NOELLI); centrodorsal, *b*, lateral, *c*, adoral, Miocene, Italy, holotype, ×4 (Noelli, 1900).

Stylometra A. H. CLARK, 1908g, p. 245 [**Antedon spinifera* CARPENTER, 1881c, p. 158; OD]. Arms as many as 30; compressed and sharply carinate, commonly with overlapping spine. Brachitaxes all of 2 brachials. Proximal brachials aborally rounded or flattened, typically spinose. First pinnule larger than second but not especially stout or basally broadened. *Holocene:* western Atlantic Ocean (sublittoral to upper bathyal).——FIG. 60,*11*. **S. spinifera* (CARPENTER); cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950, p. 43, fig. 72).

Superfamily NOTOCRINOIDEA Mortensen, 1918

[*nom. correct.* HESS & MESSING, herein, *pro* Notocrinacea RASMUSSEN, 1978, p. 902, *nom. transl. et correct. ex* family Notocrinidae MORTENSEN, 1918, p. 10] [=Notocrinida GISLÉN, 1924, p. 231 (established as a superfamily-rank taxon although named subtribe), *emend.*, CLARK & CLARK, 1967, p. 1]

Centrodorsal conical, truncated conical, or hemispherical to discoidal. Aboral area in adult specimens generally cirrus-free or with traces of obliterated cirrus sockets, commonly rugose. Most genera with 5 pits arranged radially around apex, forming dorsal star, in large specimens commonly in a depressed area. Some specimens also with shallow, indistinct, lanceolate interradial impressions around aboral pole. Centrodorsal cavity narrow to moderate, 20 to 30 percent of centrodorsal diameter, always surrounded by, or exceptionally fused with, 5 radial pits housing coelomic extensions outside chambered organ and nerve capsule of centrodorsal cavity. Cirrus sockets generally large, with more or less distinct articular tubercles, and in most fossil genera with marginal crenulae. Sockets in 10 columns on small or conical centrodorsals, increasing in number during growth and tending to form 20 columns (obliterated on aboral apex) on hemispherical to discoidal centrodorsals of larger specimens of *Glenotremites* and *Remesimetra*. Sockets small in *Semiometra*, without distinct sculpturing, and closely alternating, without forming columns on a very low discoidal centrodorsal. Rod-shaped basals commonly exposed interradially, with or without subradial cleft. Radials with low exposed surface or concealed; distal margin may be concave, reaching edge of centrodorsal only interradially. Radial articular facet generally rather low and wide, but in *Semiometra* high. Muscle fossae distinct, similar in size to interarticular ligament fossae or higher. Radial cavity narrow to wide and funnel shaped. Arms 10, divided at primibrachial 2. [*Semiometra klari* PECK & WATKINS, 1975, Lower Cretaceous, Texas, has some arms divided further at secundibrachial 2 and more distally.] Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Syzygy between secundibrachials 3 and 4 and distally at variable intervals. Arms and pinnules aborally rounded, not carinate. Pinnules short. No distal comb or aboral crest on oral pinnules. Modern genera viviparous and with ambulacral covering plates moderately developed or absent. Mouth central. *Middle Jurassic (Bathonian)–Holocene.*

Family NOTOCRINIDAE Mortensen, 1918

[Notocrinidae MORTENSEN, 1918, p. 10]

Moderate to very large Notocrinoidea with conical, truncated conical, or hemispherical to discoidal centrodorsal, commonly wider and aborally more flattened or concave in large specimens. Aboral side of centrodorsal with a distinct dorsal star except in *Schlueterometra* and adult specimens of *Notocrinus*. Commonly with shallow interradial impressions. Adoral side of centrodorsal with distinct, commonly large, and deep radial pits. Cirrus sockets in *Notocrinus* and *Semiometra* without distinct sculpturing, in other genera with distinct articular tubercles and marginal crenulae. Sockets large and in 10 to 20 columns or small and closely alternating without forming columns. Subradial cleft present or absent. Radials with low exposed surface, sometimes visible only interradially or concealed. Radial articular facet rather steep and flat or concave. *Middle Jurassic (Bathonian)–Holocene.*

Notocrinus MORTENSEN, 1917, p. 206 [**N. virilis*; M]. Centrodorsal conical or truncated conical. Dorsal star consisting of 5 radial pores surrounding central pore or pit present in juvenile specimens. Cirrus sockets without distinct sculpturing, in 10 columns, or in large specimens crowded, tending to form 20 columns. Aboral apex cirrus-free, pointed or truncated, rugose. Adoral side of centrodorsal with 5 simple, deep radial pits. Cirri stout, rather long. Cirrals rather short and wide; distal cirrals laterally compressed. Rod-shaped basals stout, centrally united, exposed interradially or concealed. No subradial cleft. Exposed surface of radial low to moderate. Radial articular facet rather steep and wide, not angularly bent or concave. Adoral muscle fossae rather wide, triangular, larger than interarticular ligament fossae; adoral edge wide, with a broad and shallow median embayment. Radial cavity moderate. Arms large. Distal syzygies at interval of 2 to 20. Pinnules with small ambulacral covering plates, but large side plates. Gonads in arm instead of in pinnules. *Paleogene (Eocene)–Holocene:* Antarctic Peninsula, *Eocene;* Southern Ocean (sublittoral to bathyal), *Holocene.*——FIG. 62,*1a–d.* **N. virilis*, Holocene; *a,* centrodorsal and base of crown, ×3 (Rasmussen, 1978); *b*, cup with centrodorsal, ×4; *c*, proximal view of 2 basals and radials, ×4; *d*, section through centrodorsal with radial pit at left, ×4 (Gislén, 1924).——FIG. 62,*1e. N. seymourensis* BAUMILLER & GAŹDZICKI; primibrachials and proximal arm, Eocene, Antarctic Peninsula, ZPAL Ca. V/5, ×5 (Baumiller & Gaździcki, 1996).

Glenotremites GOLDFUSS, 1829 in 1826–1844, p. 159, *emend.*, RASMUSSEN, 1961, p. 277; name was extended to a collective group name by GISLÉN, 1924, p. 123, but restricted by RASMUSSEN (1961) [**G. paradoxus;* M; =*Antedon semiglobosus* SCHLÜTER, 1878, p. 41; =*Antedon essenensis* SCHLÜTER, 1878, p. 40; =*Antedon rugosa* CARPENTER, 1880a, p. 49; =*Antedon perforata* CARPENTER, 1880b, p. 549; =*Antedon lundgreni* CARPENTER, 1880b, p. 550; =*Antedon striata* CARPENTER, 1880b, p. 551; =*Comatula tetensi* WEGNER, 1913, p. 182; =*Antedon minutissimus* VALETTE, 1917, p. 169; =*G. batheri* GISLÉN, 1924, p. 128; =*G. excavatus* GISLÉN, 1925a, p. 12; =*G. adregularis* GISLÉN, 1925a, p. 14; =*G. alternatus* GISLÉN, 1925a, p. 16; =*G. parvistellatus* GISLÉN, 1925a, p. 17; =*G. intermedius* GISLÉN, 1925a, p. 20; =*Sphaerometra senonica* GISLÉN, 1925a, p. 25; =*Antedon chateleti* VALETTE, 1932, p. 393] [=*Glenocrinus* D'ORBIGNY, 1852 in 1850–1852, p. 138, *nom. van.;* =*Sphaerometra* GISLÉN, 1924, p. 169 (type, *Antedon semiglobosus* SCHLÜTER, 1878, p. 41, OD)]. Centrodorsal hemispherical to discoidal with a dorsal star. Aboral apex in adult specimens cirrus-free and flattened or concave. Interradial aboral impressions may be present. Cirrus sockets large, with large axial canal, lateral articular tubercles, and marginal crenulae. Sockets irregularly crowded, tending to form columns increasing in number from 10 to 20 during growth. Centrodorsal cavity narrow, 20 to 30 percent of centrodorsal diameter, surrounded by deep, single or double radial pits, which may exceptionally fuse with the centrodorsal cavity. Rod-shaped basals exposed interradially and separated around central canal. Radials covering entire adoral side of centrodorsal with low exposed surface. Radial articular facet rather large and steep, flat or concave, with distinct muscle fossae and interarticular ligament fossae separated by oblique ridge. Radial cavity rather small to moderate. Distal arms (known only in *G. loveni*, CARPENTER, 1880a) with syzygy between secundibrachials 3 and 4, 9 and 10, and distally at interval of 5 ossicles. *Lower Cretaceous (Albian)–Upper Cretaceous (Santonian):* Czech Republic, England, Germany, Poland.——FIG. 62,*2a–f.* **G. paradoxus*, Turonian; *a–c,* centrodorsal, *a*, lateral, *b*, aboral, *c*, adoral, Germany, holotype, IPB Goldfuss 370, ×5; *d–f,* cup with centrodorsal and brachials, *d–e,* lateral, *f,* aboral, England, CAMSM B.80782, ×5 (Rasmussen, 1961).

Loriolometra GISLÉN, 1924, p. 167 [**Comaster retzii* LUNDGREN, 1875, p. 66; OD]. Centrodorsal large, high, columnar or slightly conical with rounded aboral apex bearing an aboral pit or dorsal star. Faint interradial aboral impressions may be present. Cirrus sockets large, with a wide axial canal, lateral articular tubercles, and marginal crenulae. Sockets arranged in 10 distinct columns. Centrodorsal cavity approximately 20 percent of centrodorsal diameter. Radial pits simple, very wide and deep,

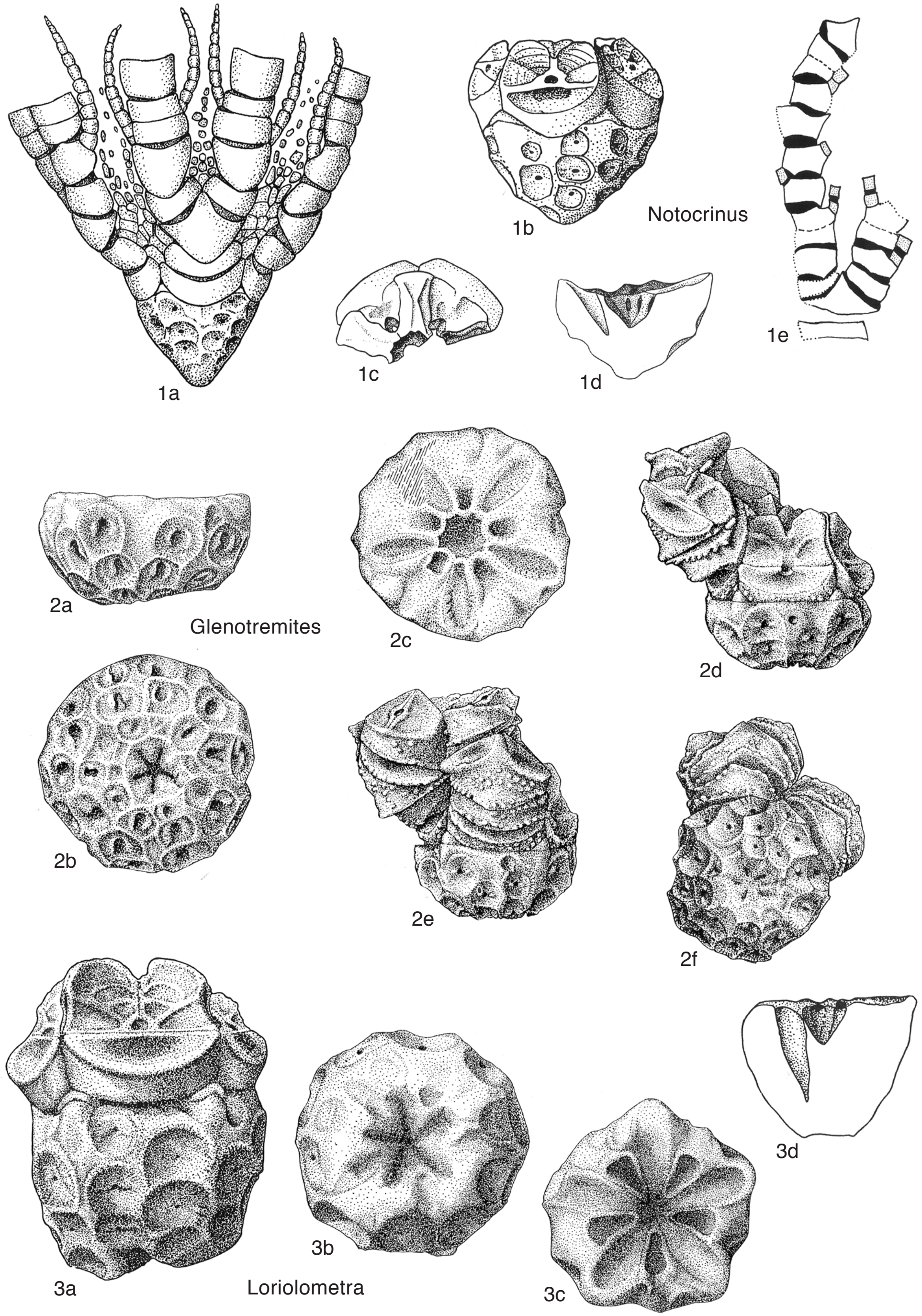

FIG. 62. Notocrinidae (p. 125–127).

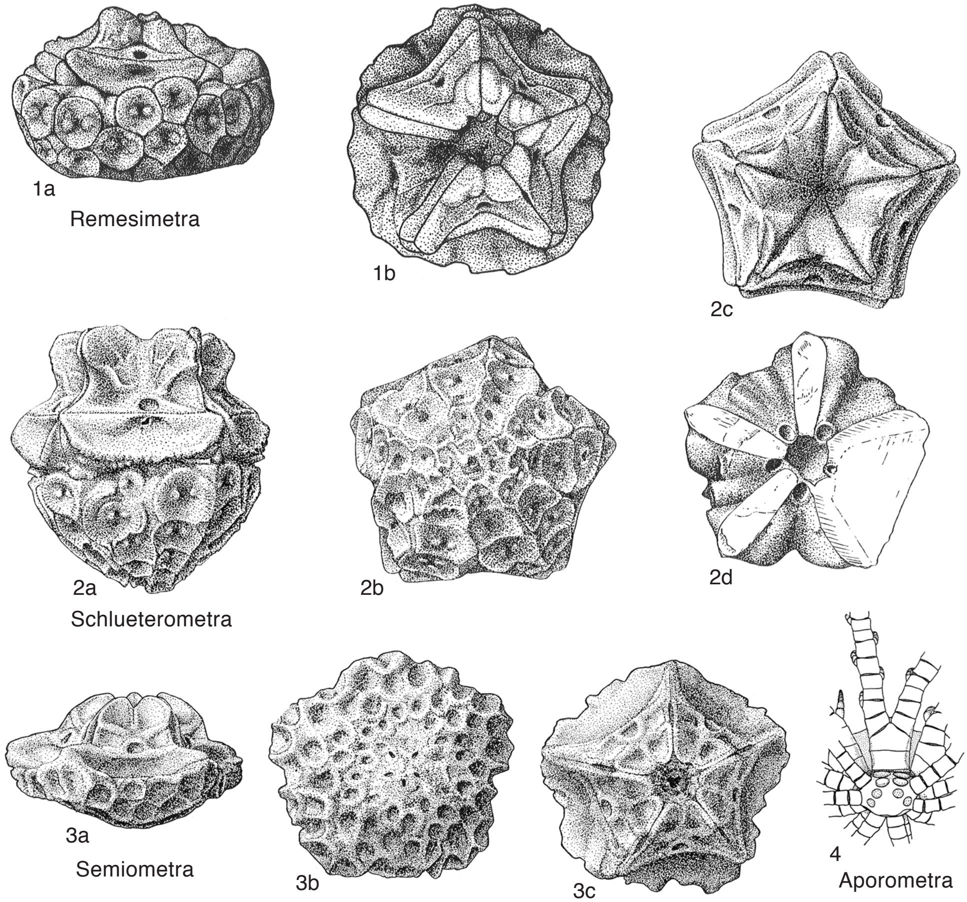

Fig. 63. Notocrinidae and Aporometridae (p. 127–128).

exceeding depth of centrodorsal cavity. Rod-shaped basals exposed interradially and separated around central canal. Radials forming complete contiguous exposed surface around centrodorsal. Deep subradial cleft. Radial articular facet steep, almost vertical, with large and wide, triangular adoral muscle fossae. Radial cavity wide. *Upper Cretaceous (Campanian):* France, Sweden.——Fig. 62,*3a–d.* **L. retzii* (Lundgren), Sweden; *a,* cup with centrodorsal, RM Ec 24541, ×4; *b*, aboral view of centrodorsal, RM Ec 24521, ×4; *c*, adoral view of centrodorsal, MGUH 8981, ×4 (Rasmussen, 1961); *d*, section through centrodorsal with radial pit at left, ×5 (Gislén, 1924).

Remesimetra Sieverts-Doreck, 1958a, p. 255 [**Glenotremites discoidalis* Gislén, 1925a, p. 10; OD]. Centrodorsal rounded subconical to large, discoidal with dorsal star. Interradial aboral impressions may be present. Large cirrus sockets with articular tubercles and marginal crenulae in 20 irregular columns in adult specimens. Centrodorsal cavity and radial pits narrow. No subradial cleft. Radials exposed only interradially. Radial articular facet flat or concave. Radial cavity rather narrow. *Lower Cretaceous (Albian)–Upper Cretaceous (Cenomanian):* Czech Republic, England.——Fig. 63,*1a–b.* **R. discoidalis* (Gislén); cup with centrodorsal, one radial missing, *a*, lateral, *b*, distal, Cenomanian, Czech Republic, ×3 (Rasmussen, 1978).

Schlueterometra Rasmussen, 1961, p. 318 [**S. voigti*; OD]. Centrodorsal conical with pointed aboral apex. No dorsal star. Cirrus sockets in 10 distinct columns, increasing in size toward base, with articular tubercles and marginal crenulae. Centrodorsal cavity narrow, approximately 20 percent of centrodorsal diameter and surrounded by deep, single radial pits. Rod-shaped basals exposed interradially and separated around central canal. Deep subradial cleft. Radials forming complete contiguously exposed surface around centrodorsal. Radial articular facet rather steep, adoral muscle fossae triangular, large, and wide. Radial cavity large, funnel shaped. *Upper Cretaceous (Coniacian–Santonian):* Germany.——Fig. 63,*2a–d.* **S. voigti*;

cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, *d*, centrodorsal adoral, Santonian, holotype, repository unkown, ×5 (Rasmussen, 1961).

Semiometra Gislén, 1924, p. 172 [**Antedon impressa* Carpenter, 1881b, p. 135; OD]. Centrodorsal low, disk shaped, with distinct dorsal star. Cirrus sockets small, crowded, commonly regularly alternating and not forming columns; sockets without distinct articular tubercles or marginal crenulae. Centrodorsal cavity approximately 20 to 30 percent of centrodorsal diameter and surrounded by small, shallow radial pits. Rod-shaped basals present but not always exposed. Radials exposed only interradially, leaving adoral surface of centrodorsal uncovered by radial plates in considerable areas along radial margins. Radial articular facet more or less concave, subtriangular with high, commonly narrow muscle fossae. Radial cavity commonly narrow, but may be funnel shaped, extended at upper edge along interradial suture. Brachials known in one putative species. Syzygies occur between secundibrachials. First pinnule on secundibrachial 2. [The Middle Jurassic (Bathonian) *Actinometra abnormis* Carpenter (1880a) and the Upper Jurassic (Oxfordian) *Antedon petitclerci* Caillet (1923) (see also Radwańska, 2007), are referred to *Semiometra*.] *Middle Jurassic (Bathonian)–Upper Cretaceous (Maastrichtian), Paleogene (?Eocene):* England, *Bathonian;* France, Poland, *Oxfordian;* USA (Texas), France, *Barremian*; *Albian;* Belgium, Czech Republic, England, France, Germany, Netherlands, Sweden, *Cenomanian–Maastrichtian*; Italy, *?Eocene.*——Fig. 63,*3a–c*. **S. impressa* (Carpenter); cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, Campanian, Sweden, MGUH 8986, ×8 (Rasmussen, 1961).

Family APOROMETRIDAE H. L. Clark, 1938

[Aporometridae H. L. Clark, 1938, p. 41]

Small Notocrinoidea with a low, hemispherical or rounded to almost conical centrodorsal with more or less flattened aboral apex, rugose due to obsolete sockets. Adoral side of centrodorsal with shallow radial pits. Aboral half of centrodorsal cavity filled with spongy stereom; no aboral pit or dorsal star. Cirrus sockets with indistinct sculpturing or with articular tubercles, but no marginal crenulae, in 10 columns of 1 to 4 sockets. Cirrals smooth, no aboral spines; distal cirrals flattened aborally-adorally. Rod-shaped basals exposed interradially or concealed. No subradial cleft. Radials with low exposed surface. Radial articular facet low and wide, angularly bent at fulcral ridge; low aboral ligament fossa almost parallel to oral-aboral axis, small interarticular ligament fossa and adoral muscle fossae almost at right angle to oral-aboral axis. Radial cavity moderate, without central plug. Syzygy between secundibrachials 3 and 4 and secundibrachials 7 and 8 and distal generally at interval of 2. No distinct ambulacral covering plates; viviparous; pinnules bearing gonads and marsupia. Aporometrids are among the few crinoids that carry different stages of larvae in and on pinnules (Helgen & Rouse, 2006). *Holocene.*

Aporometra H. L. Clark, 1938, p. 41 [**Himerometra paedophora* H. L. Clark, 1909, p. 524; OD]. Characters as for family. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* Australia (littoral to sublittoral).——Fig. 63,*4*. *A. wilsoni* (Bell); centrodorsal and base of crown, syntype, BMNH 93.7.8.8, ×3 (Clark & Clark, 1967).

Superfamily ANTEDONOIDEA Norman, 1865

[*nom. correct.* Hess & Messing, herein, *pro* Antedonacea Rasmussen, 1978, p. 906, *nom. transl. ex* family Antedonidae Norman, 1865, p. 101] [=suborder Antedonida A. H. Clark, 1908j, p. 723; =suborder Macrophreata A. H. Clark, 1909h, p. 174, excluding Atelecrinidae; *non* Antedonacea Steinmann, 1903, used for all comatulids]

Centrodorsal variable, discoidal or hemispherical to rounded subconical, conical, or columnar. Cirrus sockets generally small and numerous, closely placed, ranging from irregular alternating rows to indistinct columns, and 10 to 20 distinct columns in Zenometridae. Sockets without distinct sculpturing. Basals commonly transformed to a rosette with rod-shaped radiating portions ranging from absent through reduced to distinct in *Nanometra* and Heliometrinae, and broad, tongue-shaped, and exposed interradially in some Zenometridae. Centrodorsal cavity moderate, approximately 30 percent of centrodorsal diameter in most Antedoninae, Thysanometrinae, Heliometrinae, and Isometrinae, and large to very large in Perometrinae, Bathymetrinae, Zenometridae, and Pentametrocrinidae. Small radial pits may be present in adoral surface of centrodorsal in some specimens of *Antedon* only. Radials 10 (5 radials and 5 pararadials) in *Promachocrinus* and *Thaumatocrinus*, but 5 in all other Antedonoidea as well as in other comatulids. Adoral muscle fossae forming pair of high, thin flanges almost parallel to oral-aboral axis that meet midradially at approximately a 90 degree angle. Radial cavity narrow or funnel shaped, without central plug. Arms undivided in Pentametrocrinidae and divided at primibrachial 2 in Antedonidae. Synarthry between brachials 1 and 2 commonly embayed. Syzygy between brachials 3 and 4, generally between brachials 9 and 10, and distal at short intervals. Distal brachials strongly wedge shaped. Pinnules cylindrical to flattened, not carinate. Mouth central. *Lower Cretaceous (Albian)–Holocene.*

Family ANTEDONIDAE Norman, 1865

[Antedonidae Norman, 1865, p. 101; incl. Palaeantedonidae Gislén, 1924, p. 170; Rasmussen, 1978, p. 907]

Arms divided at primibrachial 2, rare further division at secundibrachials 2 or 4 in some arms of a few specimens. [This very large family has been subdivided into several subfamilies and includes approximately 150 nominal species, more than a quarter of all extant comatulid crinoids. A. H. Clark (1909a) distinguished 6 subfamilies on the basis of the arrangement and structure of cirri and the structure and composition of oral pinnules (modified by Clark & Clark, 1967): Antedoninae, Bathymetrinae, Heliometrinae, Isometrinae, Perometrinae, and Zenometrinae. Gislén (1924, p. 231) proposed the following groupings: (1) forms with more or less arched to hemispherical centrodorsal, moderate centrodorsal cavity, closely alternating cirrus sockets and synarthrial articulations not very narrow or strongly embayed, including Antedoninae, Perometrinae, and Thysanometrinae; and (2) forms with conical to columnar centrodorsal, large centrodorsal cavity, more or less columnar arrangement of cirrus sockets, and synarthrial articulations commonly narrow and strongly embayed, including Zenometrinae, Bathymetrinae, Heliometrinae, and Isometrinae (as well as the Pentametrocrinidae and Atelecrinidae); but this was rejected by A. H. Clark (1931 in 1915–1950). However, the occurrence of all intermediate arrangements of cirrus sockets between well-marked columns on a columnar centrodorsal and irregularly on a low hemispherical centrodorsal led A. M. Clark (1980, p. 199, footnote) to merge the Zenometrinae and Bathymetrinae. Subsequently, Messing and White (2001) removed 3 genera to a separate family, Zenometridae, leaving the remaining zenometrine genera as subfamily *incertae sedis*. A complete generic and subfamilial revision of the family is warranted.] *Lower Cretaceous (Albian)–Holocene.*

Subfamily ANTEDONINAE Norman, 1865

[*nom. transl.* A. H. Clark, 1909h, p. 176, *ex* Antedonidae Norman, 1865, p. 101]

Centrodorsal discoidal to low hemispherical or rounded subconical, generally with a small, cirrus-free, smooth, rugose or tuberculate aboral apex. Centrodorsal cavity moderate. Shallow, small radial pits may be present in specimens of *Antedon bifida*. Cirrus sockets closely placed, commonly small, forming 2 or 3 irregular rows on low centrodorsals, 3 or 4 regularly alternating rows in higher centrodorsals, and as many as 6 in conical centrodorsals; exceptionally as many as 100 sockets, including obsolete sockets on aboral apex. Cirri 10 to 60, rather short, generally with fewer than 20 cirrals, aborally rounded without aboral spines or processes and never carinate. Basal rosette; no rod-shaped basals. Radials commonly reaching edge of centrodorsal (except midradially) but may not. Radial articular facet gently sloping, wider than high. Adoral muscle fossae moderate, slightly larger than interarticular ligament fossae, and broadly rounded, more or less 4-sided, generally wider than high, separated by broad, midradial ridge with median furrow, and shallow notch. Synarthries between brachials 1 and 2 flat or slightly embayed. Some arms rarely also divided at secundibrachials 2 or 3 in *Antedon*. Holocene genera distinguished mainly on length and structure of proximal pinnules. *Paleogene (Eocene)–Holocene.*

Antedon de Fréminville, 1811, p. 349, *nom. conserv.* [**A. gorgonia*; M; name available according to ICZN, 2010, p. 51/930; =*Asterias bifida* Pennant, 1777, p. 55, *nom. nov. pro Decacnemos rosacea* Linck, 1733, p. 55] [=*Decacnemos* Bronn, 1825, p. 6–7, *ex* Linck, 1733 (type, *Decacnemos rosacea* Linck, 1733, p. 55, OD); =*Hibernula* Fleming, 1828, p. 494 (type, *Pentacrinus europaeus* Thompson, 1827, p. 1, OD); =*Phytocrinus* de Blainville, 1830, p. 235, invalid, *nom. subst. pro Hibernula* Fleming, 1828, p. 494; =*Ganymeda* Gray, 1834, p. 15 (type, *G. pulchella*, M); =?*Kallispongia* Wright, 1877, p. 754 (type, *K. archeri*, M; probably a synonym of *A. loveni* Bell, 1882a, p. 534); =*Cintedon* Munier-Chalmas, 1891, p. 22, *nom. null.*; =*Compsometra* A. H. Clark, 1908h, p. 131 (type, *Antedon loveni* Bell, 1882a, p. 534, OD); =*Repometra* A. H. Clark, 1937, p. 93 (type, *R. arabica*, M)]. Centrodorsal much broader than high; cirrus sockets irregular or alternating in arrangement. First pinnule more than 1.5 times the length of second pinnule; second similar to third; third similar to succeeding genital pinnules. *Holocene:* Atlantic Ocean, including Mediterranean, Indian, and western Pacific Oceans (sublittoral to upper bathyal).——Fig. 64,*1a*. **A. bifida* (Pennant); aboral view of holotype of *A. duebeni* Bölsche, 1866, Atlantic Ocean off Brazil, according to Hansson (2001), *A. duebeni* is synonymous with *A. bifida*, ×5 (Carpenter, 1888, pl. 32,*2*).——Fig. 64,*1b–c*. *A. mediterranea* (Lamarck); *b,* cup with centrodorsal, ×5 (A. H. Clark, 1921 in 1915–1950); *c*, adoral view of centrodorsal, ×5 (A. H. Clark, 1915a in 1915–1950, p. 261, fig. 281).

Andrometra A. H. Clark, 1917a, p. 128 [**Antedon psyche* A. H. Clark, 1908g, p. 241; OD; =*Toxometra aequipinna* Gislén, 1922, p. 129]. Second pinnule much longer than either first or third. [There is no suitable illustration available for the genus.] *Holocene:* northeastern Indian Ocean, northwestern Pacific Ocean (sublittoral).

Annametra A. H. Clark, 1936a, p. 247 (A. H. Clark, 1923b, p. 41, 52, *nom. nud.*) [**Cominia occidentalis* A. H. Clark, 1915b, p. 164; M]. Cirri short and stout, strongly recurved distally. First pinnule of 18 to 35 pinnulars no more than twice as long as broad; second pinnule slightly longer; third similar to succeeding genital pinnules. *Holocene:* southern Indian Ocean, northwestern Pacific Ocean (littoral to sublittoral).——Fig. 64,*2*. **A. occidentalis* (A. H. Clark); peripheral cirrus, Table Bay, South Africa, BMNH 1949.9.27, ×3 (Clark & Clark, 1967).

Argyrometra A. H. Clark, 1917a, p. 128 [**Iridometra crispa* A. H. Clark, 1908b, p. 218; OD]. First and second pinnules with elongate pinnulars; first pinnule either shorter or longer than third, and second intermediate. Third pinnule similar to succeeding genital pinnules. *Holocene:* western and central Pacific Ocean (sublittoral).——Fig. 64,*3*. **A. crispa* (A. H. Clark); centrodorsal with base of crown, ×3 (Clark & Clark, 1967, p. 98, fig. 7).

Ctenantedon Meyer, 1972, p. 53 [**C. kinziei*; M]. Numerous cirri formed of 12 to 14 mostly elongate segments. First 4 (sometimes first 2 or 3) pinnules with conspicuous terminal comb teeth. *Holocene:* Western tropical Atlantic Ocean (littoral).——Fig. 64,*4a–c*. **C. kinziei*; *a*, centrodorsal aboral, *b*, centrodorsal adoral, *c*, first pinnule with comb, Caribbean, holotype, USNM E11591, ×5 (Meyer, 1972).

Dorometra A. H. Clark, 1917a, p. 128 [**Antedon nana* Hartlaub, 1890, p. 170; OD]. Cirri rarely more than 40; as many as 17 cirrals with distal ends produced and overlapping; distal cirrals much longer than proximal width. Third pinnule longest and stoutest. *Holocene:* northwestern and western Pacific Ocean, Indian Ocean (littoral to upper bathyal).——Fig. 64,*5*. **D. nana* (Hartlaub); peripheral cirrus, ×10 (Clark & Clark, 1967, p. 68, fig. 3d).

Euantedon A. H. Clark, 1912h, p. 31 [**Antedon moluccana* A. H. Clark, 1912e, p. 129; OD]. First 3 pinnules progressively smaller; first pinnule with 10 to 21 segments; second with fewer segments. [There is no suitable illustration available for the genus.] *Holocene:* western and southern Pacific Ocean (littoral to upper bathyal).

Eumetra A. H. Clark, 1908l, p. 230 [**E. chamberlaini;* OD]. Cirri rarely fewer than 40 (as many as 60), of 16 to 33 cirrals with distal ends produced and overlapping; distal cirrals much longer than proximal width. Third pinnule longest and stoutest. *Holocene:* western Pacific Ocean (sublittoral).——Fig. 64,*6*. **E. chamberlaini*; centrodorsal and base of arms, Philippines, holotype, USNM 35927, ×4 (Clark & Clark, 1967).

Iridometra A. H. Clark, 1908h, p. 130 [**Antedon adrestine* A. H. Clark, 1907e, p. 340; OD; =*I. melpomene* A. H. Clark, 1911b, p. 559]. First 3 pinnules of similar form and length, usually approximately 13 to 18 segments. [There is no suitable illustration available for the genus.] *Holocene:* northwestern and western Pacific Ocean (sublittoral to upper bathyal).

Mastigometra A. H. Clark, 1908k, p. 229 [**M. flagellifera*; OD]. Distal edges of brachials thickened. First 3 pinnules progressively smaller; first pinnule with at least 20 and as many as 50 segments. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* northern Indian and western Pacific Ocean (littoral to sublittoral).——Fig. 64,*7*. *M. micropoda* A. H. Clark; part of postradial series, Ceylon, USNM 35656, ×4 (Clark & Clark, 1967).

Palaeantedon Gislén, 1924, p. 182 [**Antedon solutus* Pomel, 1887 in 1885–1887, p. 336; OD]. Centrodorsal arched to hemispherical, aborally rounded without dorsal star or depression or significant cirrus-free area. Cirrus sockets numerous, small, without distinct sculpturing or with slightly elevated margin around lumen. Sockets closely placed, alternating in rows without forming columns. Centrodorsal cavity approximately 30 percent of centrodorsal diameter. No radial pits or coelomic impressions. Indistinct interradial furrows in adoral side of centrodorsal may correspond

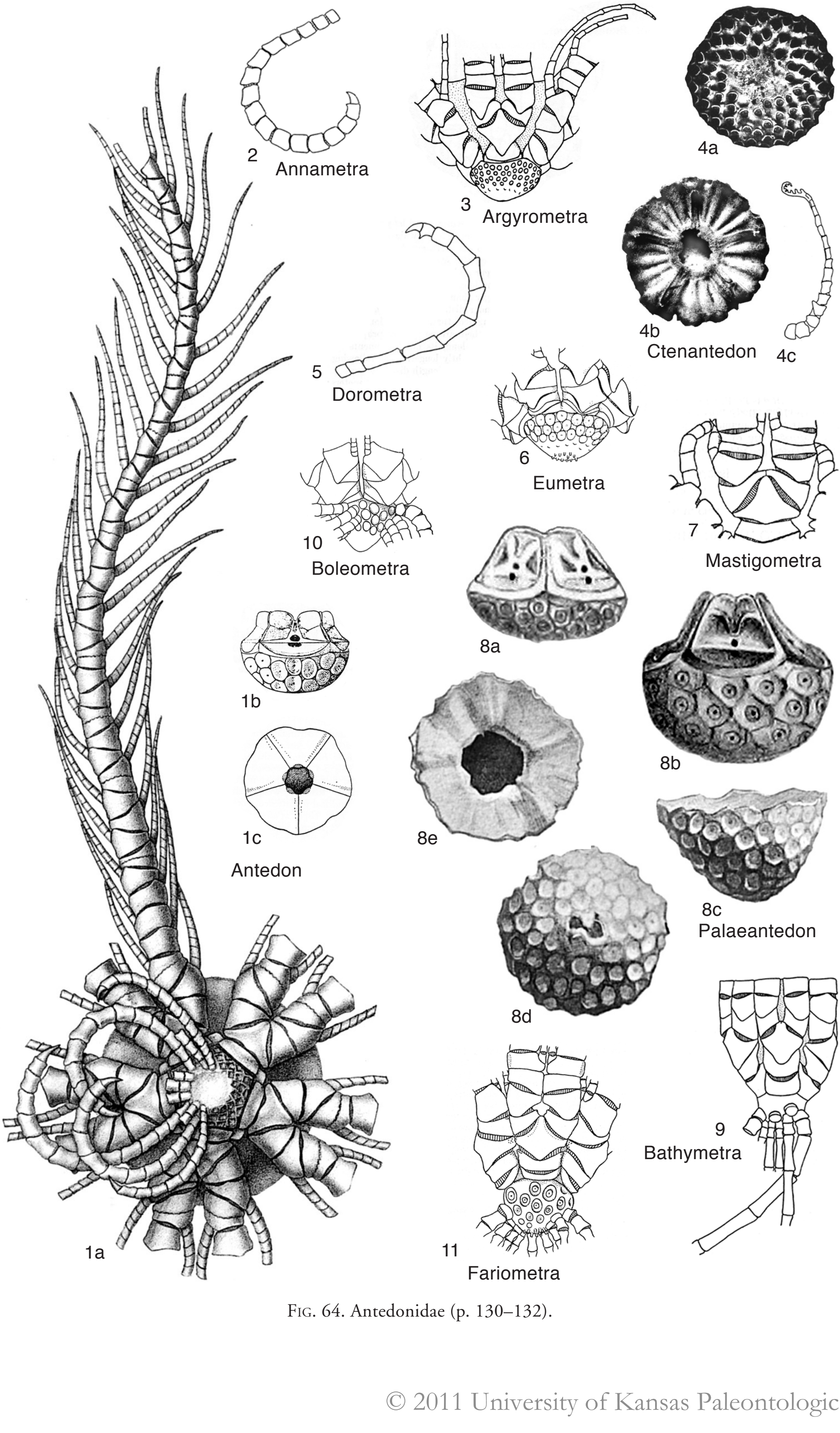

FIG. 64. Antedonidae (p. 130–132).

to reduced rod-shaped basals (not observed). Radials cover entire adoral side of centrodorsal, concealed or with low exposed surface. Radial articular facet gently sloping, rather high, with large, triangular interarticular ligament fossae. Adoral muscle fossae smaller, triangular. Radial cavity narrow to moderate. Synarthry between primibrachials 1 and 2, second primibrachial axil. *Paleogene (Eocene)–Pleistocene:* USA (South Carolina), *Eocene*; Italy, Hungary, Algeria, *Miocene*; Algeria, *Pleistocene.*——FIG. 64,*8a*. **P. soluta* (POMEL); cup with centrodorsal, Miocene, Algeria, ×10 (Pomel, 1887 in 1885–1887).——FIG. 64,*8b*. *P. ambigua* (POMEL); cup with centrodorsal, Miocene, Algeria, ×8 (Pomel, 1887 in 1885–1887).——FIG. 64,*8c–e*. *P. pannonica* (VADÁSZ); centrodorsal, *c*, lateral, *d*, aboral, *e*, adoral, Miocene, Hungary, ×10 (Vadász, 1915).

Toxometra A. H. CLARK, 1911b, p. 560 [**T. paupera*; OD] [=*Monilimetra* H. L. CLARK, 1938, p. 47 (type, *M. nomima*, OD)]. Distal ends of cirrals not produced and overlapping. Third pinnule longest and stoutest. [There is no suitable illustration available for the genus.] *Holocene:* western Pacific Ocean (littoral to sublittoral).

Subfamily BATHYMETRINAE A. H. Clark, 1909

[Bathymetrinae A. H. CLARK, 1909h, p. 177]

Centrodorsal conical to low hemispherical, rarely almost discoidal. Centrodorsal cavity large. Cirrus sockets rather small, 10 to 100 (typically 25 to 50), crowded or not, in alternating, irregular rows with tendency to form as many as 30 columns in some species; socket size may increase toward centrodorsal base. Cirrus-free aboral apex generally small, pointed to rounded, and smooth, rarely rugose. Length of cirri moderate, apical cirri rather short. Cirrals laterally compressed and generally long; length 1 to 6 times width. Distal cirrals commonly aborally carinate, sometimes with aboral spine. Basal rosette without rod-shaped basals. Exposed surface of radials generally low, concealed midradially in large species, and large in small species (*Bathymetra*). Radial articular facet high and rather steep. Interarticular ligament fossae triangular or low; narrow ridge separating interarticular fossae from adoral muscle fossae may be almost horizontal, straight or curved. Adoral muscle fossae large and high, rounded subtriangular with rounded adoral edge, separated by low narrow median ridge and small notch. Radial cavity narrow. Only 10 arms. Synarthry between primibrachials 1 and 2 commonly embayed. Primibrachial 1 commonly with parallel or converging sides and laterally overhung by primibrachial 2. First pinnule stiff and slender with elongate pinnulars. Second pinnule commonly the first genital pinnule. *Holocene.*

Bathymetra A. H. CLARK, 1908h, p. 132 [**Antedon abyssicola* CARPENTER, 1888, p. 191; OD]. Centrodorsal small, conical, with only 10 to 15 cirri; cirrus sockets well separated. Middle cirrals much longer than broad. Radials well exposed. *Holocene:* southern and central Pacific Ocean (bathyal to abyssal).——FIG. 64,*9*. **B. abyssicola* (CARPENTER); centrodorsal with cirri and base of crown, Midway, syntype, BMNH (18)88.11.9.57, ×5 (Clark & Clark, 1967).

Boleometra A. H. CLARK, 1936a, p. 248 [**Antedon clio* A. H. CLARK, 1907c, p. 79; OD]. Longest cirrals up to 3 times longer than wide; distal cirrals not longer than broad. First pinnule with as many as 30 segments. *Holocene:* northwestern Pacific Ocean (sublittoral).——FIG. 64,*10*. **B. clio* (A. H. CLARK); centrodorsal with cirri and base of 2 arms, holotype, USNM 22618, ×4 (Clark & Clark, 1967).

Fariometra A. H. CLARK, 1917a, p. 130 [**Trichometra explicata* A. H. CLARK, 19081, p. 232; OD]. Centrodorsal conical with 30 or more cirrus sockets. Peripheral cirri with 21 to 36 cirrals; longest cirrals at least 2.5 times longer than their constricted median widths; even the shorter distal cirrals still slightly longer than broad. Brachials with spinose distal margins. Proximal pinnules with short basal pinnulars but very attenuated distal ones. First pinnule with as many as 23 segments. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* Indian Ocean, western and eastern Pacific Ocean (bathyal).——FIG. 64,*11*. *F. io* (A. H. CLARK); centrodorsal with base of crown, Celebes, holotype, USNM 25452, ×7 (Clark & Clark, 1967).

Hathrometra A. H. CLARK, 1908h, p. 130 [**Alectro dentata* SAY, 1825, p. 153; OD; =*Asterias tenella* RETZIUS, 1783, p. 241]. Centrodorsal conical or convex conical with as many as 80 sockets. Cirri with as many as 33 segments, the longest more than 3 times longer than wide. First pinnule at least twice as long as second and third pinnules, of 30 to 40 segments. *Holocene:* western and northern Atlantic Ocean (sublittoral to bathyal).——FIG. 65,*1*. **H. tenella* (RETZIUS); centrodorsal with bases of 3 rays, northern Atlantic, ×5 (Messing & Dearborn, 1990).

Meteorometra A. M. CLARK, 1980, p. 199 [**M. monticola* A. M. CLARK, 1980, p. 200; OD]. Centrodorsal low hemispherical; aboral apex papillose. Cirri 25

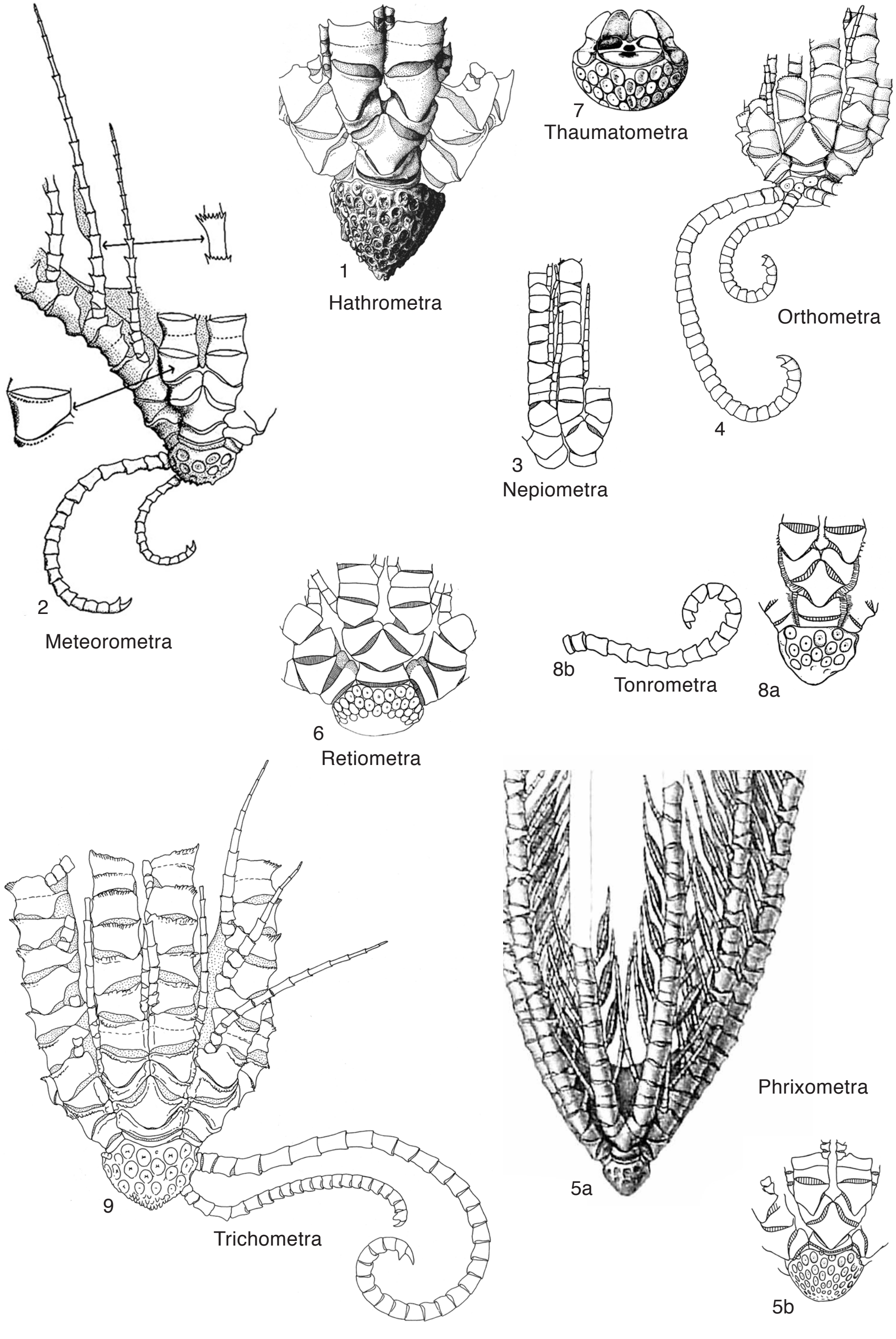

FIG. 65. Antedonidae (p. 132–134).

to 33, irregularly arranged. Largest cirri of 17 to 25 cirrals, the longest twice as long as wide. Brachials distally flared and finely spinose. Pinnulars (except basal 2) attenuated with distal ends strongly flared and spinose. First pinnule shortest. *Holocene:* northeastern Atlantic Ocean (upper bathyal).——Fig. 65,*2*. **M. monticola*; centrodorsal with cirri and proximal part of crown, with enlargement of a brachial and a pinnular to show ornamentation, holotype (centrodorsal from other specimen), paratypes, BMNH 1980.1.24.32-33, ×6 (A. M. Clark, 1980).

Nepiometra A. H. Clark, 1917a, p. 130 [**Antedon laevis* Carpenter, 1888, p. 187; OD]. Centrodorsal hemispherical with approximately 30 sockets. Cirri with as many as 30 segments, the longest less than twice as long as wide. Brachials with smooth distal margins. Primibrachials 2 laterally rugose or spinose. First pinnule with fewer than 20 segments, longer than second pinnule. *Holocene:* western Pacific Ocean (bathyal).——Fig. 65,*3*. **N. laevis* (Carpenter); parts of postradial series, Philippines, holotype, USNM 25452, ×4 (Clark & Clark, 1967).

Orthometra A. H. Clark, 1917a, p. 129 [**Trichometra hibernica* A. H. Clark, 1913b, p. 2; OD]. Centrodorsal flattened hemispherical, with as many as 30 sockets. Cirri stout and flexible with as many as 33 short cirrals, the distal ones slightly keeled aborally. Brachials highly ornamented with spinose frills. First pinnule of fewer than 15 segments, slightly longer than following pinnules. *Holocene:* northern Atlantic Ocean (bathyal).——Fig. 65,*4*. **O. hibernica* (A. H. Clark); centrodorsal with 2 cirri and bases of 3 rays, Ireland, paratype, ×5 (A. M. Clark, 1970).

Phrixometra A. H. Clark, 1917a, p. 131 [**Antedon longipinna* Carpenter, 1888, p. 185; OD]. Centrodorsal low subconical to hemispherical, with up to 50 sockets. Cirri with as many as 25 segments, the longest 2 to 3 times longer than wide. First pinnule longest. Genital pinnules of female with marsupium. *Holocene:* southwestern Atlantic Ocean, Southern Ocean (sublittoral to bathyal).——Fig. 65,*5a*. **P. longipinna* (Carpenter); centrodorsal and base of crown of adult specimen, southwestern Atlantic Ocean at 1100 m, ×4 (Carpenter, 1888, pl. 3,*2*).——Fig. 65,*5b*. *P. exigua* (Carpenter); centrodorsal with base of crown, ×5 (Clark & Clark, 1967).

Retiometra A. H. Clark, 1936a, p. 248 [**R. alascana*; OD]. Centrodorsal flattened hemispherical with wide, bare aboral surface and as many as 60 crowded sockets restricted to sides. Cirri with as many as 20 segments, the longest 3 times longer than wide; distal cirrals remain longer than wide. Brachials distally spinose. First pinnule with as many as 30 segments, twice as long as second and succeeding pinnules. *Holocene:* Arctic Ocean, northern Pacific Ocean (sublittoral to bathyal).——Fig. 65,*6*. **R. alascana*; centrodorsal with base of crown, Alaska, holotype, USNM E 1141, ×5 (Clark & Clark, 1967).

Thaumatometra A. H. Clark, 1908h, p. 127 [**Antedon ciliata* A. H. Clark, 1907c, p. 81; OD; =*Antedon tenuis* A. H. Clark, 1907c, p. 80]. Centrodorsal low subconical or hemispherical to almost discoidal with 25 to 60 sockets. Cirri of 10 to 22 segments, all longer than wide (except the first). First pinnule with 20 or fewer segments (exceptionally 35 in *T. tenuis*), usually at least slightly longer than second pinnule. *Holocene:* Indian Ocean, Pacific Ocean, northern and western Atlantic Ocean, Southern Ocean (lower sublittoral to upper abyssal).——Fig. 65,*7*. **T. tenuis* (A. H. Clark); cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950).

Tonrometra A. H. Clark, 1917a, p. 130 [**Antedon remota* Carpenter, 1888, p. 184; OD]. Centrodorsal hemispherical or rounded conical, with 30 to 50 sockets. Cirri with 18 to 37 segments, the longest strongly constricted with flared ends. Primibrachial series and arm bases in close lateral contact, brachials more or less spinose distally. First pinnule long, delicate. Second pinnule similar. *Holocene:* Southern Ocean, western Pacific Ocean (bathyal to upper abyssal).——Fig. 65,*8a–b*. **T. remota* (Carpenter), holotype, BMNH (18)88.11.9.49, Southern Ocean; *a*, centrodorsal with base of arm (Clark & Clark, 1967, p. 690, fig. 41a); *b*, apical cirrus, ×5 (Clark & Clark, 1967, p. 690, fig. 41c).

Trichometra A. H. Clark, 1908h, p. 131 [**Antedon aspera* A. H. Clark, 1908b, p. 229; OD; =*Antedon cubensis* Pourtalès, 1869, p. 356]. Centrodorsal rounded conical to hemispherical, with as many as 65 sockets arranged irregularly or in 30 columns. Cirri with 25 to 45 cirrals, the longest 2 to 3 times longer than wide. Brachitaxes and proximal brachials typically laterally flattened with more or less spinose edges. First pinnule longer than second and third pinnules. *Holocene:* northern and western Atlantic Ocean, central Pacific Ocean (sublittoral to bathyal).——Fig. 65,*9*. **T. cubensis* (Pourtalès); centrodorsal, small apical and large peripheral cirrus (note opposing spine on penultimate cirral) and bases of 3 rays with the first 3 pinnules, syzygy between secundibrachials 3 and 4 and 9 and 10 indicated by broken line, USNM, ×5 (Messing & Dearborn, 1990, p. 20, fig. 17).

Subfamily HELIOMETRINAE
A. H. Clark, 1909

[Heliometrinae A. H. Clark, 1909h, p. 176] [incl. subfamily Promachocrinae Jaekel, 1918, p. 74]

Centrodorsal rounded, commonly with cirrus-free aboral apex, to low hemispherical with small, flattened, or concave cirrus-free aboral apex or deep aboral pit. Cirrus sockets numerous, crowded, commonly regularly alternating, forming 4 to 7 circles. Centrodorsal cavity moderate. Shallow radial pits or furrows may be present at edge of centrodorsal cavity in *Florometra*. Cirri 30 to 200, long and stout, laterally compressed. Either 2 pairs of radial nerve canals and no basal rays (*Anthometrina*, *Florometra*, *Heliometra*), or only 2 radial nerve canals and basal rays present (*Solanometra*, *Promachocrinus*); vestiges of basal rays may be present in *Comatonia*. Radials with low exposed surface or concealed. Radial articular facet high, commonly rather concave with aboral ligament fossa and interarticular ligament fossae sloping outward; muscle fossae almost parallel to oral-aboral axis, narrow, higher than interarticular ligament fossae, and separated by a median ridge and notch. Radial cavity moderate to rather large. In *Promachocrinus*, the 5 basals are broad and flattened plates, united around center and with interradial rod-shaped basal rays, followed by 10 radial and pararadial ossicles. The pararadials, which lie interradially above the basals, are retarded in larval development and early growth. Arms divided at primibrachials 2; rarely with some arms also divided at secundibrachials 2. Primibrachial 1 commonly with converging sides, may be overhung by lateral edge of primibrachial 2. Synarthrial articulations commonly embayed. First pinnule long, flagellate, with numerous short pinnulars. Distal pinnulars of proximal pinnules may bear rudimentary teeth forming a comb, as in Comasteroidea but weaker. [ELÉAUME (2006) discovered the differences in basals and radial architecture that distinguish 2 groups of extant genera: *Promachocrinus* and *Solanometra* versus *Heliometra*, *Florometra,* and *Anthometrina*.] *Lower Cretaceous (Albian)–Holocene.*

Heliometra A. H. CLARK, 1907f, p. 350 [**Alecto eschrichtii* MÜLLER, 1841, p. 183; OD; =*Alecto glacialis* OWEN, 1833, p. 120; =*Antedon quadrata* CARPENTER, 1884c, p. 375; =*Antedon bartensi* CARPENTER, 1886, p. 9; =*Antedon arctica* A. H. CLARK, 1907c, p. 82; =*Heliometra juvenalis* A. H. CLARK, 1908g, p. 239]. Centrodorsal low hemispherical; cirrus sockets 45 to 100. Cirri long, stout, with 30 to 58 cirrals, the longest rarely twice as long as wide. Brachials smooth (finely spinose in some small specimens). Arm length reaches 25 cm. No rudimentary comb on oral pinnules. [Distinguished from *Florometra* by size only.] *Holocene:* Arctic Ocean, northern Atlantic and Pacific Ocean (sublittoral to bathyal).——FIG. 66,*1*. **H. glacialis* (OWEN); centrodorsal with small apical and large peripheral cirrus and bases of 3 rays with first 3 pinnules, western Atlantic, ×1.5 (Messing & Dearborn, 1990).

Allionia MICHELOTTI, 1861, p. 354 [**A. oblita*; M]. Cup and centrodorsal low, 5-sided. Centrodorsal with small, closely placed cirrus sockets and narrow aboral pit; adoral side of centrodorsal concave, with rather narrow centrodorsal cavity and furrows for rod-shaped basals. *Neogene (Miocene):* Italy.——FIG. 66,*2a–c*. **A. oblita*; cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, holotype, ×6 (Noelli, 1900).

Anthometrina ELÉAUME, HESS, & MESSING, herein, p. 224, *nom. nov. pro Anthometra* A. H. CLARK, 1915b, p. 135, *non* BOISDUVAL, 1840, p. 231 (type, *A. plumularia,* OD) [**Antedon adriani* BELL, 1908, p. 4; OD]. Brachials with high median keel. First pinnule much larger than second pinnule. [*Anthometra* was originally mentioned by A. H. CLARK, 1913d, p. 60, as a subgenus of *Promachocrinus*, without any diagnosis; it was diagnosed in 1915 by A. H. CLARK (1915b; see CLARK & CLARK, 1967, p. 448). MARC ELÉAUME was the first to recognize the junior status of *Anthometra*, but this was never published.] *Holocene:* Southern Ocean (sublittoral to bathyal).——FIG. 66,*3*. **A. adriani* (BELL); drawn from different specimens, ×1 (Bell, 1908).

Comatonia A. H. CLARK, 1916a, p. 115 [**Actinometra cristata* HARTLAUB, 1912, p. 473; OD]. Centrodorsal hemispherical or low rounded conical, with 50 to 100 crowded sockets. Cirri slender, with 12 to 23 segments, the longest up to 4 times longer than wide. Vestiges of basal rays fused to centrodorsal in one specimen. Spinose midaboral knob or ridge on some proximal brachials. First pinnule with as many as about 40 flat, round, well-developed comb teeth; weaker comb sometimes on second pinnule. [Originally placed in Comasteridae based on a well-developed comb. MESSING (1981) transferred it to Antedonidae and suggested, following GISLÉN (1924, p. 229, footnote), that it most closely approached the Heliometrinae.] *Holocene:* tropical western Atlantic Ocean (sublittoral to bathyal).——FIG. 67,*1*. **C. cristata* (HARTLAUB); proximal crown with centrodorsal and cirri, ×3 (Hartlaub, 1912).

Florometra A. H. CLARK, 1915b, p. 137 [**Antedon eschrichti var. magellanica* BELL, 1882b, p. 651; M; subsequent designation of another type species by A. H. CLARK (1914a) rejected by A. M. CLARK (in CLARK & CLARK, 1967), according to the *Code*, ICZN, 1999]. Centrodorsal subconical to almost hemispherical, commonly low or with an aboral depression. Longest cirrals may be more than twice as long as wide. Brachials typically spinose. [This genus was originally listed by A. H. CLARK (1913d, p. 62) as subgenus of *Promachocrinus*, but without any diagnosis; in 1915 (A. H. CLARK, 1915b) a diagnosis was published; see CLARK & CLARK, 1967, p. 294.] *Holocene:* Southern Ocean,

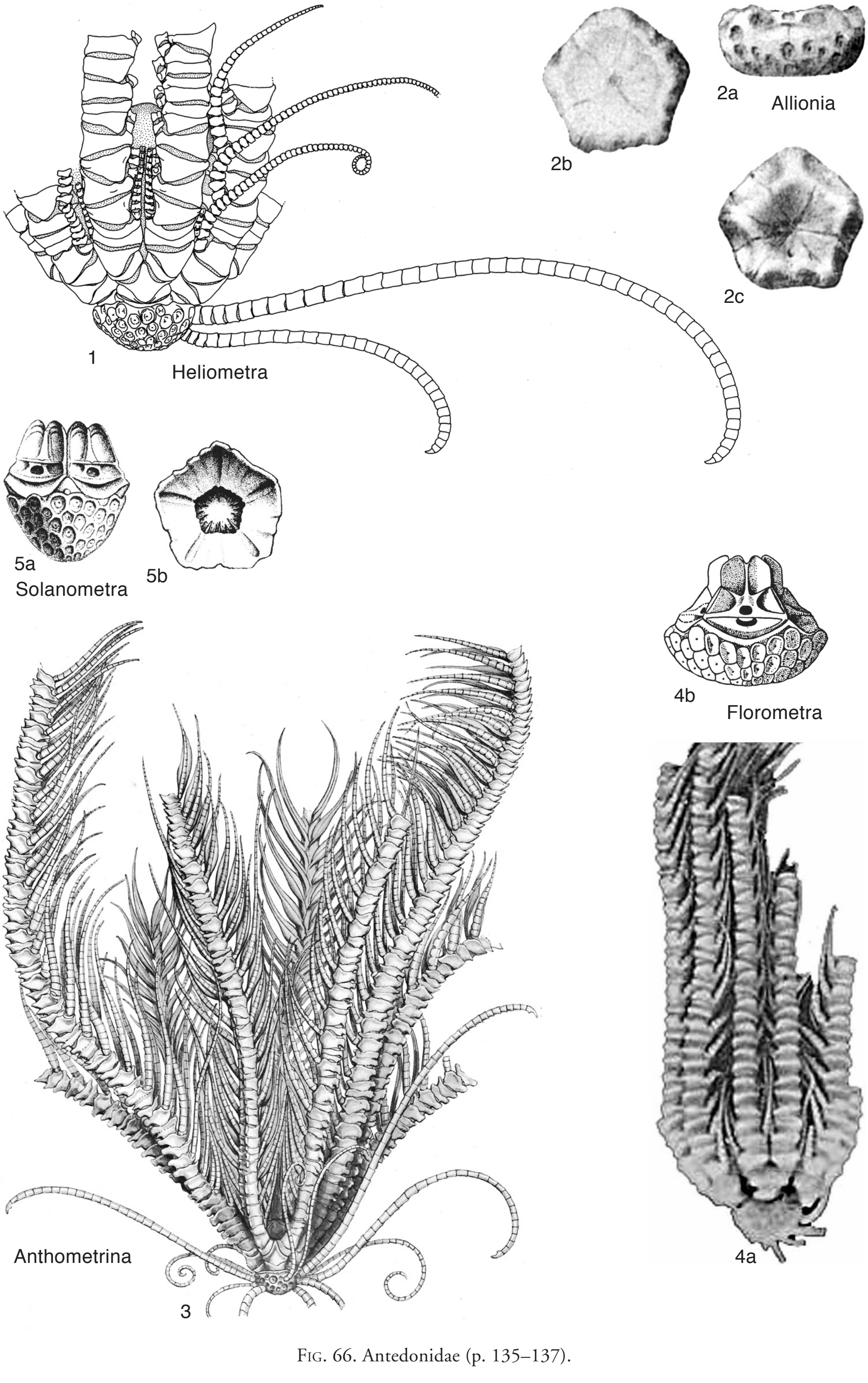

FIG. 66. Antedonidae (p. 135–137).

eastern and northern Pacific Ocean (sublittoral to bathyal).——FIG. 66,*4a*. **F. magellanica* (BELL); proximal part of intact specimen, ×1.5 (A. H. Clark, 1915b).——FIG. 66,*4b*. *F. asperrima* (A. H. CLARK); cup with centrodorsal, ×3 (A. H. Clark, 1921 in 1915–1950).

Hertha VON HAGENOW, 1840, p. 664 [**H. mystica*; M]. Centrodorsal arched, from high, rounded subconical to low discoidal, with sharp adoral edge and rounded aboral side without depression or significant cirrus-free area. No dorsal star. Cirrus sockets small, crowded, without distinct sculpturing. Adoral side of centrodorsal without radial pits or coelomic impressions. Centrodorsal cavity less than 30 percent of diameter, except in very small specimens. Rod-shaped basals present, but not exposed interradially. Radials without exposed surface, completely covering entire adoral side of centrodorsal or not. Radial articular facet high, gently sloping, commonly concave. Interarticular ligament fossae rather small; adoral muscle fossae high, rather narrow, subtriangular. Radial cavity narrow. Arms divided at primibrachial 2. Synarthry between primibrachials 1 and 2. *Upper Cretaceous (Maastrichtian)–Paleogene (Danian), Neogene (?Miocene):* Denmark, England, Germany, Sweden, *Maastrichtian;* Denmark, *Danian;* Italy, *?Miocene*.——FIG. 67,*2a–e*. **H. mystica*; cup with centrodorsal, *a*, lateral, *b*, aboral, *c*, distal, Danian, Sweden, MGUH 8996, ×7.5; *d*, distal view of cup with primibrachials, Maastrichtian, Germany, MGUH 8995, ×10; *e*, adoral view of centrodorsal, Danian, Denmark, MGUH 1213, ×7 (Rasmussen, 1961).

Promachocrinus CARPENTER, 1879b, p. 385 [**P. kerguelensis* CARPENTER, 1881a, pl. 12, SD CARPENTER, 1888, p. 348; =*P. kerguelensis* CARPENTER, 1879b, p. 385, *nom. nud.*; =*P. kerguelenensis* BELL, 1908, p. 3; =*P. vanhoeffenianus* MINCKERT, 1905, p. 496; =*P. joubini* VANEY, 1910, p. 158]. Radials 10, with one pair of nerve canals open medially. Arms 20; each ray divided at primibrachial 2. *Holocene:* Southern Ocean (sublittoral to bathyal).——FIG. 67,*3a–c*. **P. kerguelensis*; *a,* centrodorsal with cirri and base of crown, Coulman Island at 183 m, Antarctica, ×2 (Bell, 1908); *b*, cup with centrodorsal, ×4 (Carpenter, 1888, pl. 1,*1*); *c*, proximal view of cup with radials, pararadials, and basals, ×4 (Rasmussen, 1978).

Roiometra A. H. CLARK, 1944, p. 304 [**R. columbiana*; M]. Centrodorsal apparently hemispherical or subconical, covered by more than 100 crowded sockets in several alternating circles; no conspicuous cirrus-free apical area. Peripheral cirri slender, more than 100, 27 to 34 mm long, with 25 to 30 cirrals; apical cirri much shorter. Proximal cirrals as much as 3 to 4 times longer than wide; distal cirrals 1 to 1.5 times longer than wide, smooth and without aboral spines. Arms 10, divided at primibrachial 2. Synarthry between primibrachials 1 and 2. Syzygy between secundibrachials 3 and 4 and more distally. Distal edge of brachials tuberculate. Pinnules not stiff; pinnulars short, length not exceeding width. Proximal pinnulars more or less developed into a distal spine. [Genus referred by A. H. CLARK (1944) to Palaeantedonidae and compared with large specimens of *Florometra*. There is no suitable illustration available for the genus.] *Lower Cretaceous (Albian):* Colombia.

Solanometra A. H. CLARK, 1911g, p. 727 [**Antedon antarctica* CARPENTER, 1881a, p. 198; SD A. H. CLARK, 1914a, p. 3; =*Antedon australis* CARPENTER, 1888, p. 146; =*Heliometra glabra* A. H. CLARK, 1907f, p. 351, *nom. nov. pro Antedon australis* CARPENTER, 1888, p. 146, *non* CARPENTER, 1882b, p. 510]. Centrodorsal hemispherical to rounded subconical, with 80 or more sockets; cirri typically 25 to 30 cirrals, the longest rarely twice as long as wide. No rod-shaped basals. Radials 5, with one pair of nerve canals open medially. Brachials very stout. *Holocene:* Southern Ocean (sublittoral to bathyal).——FIG. 66,*5a–b*. **S. antarctica* (CARPENTER); *a,* cup with centrodorsal, ×3 (Carpenter, 1881a, pl. 1,*6a*); *b*, adoral view of centrodorsal, ×3 (Carpenter, 1888, pl. 1,*6d,* wrongly lettered *6a*).

Subfamily ISOMETRAINAE
A. H. Clark, 1917

[*nom. nov.* FET & MESSING, 2003, p. 293–296, *pro* Isometrinae A. H. CLARK, 1917a, p. 127, *non* KRAEPELIN, 1891 (Arachnida, Scorpiones); ICZN, 2005]

Centrodorsal conical to hemispherical, with 25 to 63 sockets arranged in irregular circles. Cirri stout with 30 to 75 short cirrals; apical cirri shorter. Centrodorsal cavity moderate. Rod-shaped basals apparently not present in adults. Radials generally with exposed surface, commonly diverging. Arms 10, divided at primibrachial 2. Proximal pinnules rather short and stout. Genital pinnules with expanded proximal pinnulars. Viviparous. [FET and MESSING (2003) proposed renaming the subfamily Isometrinae A. H. CLARK, 1917, as Isometrainae to remove homonymy with Isometrinae KRAEPELIN, 1891 (Arachnida, Scorpiones). The proposal was accepted by the International Commission on Zoological Nomenclature (ICZN, 2005), which also ruled to maintain A. H. CLARK as author of the family.] *Holocene.*

Isometra A. H. CLARK, 1908h, p. 133 [**Antedon challengeri* A. H. CLARK, 1907f, p. 353; OD; *nom. nov. pro Antedon lineata* CARPENTER, 1888, p. 183, *non* POMEL, 1887, p. 335]. Characters as for subfamily. [*Isometra angustipinna* CARPENTER, 1888, p. 189, is without a doubt a juvenile of *Antedon lineata* CARPENTER, 1888 (*non Antedon lineatus* POMEL, 1887). *A. lineata* was renamed *A. challengeri* by A. H. CLARK (1907f), before its relationship to *I. angustipinna* was detected.] *Holocene:* southern Atlantic Ocean,

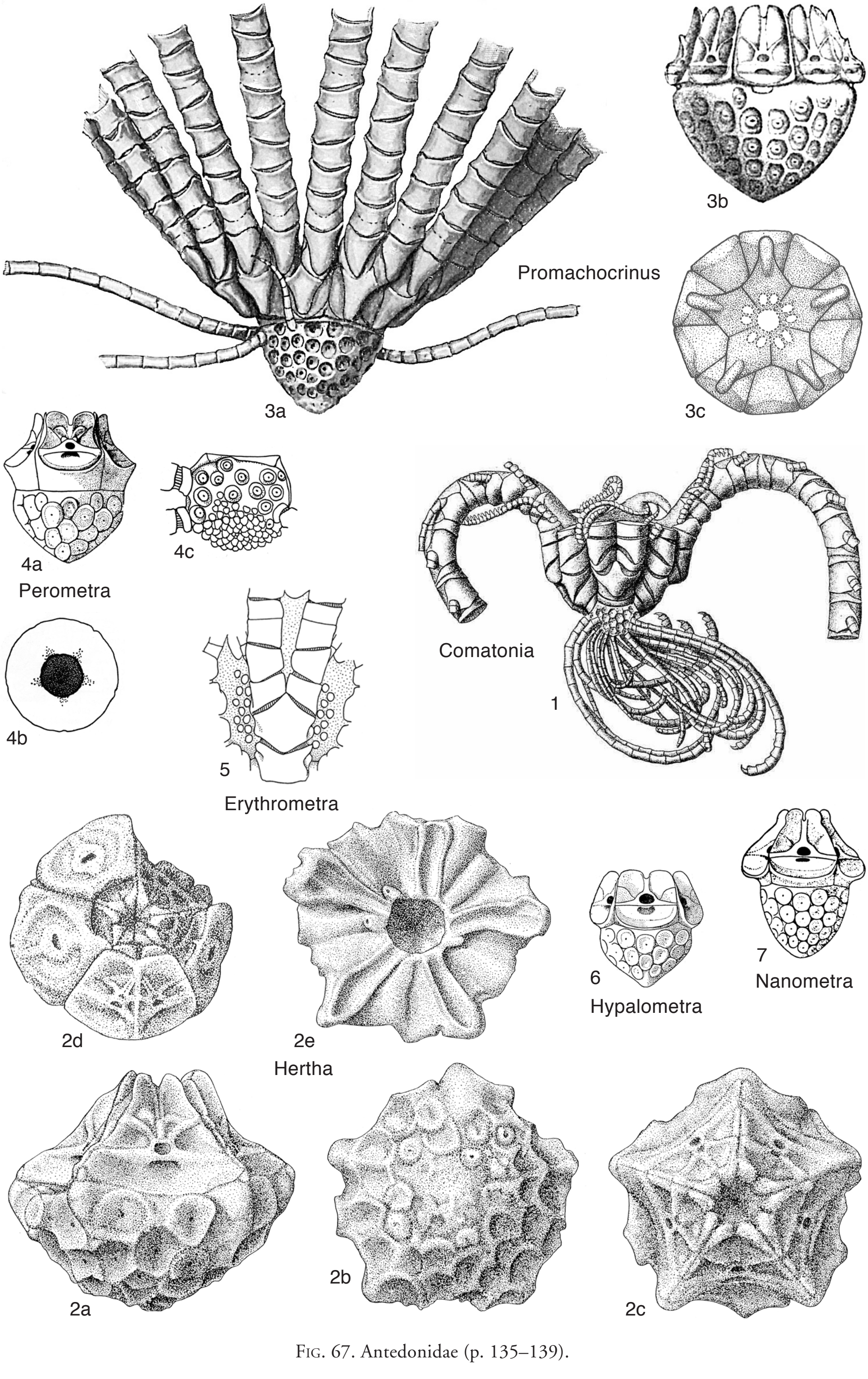

FIG. 67. Antedonidae (p. 135–139).

Southern Ocean (bathyal).——Fig. 68,*1a*. **I. challengeri* (Carpenter); proximal crown with cirri, southwestern Atlantic Ocean at 1100 m, ×4 (Carpenter, 1888, pl. 14,*4*, as *Antedon lineata*).——Fig. 68,*1b*. *I. vivipara* Mortensen; cup with centrodorsal, ×7 (Gislén, 1924).

Subfamily PEROMETRINAE
A. H. Clark, 1909

[Perometrinae A. H. Clark, 1909h, p. 176]

Centrodorsal rounded conical; aboral pole rounded, commonly rugose or tuberculate; cirrus-free portion broad or small. Cirrus sockets crowded, alternating in irregular circles, increasing in size toward base. Adoral side of centrodorsal smooth, without radial pits, interradial furrows, or ridges. Centrodorsal cavity 30 to 40 percent of centrodorsal diameter. Cirri rather long, with 25 to 55 cirrals; distal cirrals with aboral spine or process. Radials usually prominent, with exposed surface concave and projecting to low and almost concealed midradially. Radial articular facet gently sloping, rather wide, separated by narrow interradial margin. Interarticular ligament fossae triangular, approximately as high as adoral muscle fossae. Ridge separating interarticular from muscle fossa narrow, commonly indistinct. Low, commonly wide midradial ridge and notch. Radial cavity funnel shaped. Arms divided at primibrachial 2 and at secundibrachial 2 in some arms of *Perometra afra*. Primibrachial 1 low, commonly narrow and laterally overhung by proximal end of primibrachial 2. Synarthry between brachials 1 and 2 usually embayed. First pinnule stout, with fewer than 20 pinnulars. First interior pinnule frequently absent; first exterior pinnule sometimes absent. Second pinnule differs from genital pinnules. [Rod-shaped basals reported in *Nanometra clymene* but not visible in accompanying figure (Clark & Clark, 1967, p. 480) and unknown in other genera.] *Holocene.*

Perometra A. H. Clark, 1907f, p. 357 [**Antedon diomedeae* A. H. Clark, 1907d, p. 146; OD]. Proximal brachials with smooth, flattened sides apposed against those of adjacent ray. Synarthrial tubercles prominent. First interior pinnule sometimes absent. *Holocene:* Indian and western Pacific Ocean (sublittoral).——Fig. 67,*4a–b*. **P. diomedeae* (A. H. Clark); *a,* cup with centrodorsal, ×7 (A. H. Clark, 1921 in 1915–1950, p. 53, fig. 83); *b*, adoral view of centrodorsal, ×7 (A. H. Clark, 1915a in 1915–1950, p. 262, fig. 289).——Fig. 67,*4c*. *P. afra* A. H. Clark; oblique aboral view of centrodorsal, syntype, BMNH 1907.7.1.84, ×7 (Clark & Clark, 1967).

Erythrometra A. H. Clark, 1908h, p. 126 [**Antedon ruber* A. H. Clark, 1907d, p. 146; OD; =*E. ruber* A. H. Clark, 1908h, p. 126; =*E. rubra*, Gislén, 1922, p. 140]. Proximal brachials not laterally flattened, with tuberculate margins. Disk bearing rounded nodules. First interior pinnule usually absent. *Holocene:* western Pacific Ocean (sublittoral).——Fig. 67,*5*. **E. rubra* (A. H. Clark); postradial series with small interradial plates, USNM 35642, ×7 (Clark & Clark, 1967).

Hypalometra A. H. Clark, 1908h, p. 133 [**Antedon defecta* Carpenter, 1888, p. 206; OD]. Small. First interior and exterior pinnules both absent. *Holocene:* western Atlantic Ocean (sublittoral to upper bathyal).——Fig. 67,*6*. **H. defecta* (Carpenter); cup with centrodorsal, enlarged (A. H. Clark, 1921 in 1915–1950, p. 53, fig. 85).

Nanometra A. H. Clark, 1907f, p. 348 [**Antedon minor* A. H. Clark, 1907d, p. 144; OD; =*Antedon bowersi* A. H. Clark, 1907d, p. 148; =*Antedon orientalis* A. H. Clark, 1907e, p. 341; =*Nanometra minckerti* A. H. Clark, 1907f, p. 349, *nom. nov. pro Antedon minor* A. H. Clark, 1907d, p. 144, *non Antedon avenionensis* var. *minor* Nicolas, 1898, p. 406]. Proximal brachials not laterally flattened, with tuberculate margins. Disk naked. First interior pinnule present. [*Nanometra bowersi* has priority among later recognized synonyms.] *Holocene:* western Pacific Ocean (sublittoral to bathyal).——Fig. 67,*7*. **N. bowersi* (A. H. Clark); cup with centrodorsal, ×5 (A. H. Clark, 1921 in 1915–1950, p. 67, fig. 106).

Subfamily THYSANOMETRINAE
A. H. Clark, 1909

[Thysanometrinae A. H. Clark, 1909h, p. 176]

Centrodorsal hemispherical to almost discoidal, with cirrus-free aboral apex. Cirrus sockets 30 to 40, crowded, in 3 or 4 circles. Cirrals long, slender, laterally compressed, without aboral projections. No rod-shaped basals, but commonly with interradial ridges on adoral side of centrodorsal. Centrodorsal cavity moderate. Large species commonly with subradial cleft. Surface of radials low, more or less concealed midradially. Radial articular facet in *Thysanometra* steep, adoral muscle fossae wider than high, separated from interarticular ligament fossae by curved, almost horizontal ridge; in *Coccometra,* radial articular facet high and narrow, triangular, with muscle fossae high,

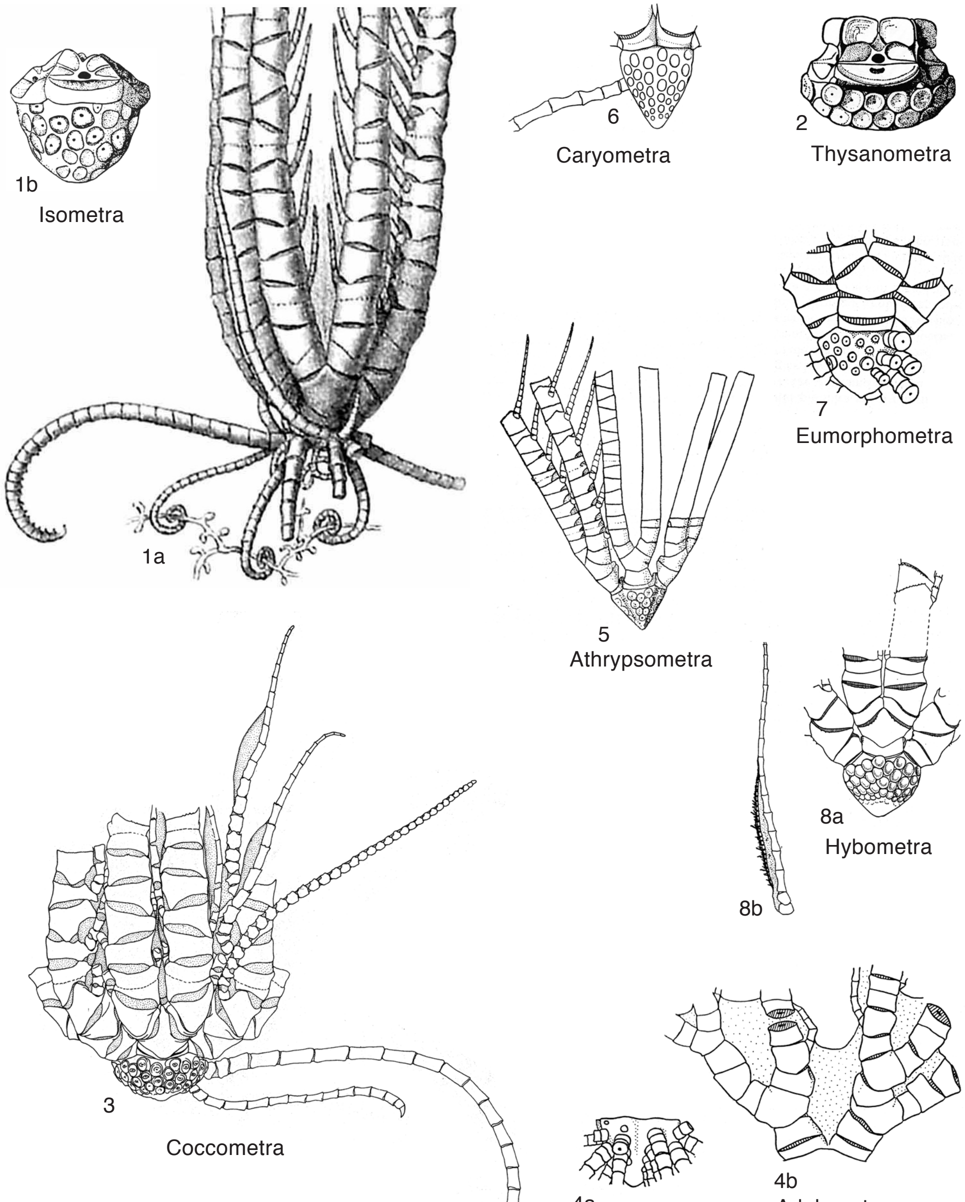

FIG. 68. Antedonidae (p. 137–143).

narrow, subtriangular, separated from interarticular ligament fossae by oblique ridge. Radial cavity in *Thysanometra* moderate to rather large, in *Coccometra* narrow. Arms 10, divided at primibrachial 2. Primibrachial 1 low, sides commonly converging and overhung by proximal part of primibrachial 2. Synarthry between brachials 1 and 2 flat to embayed. First pinnule long, flagellate, composed of 30 to 40 usually short pinnulars. Second pinnule resembles those following. *Holocene.*

Thysanometra A. H. CLARK, 1907f, p. 351 [**Antedon tenelloides* A. H. CLARK, 1907c, p. 73; OD]. Radial articular facet wider than high. Radial cavity moderate to large. Distal pinnules longer than proximal ones. *Holocene:* northwestern Pacific Ocean (sublittoral to upper bathyal).——FIG. 68,*2*. **T. tenelloides* (A. H. CLARK); cup with centrodorsal, ×4 (A. H. Clark, 1921 in 1915–1950, p. 52, fig. 89).

Coccometra A. H. CLARK, 1908h, p. 128 [**Comatula hagenii* POURTALÈS, 1868, p. 111; OD]. Radial articular facet high, narrow, and triangular. Radial cavity narrow. Distal pinnules shorter than proximal ones. *Holocene:* western Atlantic Ocean (sublittoral to bathyal).——FIG. 68,*3*. **C. hagenii* (POURTALÈS); centrodorsal, small apical and large peripheral cirrus, bases of 3 rays with first 3 pinnules, second and third pinnules with gonads, USNM E17540, ×4 (Messing & Dearborn, 1990, p. 18, fig. 14a).

Subfamily UNCERTAIN

[MESSING and WHITE (2001) removed 11 genera from Zenometrinae (see RASMUSSEN, 1978, p. 912) when they raised the subfamily to family status, Zenometridae, with only 3 genera. They assigned 4 species formerly in *Psathyrometra* to a new genus, *Athrypsometra*.]

Adelometra A. H. CLARK, 1907f, p. 363 [**Antedon angustiradia* CARPENTER, 1888, p. 253; M]. Centrodorsal conical, not higher than wide, with sockets in 10 columns, separated interradially by naked, shallow groove. Proximal brachials smooth, cylindrical, and not in lateral contact. Single known specimen has 14 arms; synarthry between primibrachials 1 and 2; secundibrachials with an axil at second or fourth ossicle or undivided; placement of syzygies depends on whether the secundibrachial series is part of the undivided arm (syzygy between secundibrachials 3 and 4) or terminates in an axil and ray division (no syzygy between secundibrachials 3 and 4). *Holocene:* western Pacific Ocean (sublittoral).——FIG. 68,*4a–b*. **A. angustiradia* (CARPENTER), Kai Islands at 256 m, holotype; *a,* interradial view of centrodorsal, ×3 (Clark & Clark, 1967, p. 506, fig. 25a); *b*, 2 radials with arm bases, ×3 (Clark & Clark, 1967, p. 506, fig. 25c).

Anisometra JOHN, 1939, p. 204 [**A. frigida*; M]. Centrodorsal slightly higher than wide, with sockets in 10 columns, separated interadially by a narrow, flat space near the centrodorsal base. Proximal brachials with conspicuously spinose margins. [There is no suitable illustration available for the genus.] *Holocene:* Southern Ocean (sublittoral).

Athrypsometra MESSING & WHITE, 2001, p. 175 [**Psathyrometra mira* A. H. CLARK, 1909j, p. 648; OD]. Centrodorsal conical, as wide across the base as high, or wider; with cirrus sockets shallow, almost flush with centrodorsal surface, not bowl-like, in 10 columns separated by interradial spaces. Basals sometimes visible interradially. Aboral surface of brachials flattened; synarthrial projections absent; proximal segments of proximal pinnules short or subtetragonal. *Holocene:* western Pacific and Indian Ocean (bathyal).——FIG. 68,*5*. **A. mira* (A. H. CLARK), centrodorsal and proximal part of crown, Andaman Islands, holotype, ×2.5 (A. H. Clark, 1912c).

Balanometra A. H. CLARK, 1909h, p. 177 [**Antedon balanoides* CARPENTER, 1888, p. 207; OD; =*Perometra elongata* A. H. CLARK, 19081, p. 229]. Centrodorsal conical, much higher than wide, with sockets in 10 columns separated interradially by furrow. First pinnule absent. *Holocene:* western Pacific Ocean (sublittoral).——FIG. 69,*1*. **B. balanoides* (CARPENTER); centrodorsal with cirri, cup, and proximal brachials, ×2 (Carpenter, 1888, pl. 33,*6*).

Caryometra A. H. CLARK, 1936a, p. 247 [**Adelometra tenuipes* A. H. CLARK, 1908b, p. 236; OD; =*Antedon arcana* HARTLAUB, 1912, p. 402; =*Psathyrometra acuta* A. H. CLARK, 1934a, p. 1]. Centrodorsal conical, higher or lower than wide, without interradial ridges, grooves, or spaces, with sockets in 10 or 15 columns not segregated into radial groups. Largest cirri with as many as 35 cirrals. Proximal brachials spiny or not. First 2 pinnules with elongate distal segments, shorter than third pinnule. *Holocene:* western Atlantic Ocean (upper bathyal).——FIG. 68,*6*. **C. tenuipes* (A. H. CLARK); centrodorsal with cirrus and radials, Puerto Rico, USNM E 3123, ×5 (Clark & Clark, 1967).

Cyclometra A. H. CLARK, 1911d, p. 87 (A. H. CLARK, 1911c, p. 51, *nom. nud.*) [**C. flavescens*; M]. Centrodorsal conical, lower than wide, without interradial ridges, grooves, or spaces, with as many as 80 sockets in 15 columns. First 2 pinnules flexible distally, with as many as 45 pinnulars, the distal segments only slightly longer than wide. [There is no suitable illustration available for the genus.] *Holocene:* Indian Ocean (bathyal).

Eometra A. H. CLARK, 1936a, p. 248 [**Psathyrometra antarctica* A. H. CLARK, 1915b, p. 116; OD]. Centrodorsal rounded conical, with sockets in 10 crowded columns of 2 or 3 each, without interradial ridges, grooves, or spaces. Cirri slender, slightly curved, tapering to a fine point; longest cirrals up to 4 times longer than wide and without aboral processes. Third and following pinnules much longer than second pinnule. [There is no suitable illustration available for the genus.] *Holocene:* Southern Ocean (bathyal).

Eumorphometra A. H. CLARK, 1915b, p. 117 [**E. concinna*; OD]. Centrodorsal conical, with sockets in 10 or 15 (rarely 20) irregular crowded columns not separated into radial groups. Cirri with 30

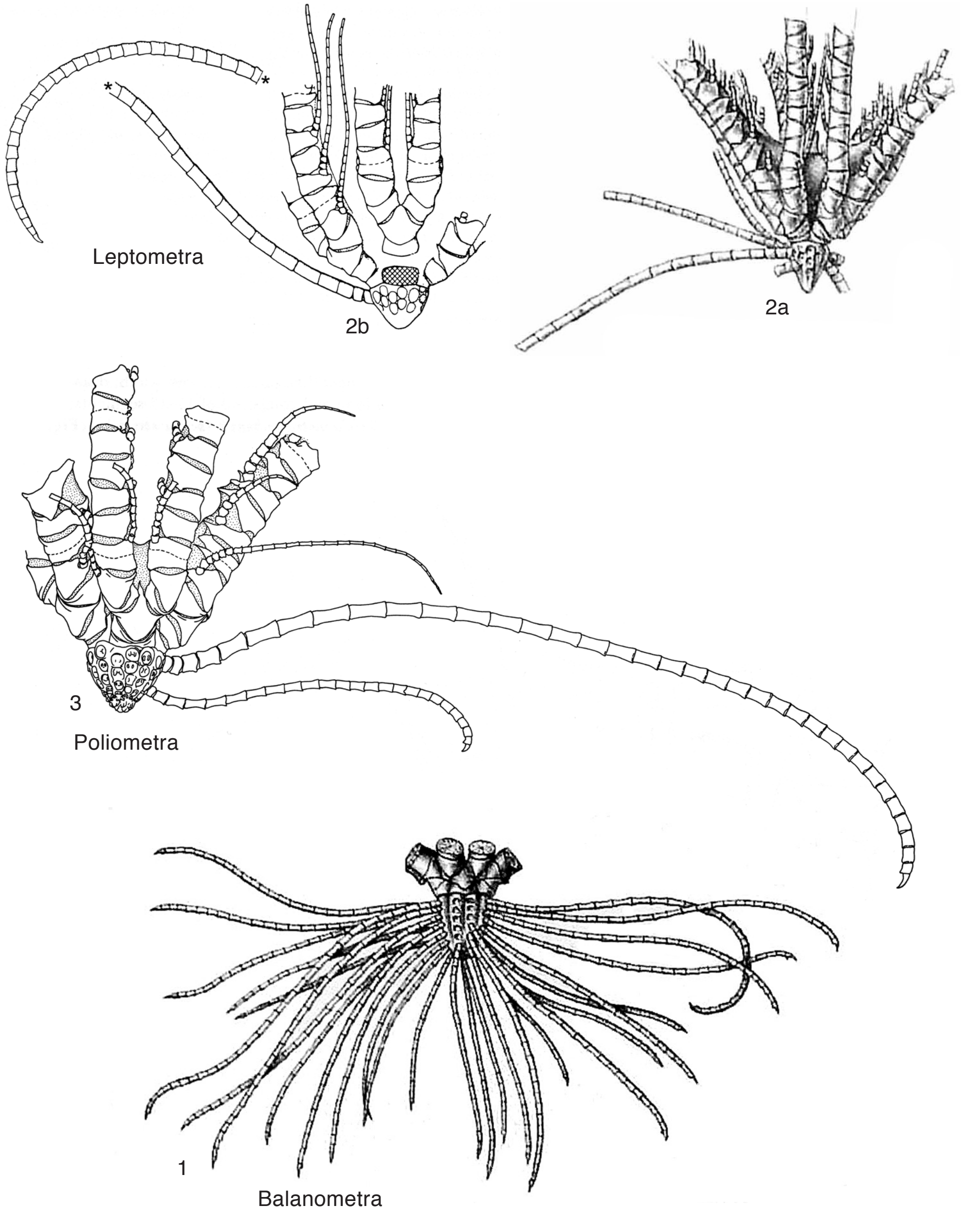

FIG. 69. Antedonidae (p. 141–143).

to 45 cirrals, the longest approximately twice as long as wide. Proximal brachials typically finely spinose and not in lateral contact. First 2 pinnules similar. Females are viviparous in the 2 species for which females are known. [Illustrations of the type species do not display the relevant characters of the genus.] *Holocene:* Southern Ocean, southern Atlantic Ocean (upper bathyal).——FIG. 68,*7*. *E. hirsuta* (CARPENTER); centrodorsal with base of crown, holotype, ×4 (Clark & Clark, 1967, p. 539, fig. 29c).

Hybometra A. H. CLARK, 1913d, p. 54 [**H. senta*; OD]. Centrodorsal conical, slightly wider than high, with sockets in 20 columns, not separated into radial groups; interradial columns of 4 sockets each; the radial ones abbreviated toward apex. Second pinnule very long, third pinnule much shorter, distal pinnules longer, with ambulacral spines. *Holocene:* western and ?southeastern Atlantic Ocean (sublittoral).——FIG. 68,*8a–b*. **H. senta*; *a,* centrodorsal with base of crown, *b,* eighteenth pinnule, Brazil, holotype, BMNH 93476, ×2.5 (Clark & Clark, 1967).

Kempometra JOHN, 1938, p. 161 [**K. grisea*; M]. Centrodorsal conical, slightly wider than high, with approximately 50 sockets in 15 crowded columns. Largest cirri of only 16 short segments. First exterior and interior pinnules absent. [There is no suitable illustration available for the genus.] *Holocene:* southern Atlantic Ocean (bathyal).

Leptometra A. H. CLARK, 1908h, p.129 [**Alecto phalangium* MÜLLER, 1841, p. 182; OD]. Centrodorsal conical, as wide as high or low and truncated, with sockets in 10 or 15 crowded columns. Cirri slender, with as many as 51 cirrals, the longest as much as 3 times longer than wide. The first 2 pinnules are similar and distinctly longer than the third. *Holocene:* northern and eastern Atlantic Ocean, including Mediterranean (sublittoral to bathyal).——FIG. 69,*2a*. **L. phalangium* (MÜLLER); base of crown with centrodorsal and cirri, Mediterranean, ×2 (Carpenter, 1888, pl. 37,*2*).——FIG. 69,*2b*. *L. celtica* (M'ANDREW & BARRETT, 1857); centrodorsal with cirrus and bases of 3 rays, Scotland, holotype, BMNH 57.10.14.2, ×3 (A. M. Clark, 1970).

Microcomatula A. H. CLARK, 1931 in 1915–1950, p. 287 (A. H. CLARK, 1911f, p. 129, *nom. nud.*) [**M. mortenseni*; OD]. Very small, 10 arms. Well-developed combs as far as second pinnule, composed of 3 segments, each with a single tooth not confluent with edge of segment; terminal segment with discrete tooth. [The holotype and only known specimen is in the Zoologisk Museum, Copenhagen; it is in poor condition and was figured for the first time by HOGGETT and ROWE (1986, fig. 2H). Following these authors, *Microcomatula* is assigned to the Antedonidae, subfamily uncertain, despite the presence of a comasterid-like pinnule comb, a feature also known from *Ctenantedon*.] *Holocene:* Caribbean (sublittoral).

Poliometra A. H. CLARK, 1923b, p. 7 [**Antedon prolixa* SLADEN in DUNCAN & SLADEN, 1881, p. 77; M; =*Antedon hystrix* CARPENTER, 1884c, p. 374]. Centrodorsal conical, approximately as wide as high, with 15 to 20 columns of cirrus sockets, not separated by interradial ridges. Cirri long, slightly curved, with as many as 50 cirrals, the longest 4 times longer than wide. First pinnule more than twice as long as second and third pinnules. *Paleogene (Eocene)–Holocene:* USA, *Eocene*; northern Atlantic and Pacific Ocean, Arctic Ocean (sublittoral to bathyal), *Holocene.*——FIG. 69,*3*. **P. prolixa* (SLADEN); centrodorsal with small apical and large peripheral cirrus and basis of 3 rays, western Atlantic, ×3 (Messing & Dearborn, 1990).

Family PENTAMETROCRINIDAE A. H. Clark, 1908

[Pentametrocrinidae A. H. CLARK, 1908h, p. 134] [=Thaumatocrinida HAECKEL, 1896, p. 469; =Thaumatocrinidae BATHER, 1899, p. 923; =Decametrocrinidae MINCKERT, 1905, p. 494; =Thaumatocrininae JAEKEL, 1918, p. 74]

Centrodorsal rounded conical to hemispherical or discoidal. Cirri covering centrodorsal or more or less restricted to margin with smooth, rugose or tuberculate aboral apex. Cirrus sockets crowded, from fewer than 20 to more than 150, in 1 to 6 irregular circles. Centrodorsal cavity rather large. Adoral side of centrodorsal may have 5 ridges or elevations, in *Pentametrocrinus* interradially, in *Thaumatocrinus* below sutures separating true radials from interradial pararadials. Cirrals long, as many as 2.5 to 5 times longer than wide, more or less laterally compressed. Basals in adult transformed to rosette; no rod-shaped basals. *Pentametrocrinus* with 5 radials, 10 in *Thaumatocrinus*, each with an undivided arm. Juvenile *Thaumatocrinus* have 5 large basal plates, each succeeded by a small, secondary radial (pararadial) from which interradial arms arise, retarded in growth compared to primary radials and arms, but gradually attaining same size and structure. Radials may be concealed or with low exposed surface that may project beyond edge of centrodorsal. Radial articular facet in *Thaumatocrinus* undescribed, in *Pentametrocrinus* rather steep, separated by lateral margins forming interradial furrows. Interarticular ligament fossae rather low, subtriangular, separated by a straight or curved, low and narrow ridge from large and high adoral muscle fossae. Paired muscle fossae forming angle of approximately 90 degrees with each other, separated by a narrow, midradial ridge and notch. Radial cavity rather narrow. Synarthry between brachials 1 and 2. Syzygy between brachials 4 and 5 and distally at variable intervals (2 to 13). First pinnule on brachial 2 or in most *Pentametrocrinus* on brachial 5. *Holocene.*

Pentametrocrinus A. H. CLARK, 1908h, p. 134 [**Eudiocrinus japonicus* CARPENTER, 1882b, p. 499; OD].

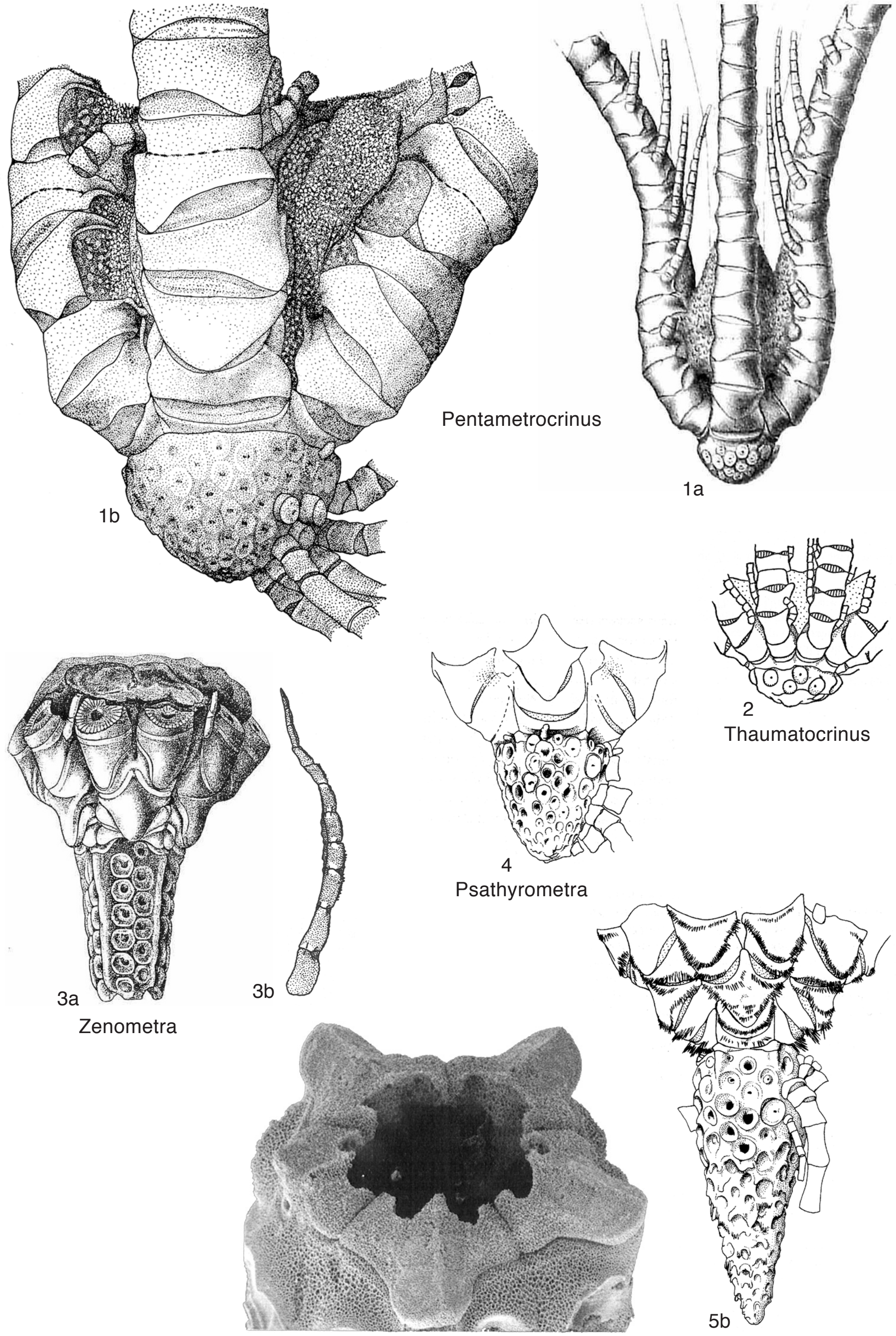

FIG. 70. Pentametrocrinidae and Zenometridae (p. 143–145).

Radials 5, each with an undivided arm. *Holocene:* Atlantic Ocean, Indian and western Pacific Ocean, Southern Ocean (sublittoral to bathyal).——FIG. 70,*1a*. **P. japonicus* (CARPENTER); centrodorsal and base of crown, Japan at 1055 m, ×3 (Carpenter, 1888, pl. 6,*1*).——FIG. 70,*1b*. *P. atlanticus* (PERRIER); centrodorsal with bases of several cirri and bases of 3 rays with interradial portion of tegmen, western Atlantic, USNM E17814, ×10 (Messing & Dearborn, 1990, p. 11, fig. 6a).

Thaumatocrinus CARPENTER, 1883, p. 143 [**T. renovatus;* OD; =*Promachocrinus abyssorum* CARPENTER, 1888, p. 351] [=*Decametrocrinus* MINCKERT, 1905, p. 494 (type, *Promachocrinus abyssorum* CARPENTER, 1888, p. 351, SD A. H. CLARK, 1908d, p. 516)]. Radials 10, each with an undivided arm. *Holocene:* northern Atlantic Ocean, eastern Indian, and western Pacific Ocean, Southern Ocean (bathyal to upper abyssal).——FIG. 70,*2*. **T. renovatus*; centrodorsal and base of crown, ×3 (Clark & Clark, 1967, p. 778, fig. 49).

Family ZENOMETRIDAE
A. H. Clark, 1909

[*nom. transl.* MESSING & WHITE, 2001, p. 159, *ex* Zenometrinae A. H. CLARK, 1909h, p. 176]

Centrodorsal completely hollow, with little if any overhanging adoral rim and without interior radial or interradial pockets or pits. Cirrus sockets with a concave fulcral bowl surrounding central lumen; proximal facet of first cirral with corresponding large boss. Basals forming a thin, complete circlet with large central lumen; each visible externally as a pentagonal extension of one of the interradial ridges (or flat strips) of the centrodorsal, commonly extending laterally as an extremely narrow strip in deep subradial clefts; adjacent basals may or may not meet midradially in external view. *Holocene.*

Zenometra A. H. CLARK, 1907f, p. 354, *emend.*, MESSING & WHITE, 2001, p. 168 [**Antedon columnaris* CARPENTER, 1881c, p. 169; OD; =*Z. pyramidalis* A. H. CLARK, 1908b, p. 237]. Centrodorsal cylindrical, with well-developed interradial ridges (truncated conical with weak ridges in small specimens); aboral apex flat or irregularly eroded and excavated. Basals narrow interradially; rosette absent. First segment of first pinnule at least twice as long as wide. *Holocene:* northern Atlantic Ocean (bathyal to upper abyssal).——FIG. 70,*3a–b*. **Z. columnaris* (CARPENTER); *a,* centrodorsal with base of 4 rays, Bahamas, ×3.5 (Hartlaub, 1912); *b*, first pinnule, western Atlantic, USNM E17962, ×3 (Messing & Dearborn, 1990, p. 16, fig. 12d).

Psathyrometra A. H. CLARK 1907f, p. 353 [**Antedon fragilis* A. H. CLARK, 1907c, p. 80; OD; =*P. borealis* A. H. CLARK, 1908b, p. 236; =*P. profundorum* A. H. CLARK, 1908b, p. 237]. Centrodorsal conical with straight or gently convex sides, rounded or truncated apically, slightly lower than wide to 1.5 times higher than wide. At least basal cirrus sockets separated interradially by narrow, flat strip or weak interradial ridge. Cirrus socket margins commonly coarsely crenulate; concave fulcral stereom spreading to lateral margins of sockets. Distal cirrals elongate and tapering; opposing spine weak or absent. Basals broad and tongue-like interradially, with a pair of interior openings surrounded by stereom that corresponds to a rosette. Proximal ray ossicles smooth, bearing very fine spinules, or with cluster of small spines restricted to projecting tips of synarthrial tubercles. First pinnular at least twice as long as wide. *Holocene:* northern, central, and eastern Pacific Ocean (bathyal).——FIG. 70,*4*. **P. fragilis* (A. H. CLARK); centrodorsal with arm bases, topotype, eastern Pacific, USNM 35739, ×4 (Messing & White, 2001).

Sarametra A. H. CLARK, 1917a, p. 129 [**Zenometra triserialis* A. H. CLARK, 1908b, p. 219; OD]. Conical centrodorsal with rounded to acutely conical aboral apex; base of centrodorsal with low, weak, interradial ridges; obsolete apical sockets with low, horseshoe-shaped rim open aborally. Basals broad and tongue-like interradially; rosette absent. First segment of first pinnule less than twice as long as wide. *Holocene:* tropical Indian Ocean, western to central Pacific Ocean (bathyal).——FIG. 70,*5a–b*. **S. triserialis* (A. H. CLARK); *a,* basal circlet on top of centrodorsal cavity, ×15; *b*, centrodorsal with bases of cirri and arms, New Caledonia, MNHN EcCh 181, ×5 (Messing & White, 2001).

Superfamily UNCERTAIN
Family JAEKELOMETRIDAE
Hess, new family

[Jaekelometridae HESS, herein] [type genus, *Jaekelometra* GISLÉN, 1924, p. 162]

Centrodorsal low to high convex conical. Cirrus sockets with more or less distinct fulcral ridge or tubercles but no projecting lateral margin, in 10 columns commonly separated by interradial or radial ridge or space. Adoral side of centrodorsal flat or concave, with increasing concavity during growth. Centrodorsal cavity rather narrow to moderate, radial depressions or pits in suture between basals may continue in centrodorsal as radial pits. Interradial furrows distinct, indistinct, or absent. Basals large, forming a high complete circlet visible externally, united as thin plates in bottom of large, deep, radial cavity, and covering adoral side of the centrodorsal except for narrow, central perforation. Radials and primibrachials thin, with aboral crest. Brachials in type species large, high, slightly recumbent, with median crest. Radial articular facet low and wide, almost triangular, with very low and indistinct interarticular ligament fossae and rather low, very wide muscle fossae. Radial cavity large. *Upper Cretaceous (Campanian)–Paleogene (Danian).*

Jaekelometra Gislén, 1924, p. 162 [**Atelecrinus belgicus* Jaekel, 1902, p. 1084; OD]. Characters as for family. [The holotype and only specimen of *J. meijeri* Rasmussen was thought by Rasmussen (1961, pl. 47,*7;* 1978, fig. 584,*1a,b*) to have reduced basals, but these are broken-off portions of larger basals distinctive for *Jaekelometra* (Jagt, 1999a, p. 90). *J. meijeri* may in fact be an extreme form of *J.* group of *concava* (Schlüter, 1878).] *Upper Cretaceous (Campanian)–Paleogene (Danian):* Belgium, Netherlands, Sweden, *Campanian–Maastrichtian;* Denmark, *Danian.*——Fig. 71,*1a–d*. **J. belgica* (Jaekel); *a–b,* cup with centrodorsal, *a*, distal, *b*, lateral, Maastrichtian, Netherlands, holotype, MNHB MB.E 710, ×4 (Gislén, 1924); *c–d*, basal circlet, *c*, oblique lateral, *d*, proximal (lower); Maastrichtian, Netherlands, RGM 396 225, ×15 (Jagt, 1999a).——Fig. 71,*1e*. *J.* sp.; oblique aboral view of radial, Maastrichtian, Netherlands, RGM 396 221, ×10 (Jagt, 1999a).——Fig. 71,*1f–g*. *J. concava* (Schlüter, 1878); centrodorsal with basal circlet, *f*, lateral, *g*, distal, Maastrichtian, Netherlands, Coll. Brussels, ×5 (Rasmussen, 1961).

Family ATOPOCRINIDAE
Messing, new family

[Atopocrinidae Messing, herein] [type genus, *Atopocrinus* A. H. Clark, 1912e, p. 150]

Centrodorsal conical, with narrow centrodorsal cavity; adoral rim with 5 interradial grooves to accommodate flat, tongue-like basals. A few small perforations between cirrus sockets connect centrodorsal cavity with exterior. Cirrus sockets initially arising as tubes along adoral surface of centrodorsal, in 10 or 15 columns, with well-developed, projecting, lateral, triangular fulcral processes. No rosette. Arms 5, undivided, composed of low triangular brachials. Synarthry between brachials 1 and 2. First syzygy between brachials 4 and 5, with few radiating ridges. First pinnule on brachial 2. *Holocene.*

Atopocrinus A. H. Clark, 1912e, p. 150 [**A. sibogae*; OD]. Characters as for family. [Only 5 specimens of *Atopocrinus* have been collected (Messing, 2003a).] *Holocene:* western Pacific Ocean (bathyal).——Fig. 71,*2*. **A. sibogae*; centrodorsal and base of crown, ×2 (A. H. Clark, 1915a in 1915–1950, p. 245, fig. 227).

Superfamily and Family UNCERTAIN

Microcrinus Emmons, 1858, p. 311 [**M. conoideus*; M]. Centrodorsal small, 5-sided, conical; circular cirrus sockets in 10 columns with as many as 6 sockets on prominent interradial bands. Centrodorsal cavity deep and wide, approximately half of centrodorsal diameter. Basals rod shaped. Isolated brachials indicate arms divided at primibrachial 2 only. Primibrachial 1 moderately high, sides converging. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Syzygy probably between secundibrachials 3 and 4 and more distally. [Referred by Gislén (1934) to Zenometrinae. Specimens of *Microcrinus conoideus* found by G. R. Baum (unpublished) in the Eocene of North America (North Carolina) have a variation from typical macrophreate structure with wide centrodorsal cavity and narrow, rod-shaped basals resting on interradial septa to forms with large and deep radial pits similar to those present in specimens of *Jaekelometra*.] *Paleogene (Eocene):* USA (North and South Carolina).——Fig. 71,*3a–b*. **M. conoideus*; centrodorsal, *a*, lateral, *b*, adoral, Lutetian–Priabonian, North Carolina, NCSM 8225, ×8 (C. N. Ciampaglio, new).

Procomaster Simms, 1988b, p. 3 [**P. pentadactylus*; M]. Small, slender comatulid with 5 arms composed throughout of very low brachials. Synarthry between primibrachials 1 and 2; syzygies at approximately every third to fifth articulation. Approximately 25 robust, strongly recurved cirri. *Lower Jurassic (Toarcian):* Germany.——Fig. 71,*4*. **P. pentadactylus*; holotype, SMNS 26993, ×1.5 (Simms, 1988b).

Suborder BOURGUETICRININA
Sieverts-Doreck, 1953

[Bourgueticrinina Sieverts-Doreck in Ubaghs, 1953, p. 762]

[Hans Hess]

Column present, attachment by irregular terminal holdfast or branched radices borne by some distal columnals; no genuine cirri. Columnal articulations synarthrial, may be synostosial or symplectial in proxistele. Cup cylindrical, spindle shaped or conical, normally composed of 2 circlets of 5 radials and 5 basals; a proximale may be present below the basals. Deviations from pentaradiate symmetry may occur. Nonmuscular brachial articulations synostosial, syzygial

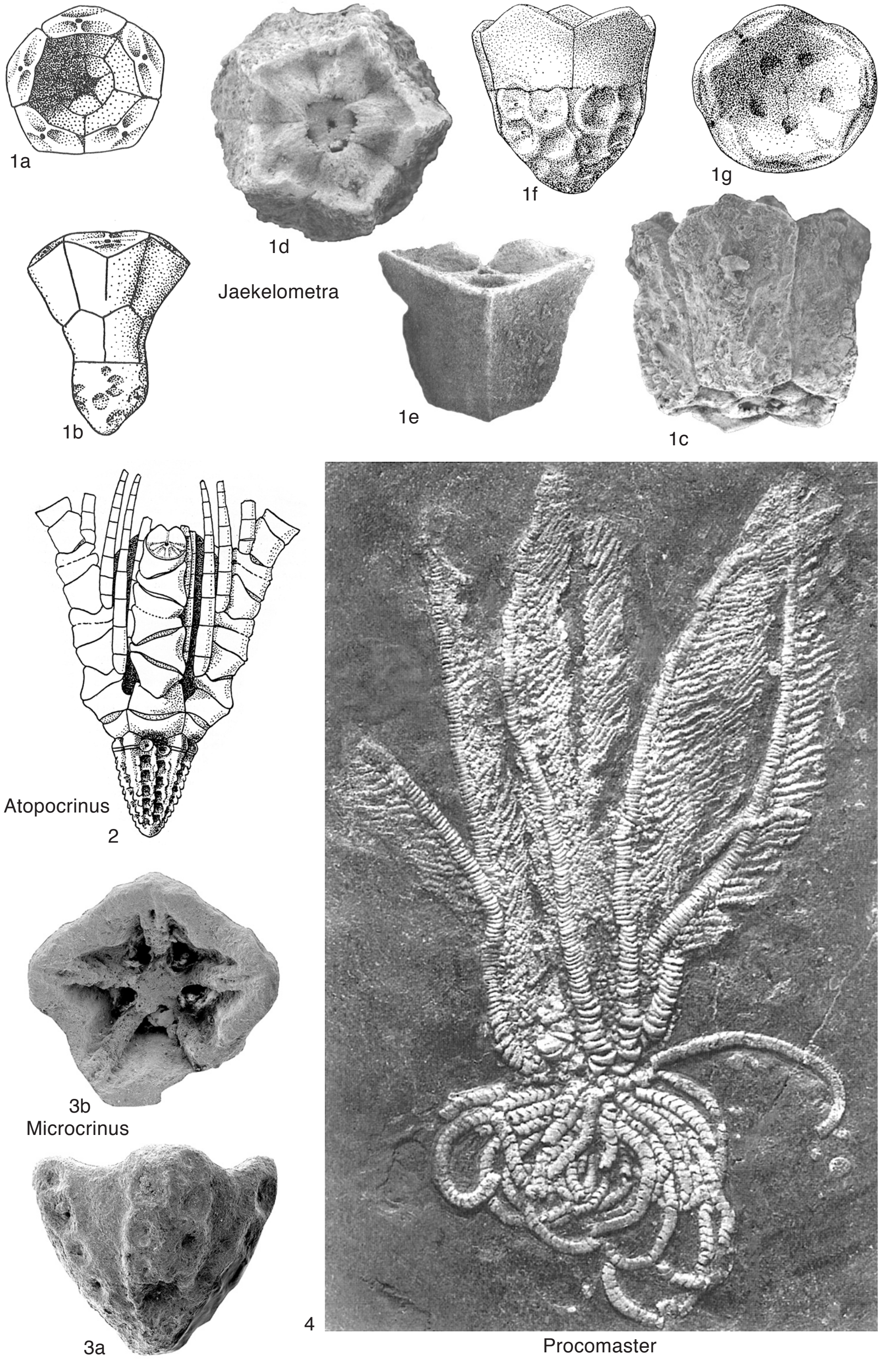

FIG. 71. Jaekelometridae, Atopocrinidae, and Uncertain (p. 146).

to cryptosyzygial, synarthrial to cryptosynarthrial, or trifascial. [Bourgueticrinids have frequently been classified with millericrinids because they entirely lack cirri. However, synarthrial columnal articulation, the characteristic feature of bourgueticrinids, is unknown in millericrinids at any ontogenetic stage but does occur in the pentacrinoid larval stage of comatulids and isocrinids. SIMMS (1988a, p. 276) considered that bourgueticrinids derived from an isocrinid or comatulid stock through paedomorphosis (neoteny), an opinion adopted herein. In view of similarities with thiolliericrinids, bourgueticrinids are, herein, treated as a suborder of Comatulida. Bourgueticrinids are characterized by a wide range of morphological variation, and many species are artificial entities based on ontogenetic stages (JAGT, 1999a). For example, KJAER and THOMSEN (1999) described a well-documented heterochronic change across the K/T boundary (Fig. 73). Adult *Bourgueticrinus constrictus* (upper Maastrichtian) and *Bourgueticrinus danicus* (lower Danian) both have a proximale, formed at a later stage in the latter. Juvenile cups of *B. danicus* and *Democrinus maximus* are very similar, but *D. maximus* completely lacks a proximale. Thus, the adult cup of *D. maximus* resembles the juvenile cup of *B. danicus* from which it developed by extension of the juvenile growth phase (neoteny). In bourgueticrinids, the column increases in length by addition of new columnals between the basals and uppermost columnal. In *Bourgueticrinus*, new columnals cease to form when the uppermost columnal transforms into a proximale that is incorporated into the cup. Loss of a proximale allows further column growth; presumably longer columns increased feeding efficiency in earliest Danian marine settings where nutrients were scarce and the bottom muddier. RASMUSSEN (1961) divided bourgueticrinines into 2 families: Bourgueticrinidae and Bathycrinidae. MOORE (1967) synonymized Bathycrinidae with Bourgueticrinidae following the discovery of intact specimens of *Dunnicrinus mississippiensis*. A. M. CLARK (1970) accepted RASMUSSEN's classification, but without differentiating between 5- and 10-armed forms. For extant bourgueticrinines, ROUX (1977b) distinguished the families Bathycrinidae (including 5- and 10-armed forms) and Phrynocrinidae. RASMUSSEN (1978, p. 847) added the extant family Porphyrocrinidae (see also ROUX, MESSING, & AMÉZIANE, 2002). SIMMS and others (1993, p. 503), followed by JAGT (1999a, p. 115), united all these families in a single family, Bourgueticrinidae. MIRONOV (2000), accepting RASMUSSEN's 4 families, added 2 genera and a new family, Septocrinidae, and subdivided the Bathycrinidae and Phrynocrinidae into 2 subfamilies each. This extensive classification is adopted herein, pending revision of this taxonomically difficult group. OJI and others (2008) reported dense colonies of a bathycrinid at a depth of over 9000 m; this is so far the deepest *in situ* observation of stalked crinoids.] *Upper Cretaceous (Cenomanian)–Holocene.*

Family BOURGUETICRINIDAE de Loriol, 1882

[*nom. correct.* CARPENTER, 1884a, p. 6, 23, *pro* Bourgueticrinidées DE LORIOL, 1882 in 1882–1889, p. 64; *emend.*, GISLÉN, 1924, p. 206]

Bourgueticrinina with 5 undivided rays. Cup mostly elongate, cylindrical to spindle shaped, composed of a proximale superposed by basals and radials of equal or nearly equal height, or high basals and shorter radials (proximale undifferentiated or absent in *Conocrinus*). Radial articular facet wide, with large muscle fossae, surrounding narrow axial canal. Articulation between brachials 1 and 2 cryptosynarthrial or synostosial (possibly muscular in *Dunnicrinus mississippiensis*). First pinnule abaxial on brachial 4. Discrete sutures in proximale of some specimens indicate derivation by fusion of a few disk-shaped proximal columnals; articular facet at base of proximale wide, circular in cross section and joined to topmost columnal by synostosis, or elliptical and joined by synarthry; uppermost free columnals cylindrical and slightly shorter than more distal ones, or elliptical in section and similar to more distal columnals; synarthrial articulation with proximale and full size of uppermost free columnal in many specimens indicate that the formation of new columnals below the proximale is restricted to juveniles; form and size of columnals changing during growth and varying through a single column (cylindrical, barrel shaped, or with elliptical section at ends and constricted medially). Branched radicular cirri present on some distal columnals. *Upper Cretaceous (Cenomanian)–Holocene.*

Bourgueticrinus d'Orbigny, 1841 in 1840–1841, p. 95 [**Apiocrinites ellipticus* Miller, 1821, p. 33; OD] [=*Mesocrinus* Carpenter, 1881b, p. 130 (type, *M. suedicus*, OD, according to ICZN, 1999, *Code*, Article 68a,i); =*Volvola* Valette, 1917, p. 86, *ex Volvola* Lhwyd, 1699, p. 56, pre-Linnean (type, *V. hureae* Valette, 1917, p. 104); =*Metapiocrinus* Jaekel, 1918, p. 70 (type, *M. minutus*, OD)]. Proximale in adults; discrete sutures in proximale of some specimens indicate its formation by fusion of a few, disk-shaped, proximal columnals. *Upper Cretaceous (Cenomanian)–Paleogene (Eocene):* Belgium, Russia, Crimea, Ukraine, Denmark, England, France, Germany, Netherlands, Poland, Sweden, USA (Alabama), *Cenomanian–Maastrichtian;* Denmark, Sweden, Italy, Belgium, Netherlands, *Danian;* USA (New Jersey), *Eocene.*——Fig. 72,*1a–d*. **B. ellipticus* (Miller); *a,* cup with proximale, Santonian, England, BMNH E45076, ×2 (Rasmussen, 1961); *b–d*, cup with proximale, *b*, lateral, *c*, lower, *d*, distal, Santonian, England, BMNH E45069, ×2 (Rasmussen, 1961).——Fig. 72,*1e–i*. *B. danicus* Nielsen, 1913; *e–g,* cup with proximale, *e*, lateral, *f*, lower, *g*, distal, Danian, Denmark, MGUH 8942, ×5 (Rasmussen, 1961); *h–i*, distal columnals, *h*, lateral, *i*, facet, Danian, Denmark, MGUH 8947, ×5 (Rasmussen, 1961).——Fig. 72,*1j–m*. *B. hagenowii* (Goldfuss in Hagenow, 1840); proximale with basal circlet and 3 radials, *j*, lateral, *k*, upper end of proximale when basals and radials removed, *l*, lower facet of proximale, *m*, distal, Maastrichtian, Denmark, MGUH 8935, ×2.5 (Rasmussen, 1961).——Fig. 72,*1n*. *B. hureae* (Valette, 1917); proximale and cup with associated bourgueticrinid columnal, Santonian, England, BMNH E50018, ×5 (Smith & Wright, 2002).——Fig. 73. *Bourgueticrinus–Democrinus;* phylogeny, ontogeny, and degree of paedomorphic change in the Maastrichtian *Bourgueticrinus constrictus* and the Danian *B. danicus* and *Democrinus maximus*, approximately ×2 (Kjaer & Thomsen, 1999).

Conocrinus d'Orbigny, 1850 in 1850–1852, p. 332 [**Bourgueticrinus thorenti* d'Archiac, 1846, p. 200; M] [=*Rhizocrinus* Sars, 1868, p. 38 (type, *R. lofotensis* Sars, 1864, p. 127, *nom. nud.*; Sars, 1868, p. 39, available according to Dir. 73, ICZN, 2010, p. 489–499); =*Tormocrinus* Jaekel, 1891, p. 657 (type, *T. veronensis*, M); =*Formocrinus* Pompeckj, 1913, p. 481, *nom. null.*, *error pro Tormocrinus* Jaekel, 1891, p. 657)]. Sutures between cup plates indistinct; basals commonly fused. Number of radials and arms generally 5, rarely 4 to 7. Every second brachial articulation synostosial or cryptosynarthrial. Articulation between cup and column commonly constricted, distinct proximale absent. Facets of elliptical distal columnals with ligament fossae forming a low, fat figure 8. [*Rhizocrinus* was first treated as a synonym under *Conocrinus* by Roux (1985b).] *Paleogene (Paleocene)–Holocene:* southern Europe, Crimea, Iran, *Eocene–Miocene*; northern and eastern Atlantic Ocean, rarely in Caribbean and Indonesia, *Holocene.*——Fig. 72,*2a*. **C. thorenti* (d'Archiac); cup, Eocene, France, lectotype, MNHN R54426, ×3 (Roux, 1978c, fig. 1B-a).——Fig. 72,*2b*. *C. cherbonnieri* Roux, 1976; proximal column and base of crown, Holocene, holotype, MNHN EcPs240, ×8 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).——Fig. 72,*2c–d*. *C. tauricus* Klikushin, 1982b; *c,* facet of proximal columnal, Paleocene, Crimea, LGI PK-2-6, ×15; *d*, proximal facet of primibrachial, Paleocene, Crimea, LGI PK-2-2, ×10 (Klikushin, 1982b).——Fig. 72,*2e*. *C. lofotensis* (Sars); proximal column and base of crown, Holocene, ×8 (Rasmussen, 1978).

Democrinus Perrier, 1883, p. 450 [**D. parfaiti*; M] [=*Rhizocrinus (Bythocrinus)* Döderlein, 1912, p. 4, 11 (introduced as subgenus for *Rhizocrinus chuni* Döderlein, 1907, and *R. (Bythocrinus) braueri* Döderlein, 1912, without designation of type species)]. Cup of 5 high, slender basals and 5 much lower radials surrounding narrow central canal. Sutures between basals and radials distinct, irregular, or hardly visible. Radial articular facet large. Articulation of basal circlet with top of column smooth and circular, with diameter corresponding to base of cup. Growth of cup mainly affects basal circlet, with height increasing more than width, so that mature specimens become more slender and cylindrical. Interradial nerve canal extending from basals in sutures between radials before dividing. Every second brachial articulation synostosial, synarthrial, or trifascial. Synostosial articulations may be modified, with short, median ridge from axial canal to aboral edge of proximal articular facet fitting into a furrow in distal facet of preceding brachial. Proximale not developed in adults. A few (generally fewer than 6) low proximal columnals have synostosial articulations. More distal columnals resemble those of Bathycrinidae. *Upper Cretaceous (Maastrichtian)–Holocene:* Denmark, Germany, *Maastrichtian;* Denmark, Sweden, England, USA, *Danian, Eocene;* worldwide (sublittoral to bathyal), *Holocene.*——Fig. 72,*3a–b*. **D. parfaiti*; *a*, proximal column and base of crown, ×5; *b*, columnals from mesistele, Holocene, MNHN EcPs231, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).——Fig.

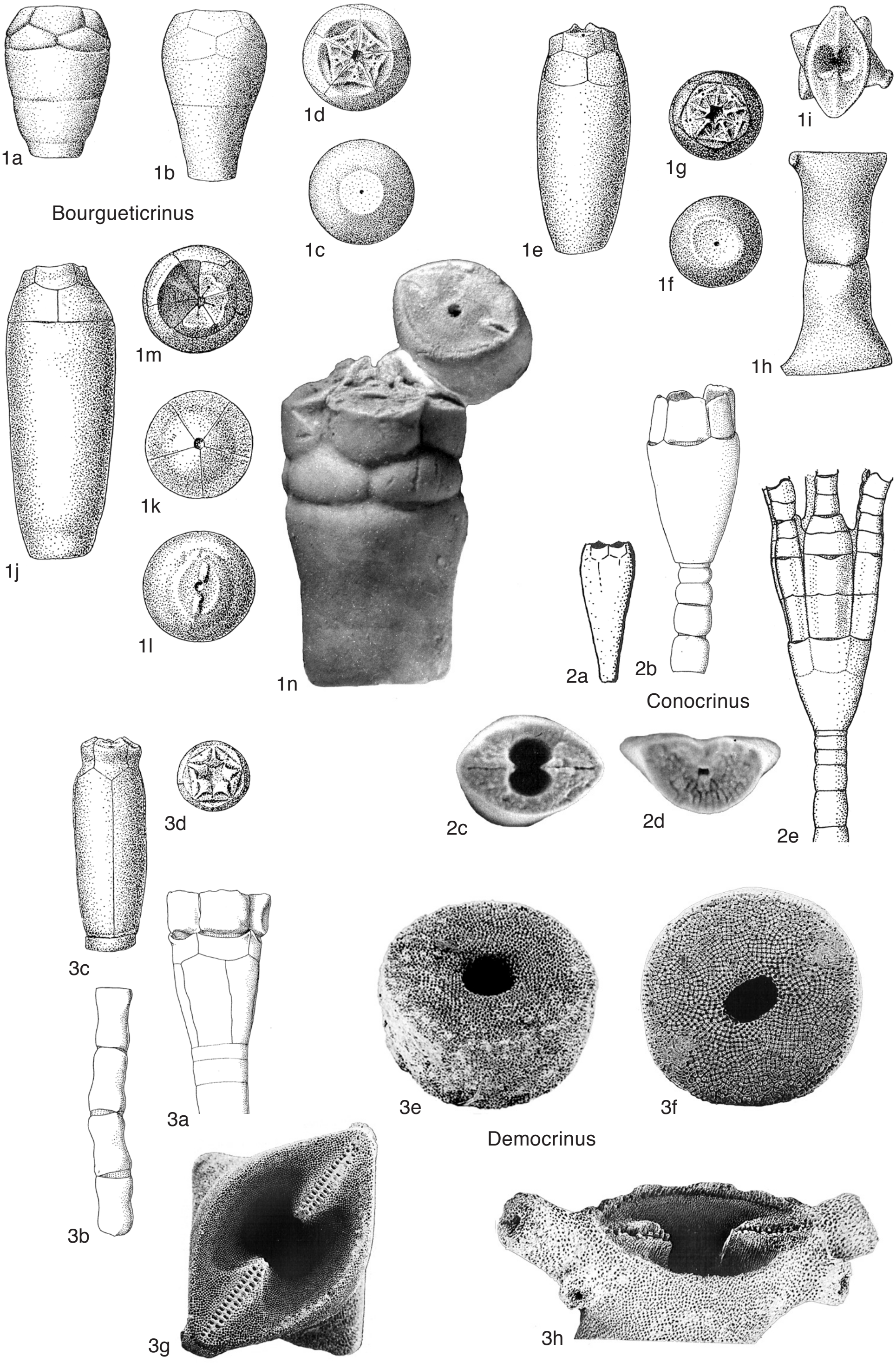

FIG. 72. Bourgueticrinidae (p. 149–151).

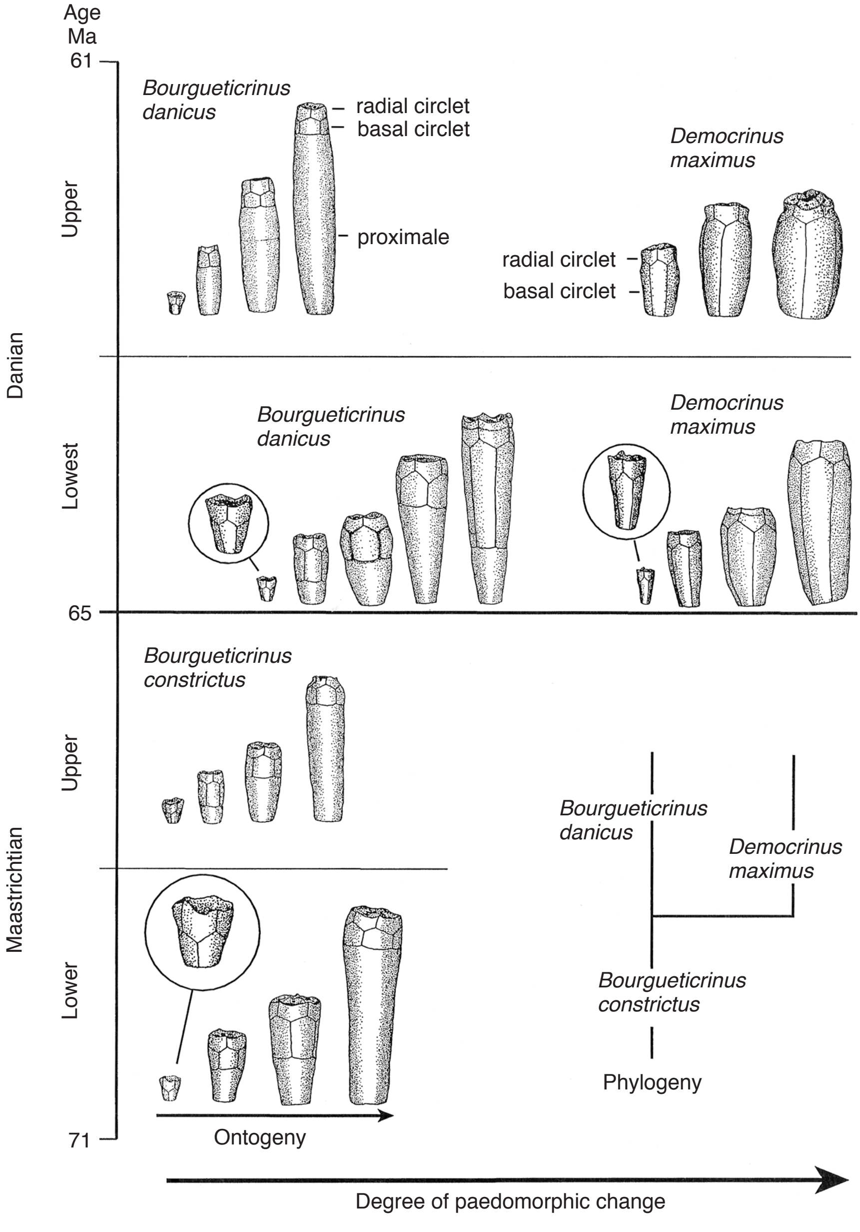

FIG. 73. Bourgueticrinidae (p. 149).

72,*3c–d*. *D. maximus* (NIELSEN, 1915); cup with columnal, *c*, lateral, *d*, distal, Danian, Denmark, MGUH 8958, ×5 (Rasmussen, 1961).——FIG. 72,*3e–h*. *D. brevis* (A. H. CLARK, 1909k), Caribbean, Santa Marta, Colombia, at approximately 170 m; *e*, oblique view of proximal columnal with synostosis, USNM E17992/box V/stub 4, ×30; *f*, proximal columnal with weakly formed synarthry, USNM E17992/box V/stub 5, ×30; *g*, synarthrial facet of columnal from mesistele, USNM E17992/box 6/stub 11, ×20; *h*, oblique view of proximal columnal facet with radicular extensions, USNM E17992/box 6/stub 12, ×20 (Donovan, 1996).

Dunnicrinus MOORE, 1967, p. 8 [**D. mississippiensis*; M]. Cup slightly conical, almost cylindrical, approximately as high as wide, of similarly

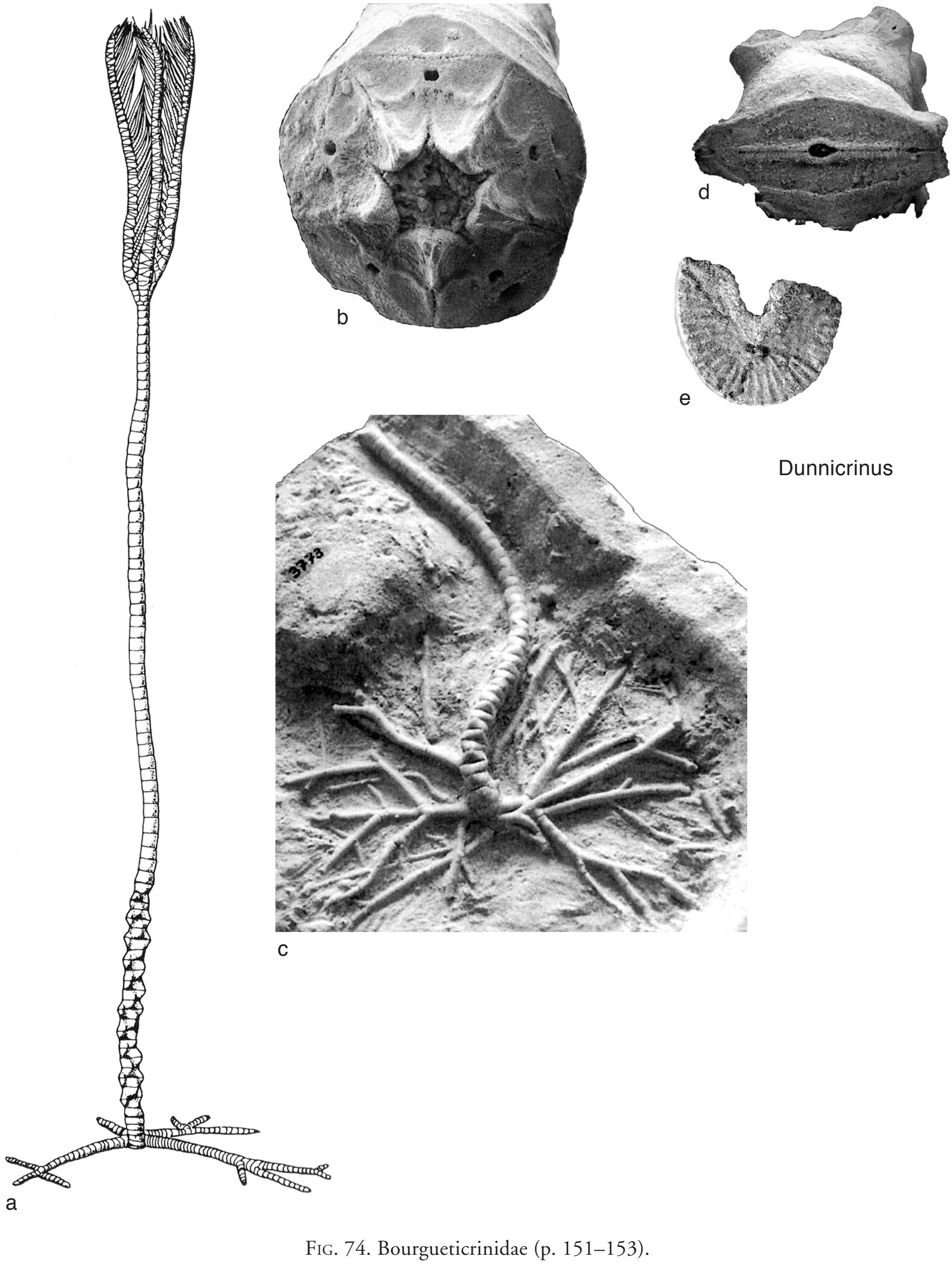

Fig. 74. Bourgueticrinidae (p. 151–153).

sized basals and radials separated by distinct sutures. Base circular, corresponding to top of column. Most fossil specimens broken along suture between basals and radials. Radial articular facet with steep, high, and narrow muscle fossae; radial cavity narrow. Arms 5, undivided, exceptionally with 4, 6, or 8 rays (Jagt, 1999a, p. 119). Brachials rounded aborally, strongly wedge shaped with oblique muscular articulations distal to brachial 2. Cryptosynarthry between brachials 1 and 2 in *D. aequalis* (possibly muscular in *D. mississippiensis*), other articulations muscular and cryptosyzygial to syzygial, distributed randomly (Jagt, 1999a). Pinnulation complete; first pinnule on brachial 2; each pinnule with approximately 25 pinnulars, equal in length and diameter, and with straight muscular articulations. Proximalmost columnals generally thin; new, extremely thin columnals introduced immediately below basal circlet during juvenile growth, first appearing externally midradially below interbasal sutures, thus resembling infrabasals. After formation of new columnals has ceased in adults, the uppermost columnal grows to a size equal to other columnals, similar in diameter, but in some specimens higher, thus approaching the proximale of *Bourgueticrinus*. Proxistele with cylindrical to slightly barrel-shaped columnals, height similar to diameter, circular to slightly elliptical in section and with articulations almost synostosial in the few uppermost columnals, at least in juvenile specimens. Distal columnals stout, similar to *Bourgueticrinus*, with narrow lumen, elliptical in section and joined by synarthries. Distalmost column bearing branched radicular cirri. [JAGT (1999a, p. 129) noted that *Mesocrinus suedicus* CARPENTER (1881b), Campanian, may be assignable to *Dunnicrinus* based on brachial morphology; unfortunately, there is not enough material known to be certain about this.] *Upper Cretaceous (Maastrichtian):* Netherlands, USA (Mississippi).——FIG. 74*a*. **D. mississippiensis*; reconstruction, Maastrichtian, USA, ×0.5 (Moore, 1967).——FIG. 74*b–e*. *D. aequalis* (D'ORBIGNY, 1841 in 1840–1841), Maastrichtian, Netherlands; *b,* distal view of cup, MHMM 1997101-1, ×10; *c*, radix with part of column, MHMM MD 3773, ×0.7; *d*, proximal facet of columnal from dististele, MHMM 1997102-1, ×5; *e*, distal facet of brachial with syzygy, MHMM 1997100-3, ×10 (Jagt & others, 1998).

Family BATHYCRINIDAE Bather, 1899

[Bathycrinidae BATHER, 1899, p. 922; *emend.*, GISLÉN, 1924, p. 206–212] [=Rhizocrinidae JAEKEL, 1894, *nom. nud.;* =Rhizocrinidae JAEKEL, 1918, p. 72, *partim,* excluding *Drepanocrinus* (=*Roveacrinus*)]

Ten-armed Bourgueticrinina with pinnulars V-shaped in cross section; cover plates present. Large, rodlike spicules absent in ambulacra. Cup shape variable; basals present or absent. Arms divided at primibrachial 2. Primibrachials wide, flattened, joined by cryptosynarthry and covering tegmen. Secundibrachial articulations muscular and cryptosynarthrial or cryptosyzygial. First pinnule from secundibrachial 4 to 14. Lateral (additional) plates on pinnules present or absent. Several proximal columnals (generally more than 10) discoidal in adult. Column attached by radicular cirri or expanded terminal disk. *Paleogene (Danian)–Holocene.*

Subfamily BATHYCRININAE Bather, 1899

[*nom. transl.* MIRONOV, 2000, p. 713, *ex* Bathycrinidae BATHER, 1899, p. 922]

Cup conical to funnel shaped, or with median constriction. Basals may be fused, absent or possibly small and covered by the radials in *Naumachocrinus*. Every second or third brachial articulation ligamentary (cryptosynarthrial). Proximal columnals low and discoidal in adults. Elongate columnals in mesistele, with exception of *Cingocrinus*. Fixation by radicular cirri, in *Naumachocrinus* by terminal disk. *Paleogene (Danian)–Holocene.*

Bathycrinus THOMSON, 1872, p. 772 [**B. gracilis*; M; ICZN, 2010, Opinion 73, Dir. 72, p. 95/930] [=*Ilycrinus* DANIELSSEN & KOREN, 1877, p. 45 (type, *I. carpenterii*, OD); =*Paleobathycrinus* ROUX, 1978a (unpublished), p. A19 (type, *Bathycrinus windi* RASMUSSEN, 1961, p. 201), *nom. nud.*]. Cup with low ring of fused basals commonly at an angle to higher, conical circlet of 5 radials separated by sutures; radial cavity wide and shallow. Basals with sutures in Paleocene *B. windi*. *Paleogene (Danian)–Holocene:* Denmark, *Danian;* worldwide (bathyal to abyssal), *Holocene.*——FIG. 75,*1a–b*. **B. gracilis*; *a*, proximal part of column and base of crown, *b*, columnals from mesistele, Holocene, USNM E16288, ×8 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).——FIG. 75,*1c–l*. *B. windi* RASMUSSEN, 1961, Danian; *c–e,* cup, *c*, lateral, *d*, proximal, *e*, distal, holotype, Coll. Wind 71, ×10; *f–i*, first primibrachial, *f*, aboral, *g*, adoral, *h*, proximal, *i*, distal, Coll. Wind 73, ×10; *j*, adoral view of primibrachial 2, Coll. Wind 74, ×10; *k–l*, proximal column, *k*, lateral, *l*, facet, Coll. Wind 75, ×10 (Rasmussen, 1961).——FIG. 75,*1m–n*. *B. aldrichianaus* THOMSON, 1876, Gulf of Guinea at 3587 m, USNM E17896; *m,* distal column with synarthrial joints and part of radix, ×2.5; *n,* facet from mesistele, ×30 (Macurda & Meyer, 1976).

Cingocrinus MIRONOV, 2000, p. 719 [**C. radicatus*; M]. Cup with sharp median restriction at sutures between basals and radials; basals convex; radial circlet conical. Brachial formula unstable. First pinnule on secundibrachials 5 to 7. Lateral (additional) plates of pinnules absent; movable joints in pinnules alternating with nonmovable joints. Each tube foot covered by 3 or 4 small plates. As many as 44 proximal columnals have height less than diameter. No elongate columnals. *Holocene:* northwestern Pacific Ocean (abyssal).——FIG. 75,*2a–b*. **C. radicatus*; Commander Islands at 4570 m, holotype, IO RAS XV-63-2; *a,* base of crown, ×4; *b,* proximal column, ×3 (Mironov, 2000).

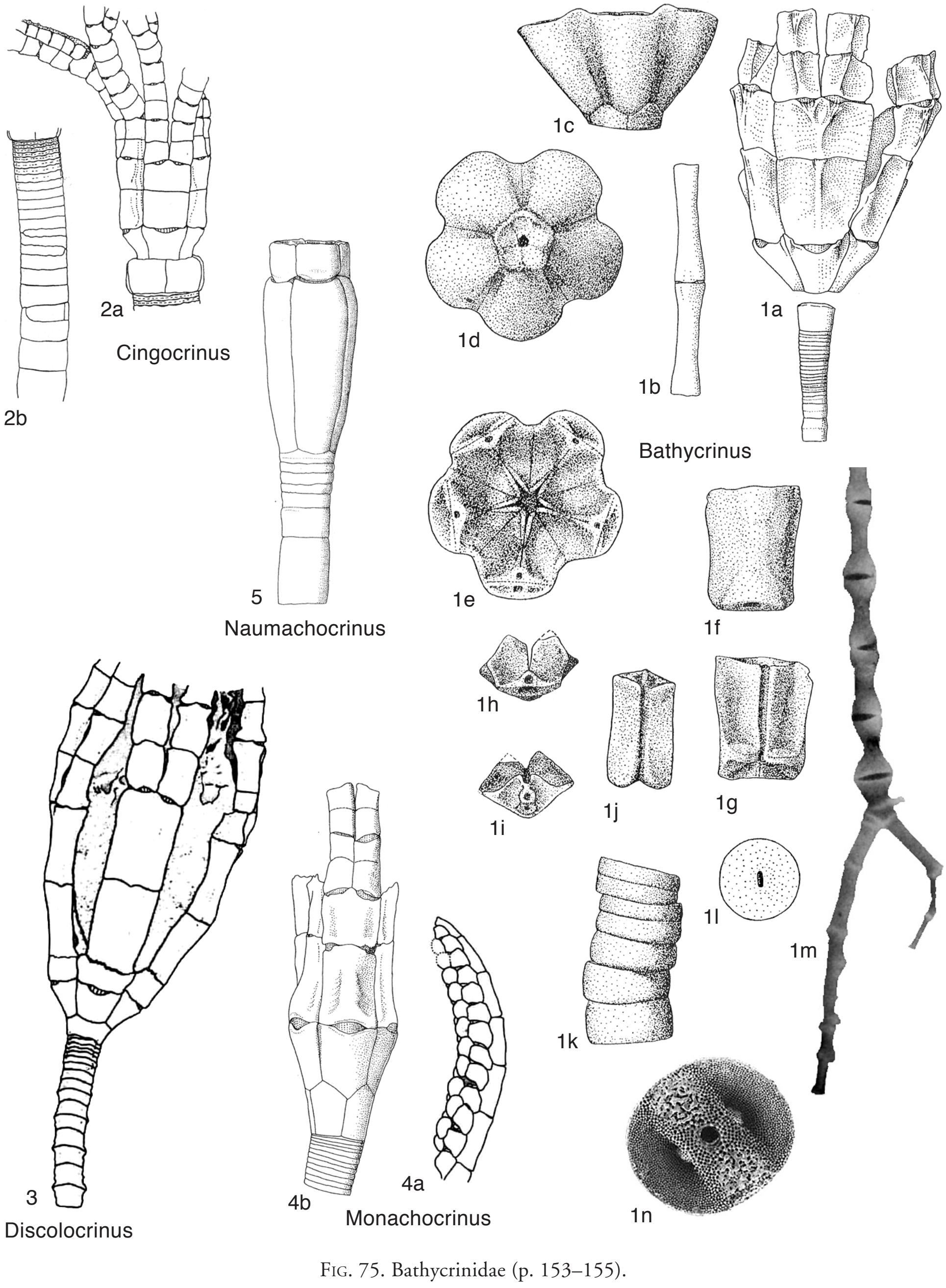

FIG. 75. Bathycrinidae (p. 153–155).

Discolocrinus MIRONOV, 2008, p. 146 [**D. thieli*; M]. Primibrachials elongate; pinnules laterally compressed, without cover plates. Proximal columnals with thorns. *Holocene:* eastern Pacific Ocean (abyssal).——FIG. 75,*3*. **D. thieli*; proximal column and base of crown, Peru Basin at 4131 m, holotype, SMF 2079, ×2 (Mironov, 2008).

Monachocrinus A. H. CLARK, 1917b, p. 390 [**M. sexradiatus*; OD]. No angular boundary between basals and radials. Circlet of unfused basals approximately as high as wide; radial circlet of similar height, widening upward. Generally more than 10 proximal columnals, thin and disk shaped. [A. H. CLARK (in ZITTEL, 1913, p. 230) recorded and characterized the genus and included it (A. H. CLARK, 1915b) in a key to the genera of the Bourgueticrinidae. Seven species were indicated, but not by name. A. H. CLARK (1915a in 1915–1950) assigned *Bathycrinus caribbeus* A. H. CLARK (1908g) and *B. paradoxus* A. H. CLARK (1909g) to this genus. He diagnosed it (A. H. CLARK, 1917b, p. 390) and briefly described the type species, *M. sexradiatus*, but later offered a full description of the type as a new species (A. H. CLARK, 1923b, p. 19). According to JAGT (1999a, p. 131), none of the Santonian–Maastrichtian species tentatively assigned by RASMUSSEN (1961) to *Monachocrinus* belongs in this genus. According to ROUX (1977b, p. 28), *M. recuperatus* is the most typical of the genus. According to MIRONOV (2008, p. 148) pinnules with rows of large covering plates bordering the ambulacral groove are characteristic of bathycrinids.] *Holocene:* worldwide (bathyal, abyssal in temperate and tropical seas).——FIG. 75,*4a*. **M. sexradiatus*; lateral view of pinnule with covering plates, northern Atlantic at 2075 m, syntype, CM Cri-65, ×15 (Mironov, 2008).——FIG. 75,*4b*. *M. recuperatus* (PERRIER, 1883); proximal column and base of crown, holotype, MNHN EcPh26, ×5 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

Naumachocrinus A. H. CLARK, 1912f, p. 196 [**N. hawaiiensis*; M]. Radials high; arms delicate. Basals absent or small and covered by the radials. [*Naumachocrinus* was assigned to the Caledonicrininae by MIRONOV (2000) because of a basal circlet not visible from the outside. However, MIRONOV (2008, p. 151) questioned his previous assignment of *Naumachocrinus* to the Caledonicrininae because the cryptic basal circlet may be convergent with *Caledonicrinus*. Following BOURSEAU and others (1991, p. 272) and OJI and KITAZAWA (2008), it is here placed in the Bathycrininae.] *Holocene:* southwestern and central Pacific Ocean (bathyal).——FIG. 75,*5*. **N. hawaiiensis;* proximal column and base of crown, MNHN EcPs130, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

Subfamily CALEDONICRININAE Mironov, 2000

[Caledonicrininae MIRONOV, 2000, p. 721]

Cup convex in profile, only radials visible from outside. Radials large, bulging; arms robust. Basals high, covered by large radials. First pinnule on secundibrachials 4 or 5. First proximal columnals articulated by flat synostosis, middle and distal columnals by synarthries without deep ligament fossae. Columnals of mesistele cylindrical or barrel shaped, not elongate. Attachment by expanded terminal plate; radicular cirri absent. [*Caledonicrinus* has a special type of nervous system that sets it aside from other Bourgueticrinina (HEINZELLER, 1998; BOHN & HEINZELLER, 1999). A molecular analysis by COHEN and others (2004) placed *Caledonicrinus* among cyrtocrinids, but a cladistic morphological analysis did not link it with any clade. Synarthrial facets in the mesistele of *Caledonicrinus* are missing in cyrtocrinids, so the form is herein retained in the Bourgueticrinina pending further studies.] *Holocene.*

Caledonicrinus AVOCAT & ROUX in AMÉZIANE-COMINARDI & others, 1990, p. 118 [**C. vaubani*; M]. Characters as for subfamily. *Holocene:* southwestern Pacific Ocean (bathyal).——FIG. 76*a–e*. **C. vaubani*; *a,* proximal column and base of crown, MNHN EcPs23, ×2 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*); *b*, complete, smooth specimen, New Caledonia at 410–440 m, paratype, MNHN EcPs19, ×1 (Améziane, new); *c*, symplectial facet on proximal columnal, New Caledonia at 410–440 m, holotype, MNHN EcPs19, ×8; *d*, synarthrial facet on distal columnal, holotype, MNHN EcPs19, ×7; *e*, oblique distal view of cup with 2 radials (*R*) removed to show the hidden basal complex, ×5 (Bourseau & others, 1991).

Family PHRYNOCRINIDAE A. H. Clark, 1907

[Phrynocrinidae A. H. CLARK, 1907a, p. 510; *emend*., A. M. CLARK, 1973b, p. 276]

Arms diverging from their base, divided at primibrachial 2 or distally; undivided in Porphyrocrininae. Nonmuscular articulations between primibrachials 1 and 2 and more distally at variable (usually 3 or 4) intervals. First pinnule on brachial 8 to 10. No proximale. Proximal columnals low, 1 or 2 uppermost discoidal in adults. Columnals stout, as wide as base of cup, circular to elliptical in section, all joined by synarthry. Fixation by irregular terminal disk. *Holocene.*

Subfamily PHRYNOCRININAE A. H. Clark, 1907

[*nom. transl.* MIRONOV, 2000, p. 713, *ex* Phrynocrinidae A. H. CLARK, 1907a, p. 510]

Cup low and broad conical, almost discoidal, with 5 basals and 5 slightly larger radials separated by distinct sutures. Arms branching only distally, as many as 3 times. *Holocene*.

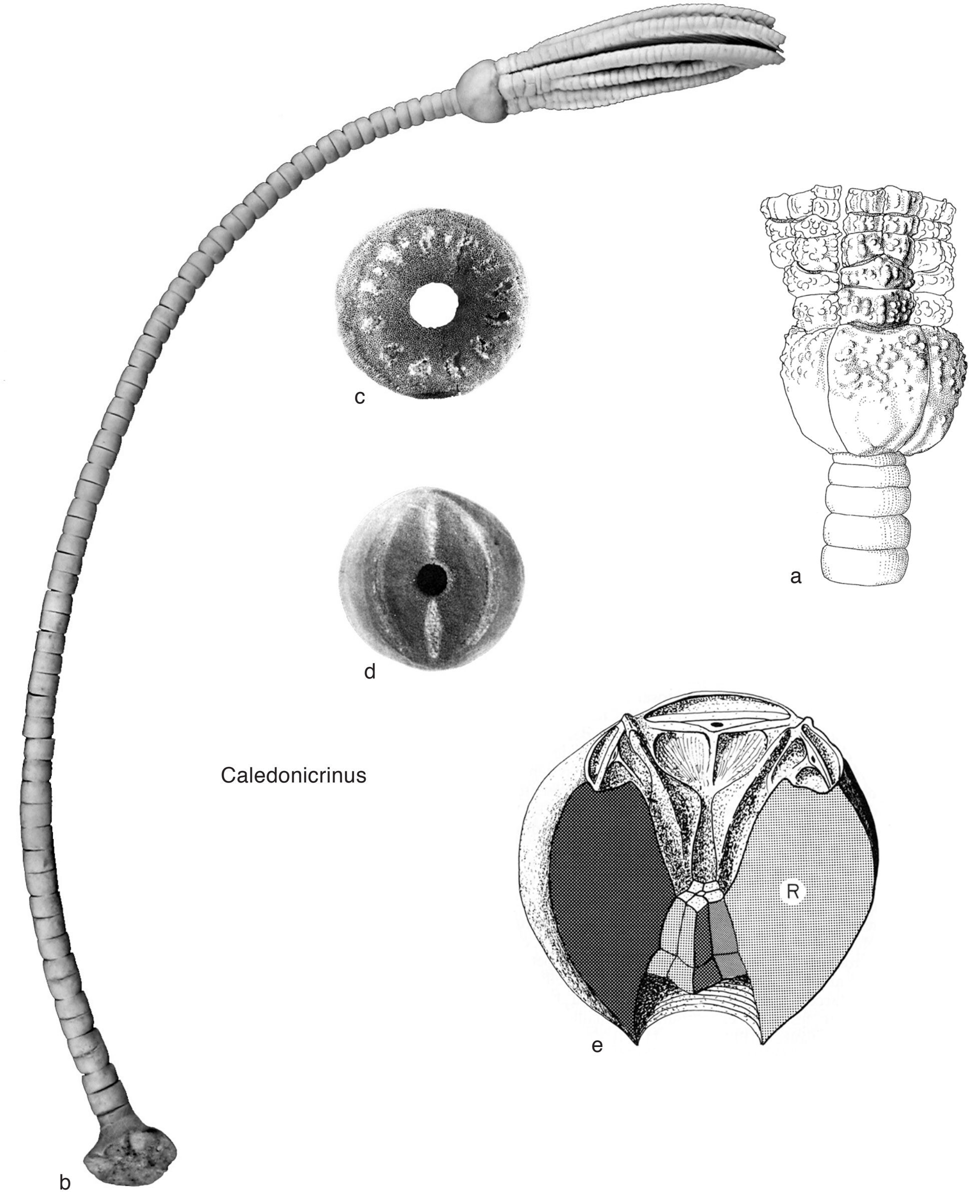

FIG. 76. Bathycrinidae (p. 155).

Phrynocrinus A. H. CLARK, 1907a, p. 507 [**P. nudus*; M]. Characters as for subfamily. *Holocene:* western Pacific Ocean (bathyal to abyssal).——FIG. 77,*1a–c*. **P. nudus*; *a,* proximal column and base of crown, NIWA Z8481, ×1.5 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*); *b*, facet from mesistele, NMNZ Ech. 6534, ×2 (Donovan & Pawson, 1994); *c*, proximal column and base of crown, holotype, USNM 22601, ×0.9 (A. H. Clark, 1907a).

Subfamily PORPHYROCRININAE A. M. Clark, 1973

[*nom. transl.* MIRONOV, 2000, p. 713, *ex* Porphyrocrinidae A. M. CLARK, 1973b, p. 281]

Cup slightly conical, radials slightly higher than basals. Arms undivided; adjacent first brachials apposed in small specimens; every second to third brachial articula-

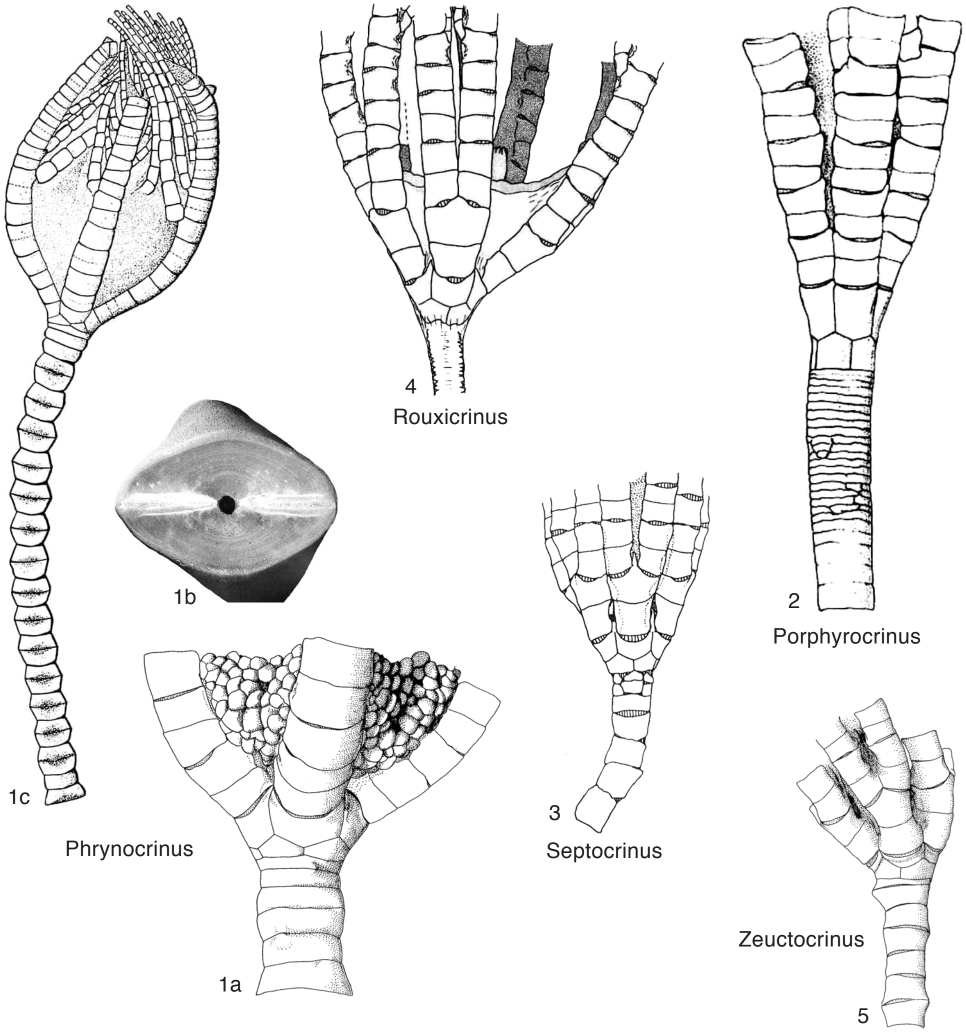

FIG. 77. Phrynocrinidae and Septocrinidae (p. 156–158).

tion nonmuscular. Column long and stout, diameter equal to cup. Several proximal columnals thin discoidal, circular in section with synostosial or symplectial articulations. More distal columnals subcircular to elliptical in section, joined by synarthry. Facets of a few distal columnals may bear marginal crenulae. *Holocene.*

Porphyrocrinus GISLÉN, 1925b, p. 91 [**P. verrucosus;* M]. Characters as for subfamily. *Holocene:* western Pacific Ocean, southwestern Indian Ocean, northeastern and south-central Atlantic Ocean (upper bathyal).——FIG. 77,*2.* **P. verrucosus;* proximal column and base of crown, Palau at 310 m, CRRF crech 147, ×3 (Messing, 2007).

Family SEPTOCRINIDAE Mironov, 2000

[Septocrinidae MIRONOV, 2000, p. 721]

Cup conical; 5 basals and 5 radials almost equal in height. Synostosis between primibrachials 1 and 2. Arms 10, divided at primibrachial 2. Tegmen incompletely covered by primibrachials 1 and 2. Proximal synostoses in most cases between secundibrachials 1 and 2 and 3 and 4, then at variable intervals. First pinnule from brachials 6 to 12, commonly 10. Pinnulars semicircular in cross section, without cover or lateral plates. Large, rodlike spicules in ambulacra. Column attached by radicular cirri in *Septocrinus* (unknown in *Zeuctocrinus*). *Holocene.*

Septocrinus Mironov, 2000, p. 722 [**S. disjunctus*; M]. Cup with laminar, interradial projections. First primibrachials not contiguous; second primibrachials with median prolongation. Three proximalmost columnals composed of 4 to 6 fused or separate plates. Irregular relief on fulcral ridge of distal columnals. No elongate columnals. *Holocene:* southwestern Atlantic Ocean (abyssal).——Fig. 77,*3*. **S. disjunctus*; proximal column and base of crown, Argentina Basin at 5180 m, holotype, IO RAS XV-63-4, ×1.5 (Mironov, 2000).

Rouxicrinus Mironov & Pawson, 2010, p. 51 [**R. vestitus*; M]. Brachials and pinnulars with thorns. Proxistele with numerous low columnals, tapering toward cup. *Holocene:* western Atlantic Ocean (bathyal).——Fig. 77,*4*. **R. vestitus*; proximal column and base of crown, Barbados at 747 m, holotype, USNM E00042699, ×4 (Mironov & Pawson, 2010).

Zeuctocrinus A. M. Clark, 1973b, p. 276 [**Z. gisleni*; M]. First primibrachials in adults proximally in contact laterally. Proximal column articulations elliptical, middle and distal columnals cylindrical. Attachment unknown. *Holocene:* northeastern Atlantic Ocean (lower bathyal).——Fig. 77,*5*. **Z. gisleni*; proximal column and base of crown, holotype, BMNH 1972.12.5.4, ×2 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

Suborder GUILLECRININA Mironov & Sorokina, 1998

[Guillecrinina Mironov & Sorokina, 1998b, p. 11]

[Hans Hess]

Cup small, low; basals usually rounded, swollen. Radials and following brachials of similar size. Arms undivided or divided at more distal brachials. Nonmuscular brachial articulations syzygial or cryptosyzygial. Tegmen high. Fine, flexible pinnules. First pinnule from primibrachials 2 or 3 on either sides of arm. Pinnulars semicircular (crescent shaped) in cross section, with shallow furrow on inner side. Additional plates of genital expansions not arranged in rows. Juvenile column xenomorphic, of various symmetries; adult column homeomorphic; proximal columnals commonly with symplectial facets and grouped crenulae; distal facets with radial, syzygial-like crenulae that may be separated by deep ligamentary pits; adult columnals never with synarthries. Attachment by terminal disk. [The extant genus *Guillecrinus* was placed by Roux (1985a) and Bourseau and others (1991) in the Paleozoic Inadunata because of the presence of infrabasals. However, closer analysis by Améziane and Roux (2005) revealed the absence of infrabasals. These authors also discussed affinities with the Hyocrinidae and Bourgueticrinina. Mironov and Sorokina (1998b, p. 86) assigned the suborder to the Hyocrinida on the basis of a number of common characters. The Guillecrinina are herein tentatively assigned to Comatulida based on a molecular analysis by Cohen and others (2004).] *Holocene.*

Family GUILLECRINIDAE Mironov & Sorokina, 1998

[Guillecrinidae Mironov & Sorokina, 1998b, p. 11]

Characters as for suborder. [Mironov and Sorokina (1998b, p. 14) established the family Vityazicrinidae for the monospecific genus *Vityazicrinus* based on a single, possibly juvenile, specimen; they assigned the family to Hyocrinida. In view of the differences between juvenile and adult columns demonstrated by Améziane and Roux (2005) for *Guillecrinus*, the establishment of a separate family for *Vityazicrinus* is premature.] *Holocene.*

Guillecrinus Roux, 1985a, p. 505 [**G. reunionensis*; OD]. Cup smooth, with 5 basals. First primibrachial as wide as radial. Syzygy between primibrachials 1 and 2 or 1 and 2 and 3, and between primibrachials 4 and 5. First pinnule on primibrachial 2. Additional plates of the genital expansions numerous and small. Ambulacral podia large, including those on proximal pinnules. Tegmen with 5 deep interradial holes, at the upper margin of the radials; anal cone absent. Proximal columnals in one piece, cylindrical, without spines; symplectial articulations with broad, star-shaped crenulae and deep triangular depressions. *Holocene:* western and eastern Indian Ocean, southwestern Pacific Ocean (bathyal).——Fig. 78,*1a*. **G. reunionensis*; proximal column and base of crown, Réunion at approximately 1800 m, holotype, MNHN EcPs 34, ×2 (C. Ferrara, new).——Fig. 78,*1b–e*. *G. neocaledonicus* Bourseau & others, 1991, holotype;

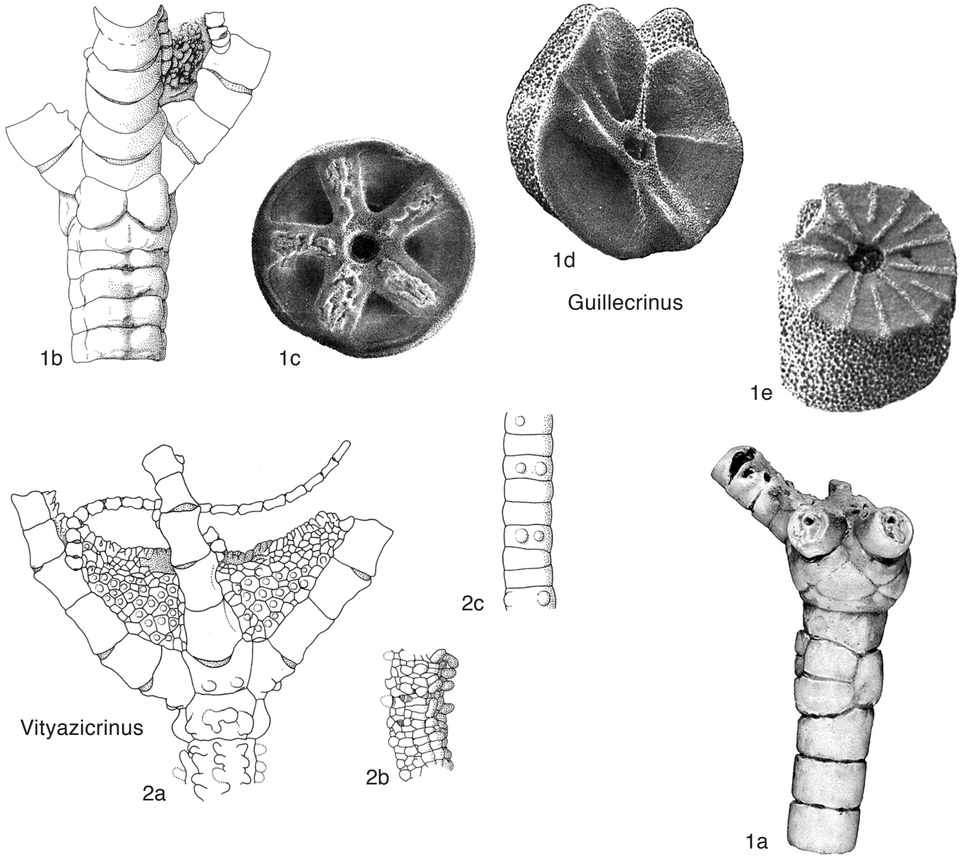

FIG. 78. Guillecrinidae (p. 158–159).

b, proximal column and base of crown, MNHN EcPs10269, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*); *c*, facet of distal columnal with deep ligamentary lobes, MNHN EcPs10269, ×8; *d*, muscular facet of proximal brachial, MNHN EcPs10269, ×8; *e*, syzygy on proximal brachial, MNHN EcPs10269, ×8 (Bourseau & others, 1991).

Vityazicrinus MIRONOV & SOROKINA, 1998b, p. 15 [**V. petrachenkoi*; M]. Cup with 3 basals and 5 radials, bearing large tubercles. Arms divided at primibrachial 7 and more distally. First primibrachial narrower than radial. Nonmuscular brachial articulations cryptosyzygial or approaching syzygies with a few broad culmina; position of cryptosyzygies variable on proximal arms. First pinnule on primibrachial 2 or 3. Ambulacral podia and cover plates of the proximalmost pinnules reduced. Tegmen without holes; anal cone present. Proximal columnals composed of several plates, discoidal, 8-sided or 6-sided, with blunt spines; symplectial articulations with 4 to 5 slightly developed crenulae and shallow depressions. *Holocene:* central Pacific Ocean (upper abyssal).——FIG. 78,*2a–c*. **V. petrachenkoi*; *a*, proximal column and base of crown; *b*, proxistele near cup; *c*, mesistele, central Pacific Ocean at 4100–4400 m, holotype, ZMM C-14, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

MILLERICRINIDA

HANS HESS

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Order MILLERICRINIDA Sieverts-Doreck, 1952

[Millericrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952, p. 614; *emend.*, RASMUSSEN, 1978, p. 817, to include Hyocrinina and exclude Bourgueticrinina; *emend.*, HESS, herein, to exclude Dadocrinidae and Hyocrinina] [=Apiocrinacea STEINMANN, 1903, p. 185, *partim*, excluding Bourgueticrinidae]

Cup large, stout, thick walled. Five basals and radials. Basals contiguous. Primibrachials in most species joined laterally or connected by interradial plates. Synarthries or synostoses between primibrachials 1 and 2 and secundibrachials 1 and 2. Syzygies and cryptosyzygies common. First syzygy between secundibrachials 4 and 5. Tegmen covered with small polygonal plates. Column cylindrical, may be pentagonal proximally with nodals. Cirri absent; attachment by terminal root or encrusting disk, except in *Ailsacrinus*. Columnal articular facets with radiating crenulae, restricted to marginal zone in pentagonal columnals; never synarthrial or cryptosymplectial at infranodals. [Millericrinida are characterized by cylindrical columnals with multiradiate facets and a holdfast of several, laterally enlarged, low columnals. Such features are known from the Middle Triassic Bangtoupocrinidae (including *Silesiacrinus*); but, unfortunately, no intact or partly articulated specimens have been reported from these sediments (HAGDORN, GŁUCHOWSKI, & BOCZAROWSKI, 1996; STILLER, 2000). The origin of millericrinids is rather obscure, but the extant isocrinid *Proisocrinus* with a cirriferous proximal column and a cylindrical distal column, attached by a terminal disk, may be representative of an unknown ancestral form derived from the holocrinids. Relationships of millericrinids to other crinoids with a cylindrical column devoid of cirri, such as cyrtocrinids and hyocrinids, are controversial.] *Middle Triassic–Lower Cretaceous.*

Family MILLERICRINIDAE Jaekel, 1918

[Millericrinidae JAEKEL, 1918, p. 69]

Cup low cone, bowl, or globe shaped. Sharp distinction between cup and column in most forms. Few or generally no interradial plates. *Lower Jurassic–Upper Jurassic.*

Millericrinus D'ORBIGNY, 1840 in 1840–1841, p. 36, *emend.*, ROLLIER, 1911, p. 7 [**Encrinites milleri* VON SCHLOTHEIM, 1823 in 1822–1823, p. 89; SD ROLLIER, 1911, p. 7] [=*Ceriocrinus* KOENIG, 1825, pl. 11,*128* (*nom. nud.*), *non* DESOR, 1845, p. 215, obj., *non* WHITE, 1880, p. 127, obj.; =*Millericrinites* BUVIGNIER, 1852, p. 263, *nom. van.*] Cup large, more or less 5-sided, commonly rather low and wide. Basals forming more or less horizontal underside of cup and commonly part of sides. Radials steep. Radial articular facets separated or laterally in contact. Arms unknown. Column cylindrical or proximally pentagonal; proximal part not widening toward cup. Uppermost columnal enlarged as a 5-sided proximale included in cup, with proximal end reaching the central cavity, and with articular facet toward surrounding basals, forming steep pyramid. Columnal articular facets with crenulae generally arranged in 5 groups. [DESOR (1845, p. 215–216) recorded *Ceriocrinus* KOENIG with the type species *Apiocrinus milleri*, although KOENIG used *Ceriocrinus* in the unpublished second part of *Icones Fossilium Sectiles* in the combination *C. celator* for a figured specimen never identified, and with reservation for *C.? milleri.* Because KOENIG never published the name, and AGASSIZ (1836) only listed *Ceriocrinus* among synonyms of *Apiocrinus*, RASMUSSEN (1978, p. 819) considered *Ceriocrinus* a junior synonym of *Millericrinus*, taking the name and date from DESOR (1845). ROLLIER (1911) subdivided the genus into subgenera *Millericrinus*, *Angulocrinus*, *Liliocrinus*, and "*Cupulocrinus*" (=*Orbignycrinus*), herein treated as genera.] *Middle Jurassic–Upper Jurassic:* England, France, Germany, Poland, Portugal, Switzerland, Crimea.——FIG. 79,*1a–i*. **M. milleri* (VON SCHLOTHEIM), Oxfordian; *a,* cup and proximal column, France, ×1 (de Loriol, 1884 in 1882–1889); *b–c*, cup, *b,* proximal, *c,* distal, Switzerland, NMB 287, ×1 (de Loriol, 1879 in 1877–1879); *d*, proximal view of juvenile cup, Switzerland, NMB 285, ×1 (de Loriol, 1879 in 1877–1879); *e*, distal view of basal circlet, France, ×1 (de Loriol, 1884 in 1882–1889); *f–g*, radial, *f,* aboral, *g,* adoral, Switzerland, MGL 17443, ×1;

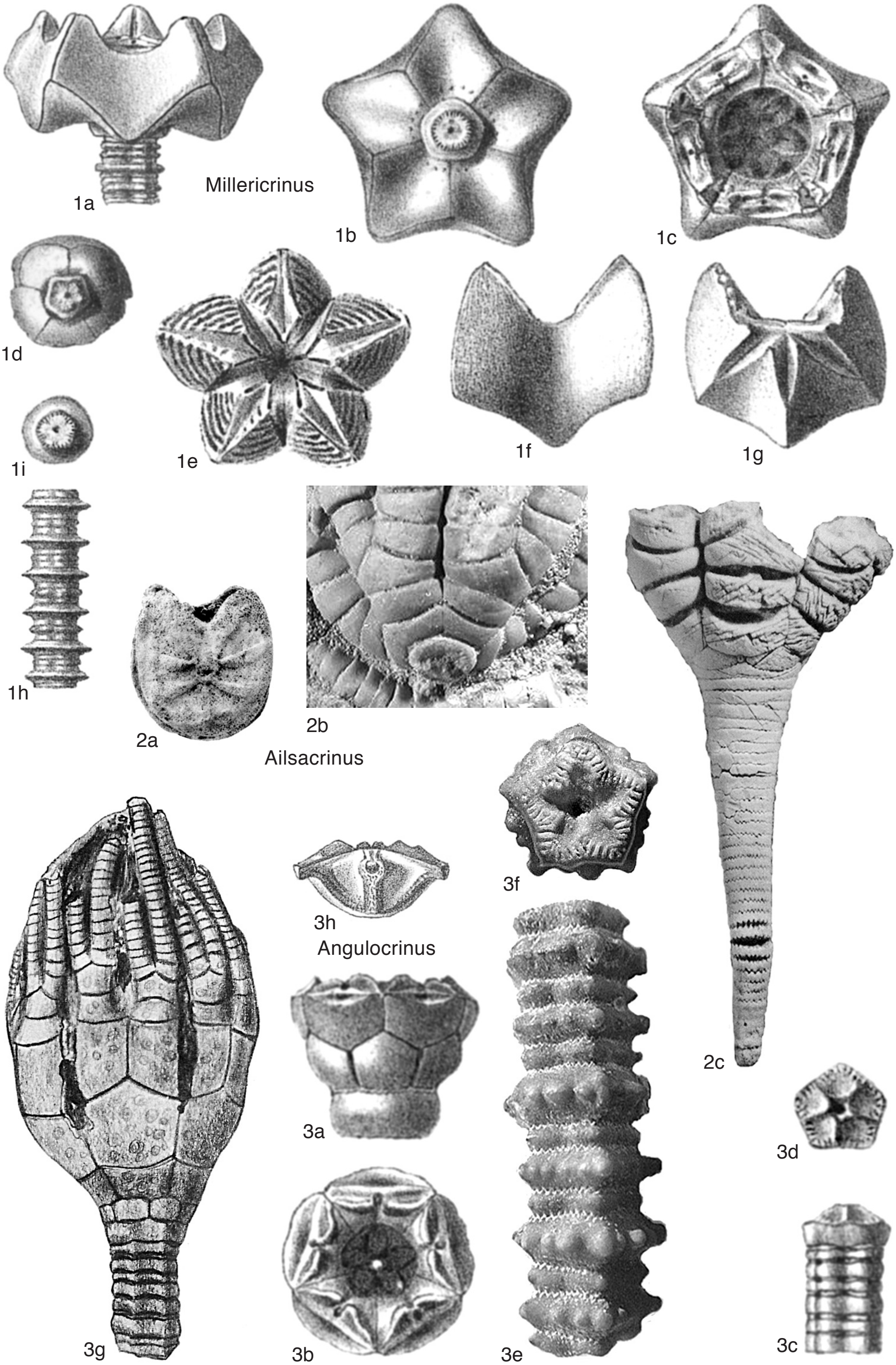

FIG. 79. Millericrinidae (p. 160–162).

h–i, column, *h,* lateral, *i,* facet, Switzerland, NMB 286, ×1 (de Loriol, 1879 in 1877–1879).

Ailsacrinus Taylor, 1983, p. 42 [**A. abbreviatus*; M]. Cup bowl shaped to conical with small basals and commonly with irregularly developed, tiny accessory plates between basals. Synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2. Arms with frequent syzygies. First pinnule on secundibrachial 2. Pinnules differentiated into oral and distal series; short, oral pinnules without groove and cover plates but an adoral transverse ridge, and more elongate distal pinnules with groove and cover plates. Column reduced, tapering distally and terminating in a rounded columnal; incomplete lenticular columnals may be present. No holdfast. [The genus includes *A. prattii* (Gray, 1828), with a column of highly variable length, of 1 to more than 66 columnals (Taylor, 1983, p. 43).] *Middle Jurassic (Bathonian):* England.——Fig. 79,*2a–b.* **A. abbreviatus*; *a,* syzygial facet of brachial, syntype, BMNH E68080, ×9 (Taylor, 1983); *b,* base of crown with top columnal, topotype, NMB M10531, ×3.2 (Hess, new).——Fig. 79,*2c. A. prattii* (Gray); column and base of crown, CAMSM J.33695, ×2.5 (Taylor, 1983).

Angulocrinus Rollier, 1911, p. 4 [**Millericrinus nodotianus* d'Orbigny, 1841 in 1840–1841, p. 59; SD Rasmussen, 1978, p. 819]. Cup truncated conical, not tumid, increasing in diameter upward from edge of enlarged uppermost columnal, which is more or less included as a rounded to 5-sided proximale in cup with a 5-sided pyramidal proximal facet toward the basals. Synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2. Proximal part of column 5-sided with columnals that may alternate in height and diameter. Mesistele mostly cylindrical, commonly ornamented with tubercles, spines, or strands of stereom attached to each other; attachment by radicular cirri as creeping roots or runners along the substrate but also by terminal root. Columnal articular facets with radiating crenulae commonly arranged in 5 groups, especially in proximal part of column. Crenulae may, in some species, be restricted to a marginal zone of facet. [Rollier (1911) based this genus on the cup of *Millericrinus regularis* d'Orbigny and *M. nodotianus* d'Orbigny as figured by de Loriol (1883 in 1882–1889). Rasmussen (1978, p. 819) designated *M. nodotianus* as the type of the genus, because it was the only species based on specimens with a preserved cup by d'Orbigny (1841 in 1840–1841). De Loriol (1884 in 1882–1889, pl. 116,*1c*) found small, concealed infrabasals in specimens of *A. orbignyi.* Numerous species from Oxfordian strata assigned by d'Orbigny (1841 in 1840–1841) and de Loriol (1878, 1883–1884 in 1882–1889) to *Millericrinus* are based on columns only. Most of them appear to belong to *Angulocrinus*; in view of the heteromorphic nature and high variability of the columns, a number of these species may well be identical.] *Middle Jurassic (Callovian)–Upper Jurassic (Kimmeridgian):* France, Germany, Portugal, Switzerland, Crimea.——Fig. 79,*3a–g.* **A. nodotianus* (d'Orbigny); *a–b,* cup, *a*, lateral, *b*, distal, Oxfordian, France, Dijon Museum, ×1; *c–d*, proximal column with proximale, *c*, lateral, *d*, proximal, Oxfordian, France, ×1 (de Loriol, 1883 in 1882–1889); *e–f*, column, *e*, lateral, *f*, facet, Oxfordian, France, NMB M10608, ×4 (Hess, new); *g*, crown and proximal column, base of crown with sutures poorly preserved; there are 2 primibrachials and probably 5 secundibrachials, Oxfordian, Switzerland, ETH 5431, ×1 (Rollier, 1911).——Fig. 79,*3h. A. horridus* (d'Orbigny, 1841 in 1840–1841); proximal view of primibrachial 2, Oxfordian, France, ×2 (de Loriol, 1883 in 1882–1889, as *Millericrinus beaudouini* de Loriol).

Liliocrinus Rollier, 1911, p. 6 [**Millericrinus polydactylus* d'Orbigny, 1841 in 1840–1841, p. 41; SD Rasmussen, 1978, p. 819]. Cup low conical to bowl shaped, not tumid, increasing in diameter upward from edge of rather wide, uppermost columnal. Basals and radials large. Radial articular facet low and wide. Synostosis with marginal crenulae between primibrachials 1 and 2, synarthry between secundibrachials 1 and 2. Column cylindrical, proximal columnals slightly increasing in diameter toward cup, not 5-sided. Columnal articular facets covered by radiating crenulae not separated in groups. Proximal articular facet of uppermost columnal more or less pyramidal or conical to almost flat. Attachment by root. [Rollier (1911) based this genus on *Apiocrinites rosaceus* (von Schlotheim, 1823 in 1822–1823) as figured by Goldfuss (1831 in 1826–1844, pl. 56,*3*) and Quenstedt (1858, pl. 87,*20*), and on *Millericrinus polydactylus* d'Orbigny as figured by de Loriol (1884 in 1882–1889, pl. 109). Because Desor (1845, p. 217) demonstrated that the identity of the first recorded species is ambiguous, Rasmussen (1978, p. 819) designated *M. polydactylus* as the type species. Most specimens from the Upper Jurassic of France and Switzerland described as *Apiocrinites rosaceus* belong to *Liliocrinus munsterianus* (d'Orbigny), the best documented species of the genus. De Loriol (1884 in 1882–1889, pl. 110,*2a*) showed small, concealed infrabasals in specimens of *L. polydactylus.*] *Middle Jurassic (Bathonian)–Upper Jurassic (Kimmeridgian):* England, France, Germany, Switzerland.——Fig. 80,*1a–b.* **L. polydactylus* (d'Orbigny), Oxfordian, France; *a,* crown, ×0.8; *b*, proximal column with cup, MNHN R62602, ×1 (de Loriol, 1884 in 1882–1889).——Fig. 80,*1c–g. L. munsterianus* (d'Orbigny, 1841 in 1840–1841), Oxfordian, Switzerland; *c–e,* cup with a primibrachial 1 still attached and a primibrachial 2 in the radial cavity, *c*, lateral, *d,* proximal, *e*, distal, NMB M10602, ×1; *f–g*, column, *f*, lateral, *g*, facet, NMB M10609, ×1.3 (Hess, new).

Orbignycrinus Biese, 1935 in 1935–1937, p. 478, *nom. nov. pro Cupulocrinus* Rollier, 1911, p. 7, *non* d'Orbigny, 1850 in 1850–1852, p. 23, 46 [**Millericrinus cupuliformis* d'Orbigny, 1841 in 1840–1841, p. 51; SD Sieverts-Doreck in Rasmussen, 1978, p. 822]. Cup smooth, bowl shaped, almost

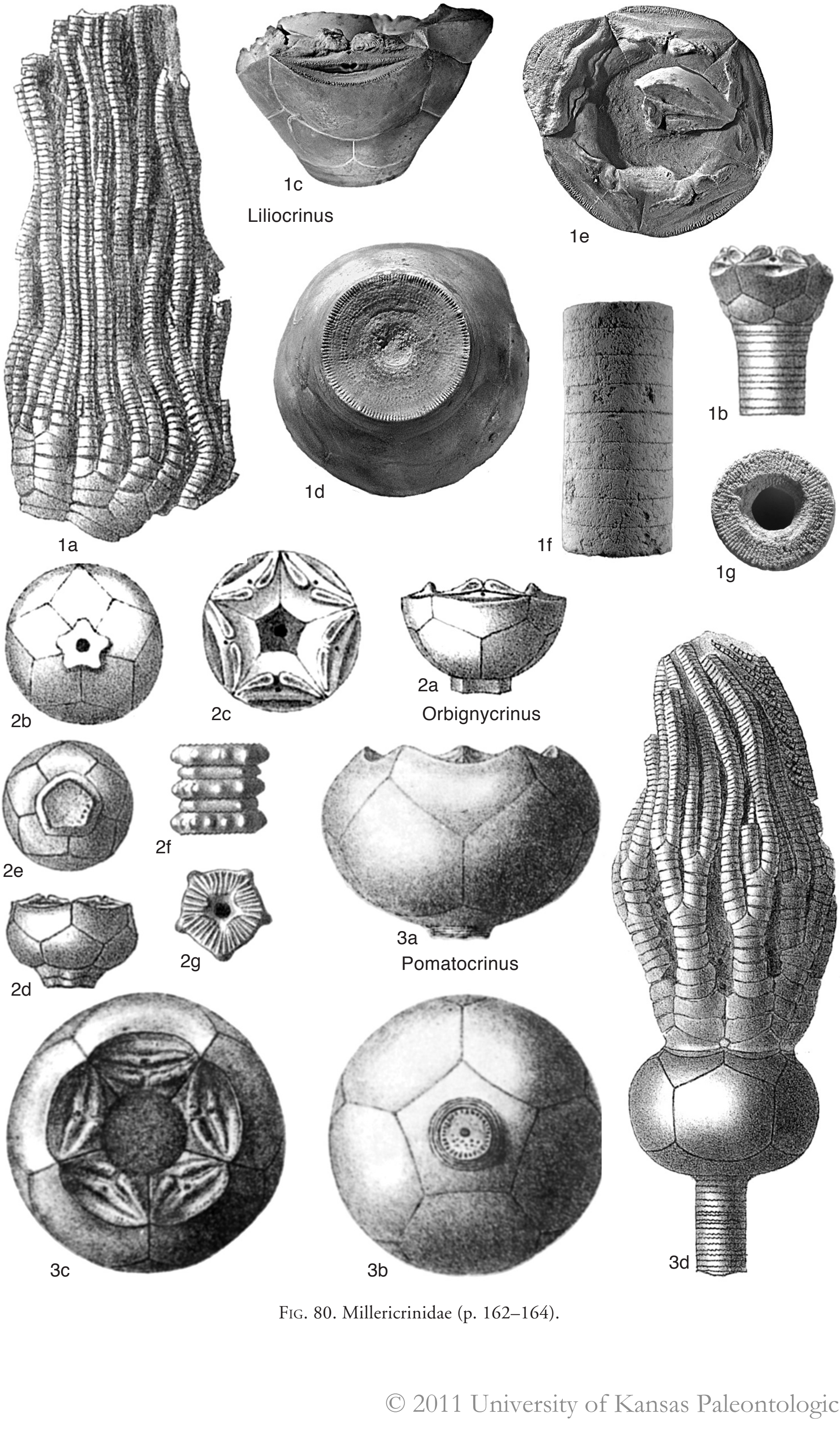

FIG. 80. Millericrinidae (p. 162–164).

hemispherical, composed of large and high basals and somewhat lower radials. Rather small proximale with pentalobate articulation for the column. Distal side of cup almost circular. Radial articular facet low and wide, almost horizontal, meeting in interradial sutures and surrounding shallow radial cavity; with distinct ridge, aboral and interarticular ligament fossae low and wide, adoral muscle fossae not distinct. Arms unknown. Column 5-sided; columnals strongly alternating, crenulae arranged in 5 groups and more or less restricted to a marginal zone. Attachment by root. *Middle Jurassic (Bathonian)–Upper Jurassic (Kimmeridgian):* France, Switzerland.——Fig. 80,*2a–c*. **O. cupuliformis* (d'Orbigny); cup, *a*, lateral, *b*, proximal, *c*, distal, Oxfordian, France, ×2 (de Loriol, 1884 in 1882–1889).——Fig. 80,*2d–g*. *O. cotteaui* (de Loriol, 1883 in 1882–1889), Bathonian, France; *d–e,* cup, *d*, lateral, *e*, proximal, MNHN R61911, ×1 (de Loriol, 1883 in 1882–1889); *f–g*, column, *f*, lateral, *g*, facet, ×1.5 (de Loriol, 1883 in 1882–1889).

Pomatocrinus Desor, 1845, p. 217 [**Encrinites mespiliformis* von Schlotheim, 1820, p. 332; M]. Cup large, globe shaped, thick walled, composed of very large basals, smaller radials, and a rather large proximale surrounding an almost spherical central cavity. Sutures distinct. All cup plates with flat, slightly rough facets. No trace of infrabasals. Radial articular facet large, wide, meeting along interradial sutures; articulation with distinct fulcral ridge, aboral and interarticular ligament fossae, and small adoral muscle fossae. Primibrachials meet laterally. Arms divided at primibrachials 2 and more distally; first pinnule on secundibrachial 2. Synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2. Proximalmost columnal 5-sided, forming aboral pole of spherical cup, and continued as high, 5-sided, truncated pyramid inside basal circlet to bottom of central cavity; underside has a concave, circular, articular facet to receive finely granulated proximal facet of next columnal, which together with a few succeeding, very low columnals form very short, slightly conical transition to cylindrical column. Columnal articular facets with fine, radiating crenulae, closely placed, not in separate groups; crenulae may be modified to granules in central area. [Koenig (1825, pl. 11,*129*) introduced this genus name in the combination *P. jaegeri* in the second part of *Icones Fossilium Sectiles,* which was never published; but it was distributed to a few people. The specimen figured by Koenig but undescribed has never been identified. It resembles *E. mespiliformis*, although this species was figured on the same plate as *Symphytocrinus*? *mespiliformis*. Agassiz (1836, p. 195) recorded *Pomatocrinus* as one of several synonyms of *Apiocrinus*; Desor (1845) first used the name for *Encrinites mespiliformis*. Rollier (1911, p. 6) used the name *Pomatocrinus* for one of his subgroups of *Millericrinus*. Quenstedt (1858, p. 715), described *Apiocrinites mespiliformis* as resembling the fruit of medlar (*Mespilus*); the name *Mespilicrinus* therefore was considered suitable, but it was not established for this genus. Quenstedt (1858, p. 198, 514) also used the name *Mespilocrinites*. He used *Mespilocrinus* in later publications (Quenstedt, 1876, pl. 104,*138–152,* pl. 105,*1–4, 8–12;* 1885, p. 931, fig. 344, pl. 73,*40–44*) for species of *Cyclocrinus*, but this name was preoccupied by de Koninck and Le Hon (1854). Genus is closely similar to a group of *Apiocrinites* except for the unmodified radial articular facet and proximal brachials. It differs from *Orbignycrinus* in column and proximale.] *Lower Jurassic–Upper Jurassic:* Germany, France, Poland, Portugal, Spain, Switzerland, Russia.——Fig. 80,*3a–c*. **P. mespiliformis* (von Schlotheim); cup, *a*, lateral, *b*, proximal, *c*, distal, Upper Jurassic, Portugal, ×1 (de Loriol, 1891).——Fig. 80,*3d*. *P. magnificus* (d'Orbigny, 1850 in 1850–1852); crown and proximal column, Oxfordian, France, lectotype, MNHN B11439, ×0.75 (de Loriol, 1883 in 1882–1889).

Shroshaecrinus Klikushin 1987a, p. 249 [**S. shroshaensis*; M]. Cup sharply differentiated from column, base with concave facet for column. Basals unfused; diameter of radial cavity at upper edge one-quarter of cup diameter. Columnals cylindrical throughout, low, with variable height near cup; columnals not higher in dististele than those in proxistele. Columnal facets with short, coarse crenulae separated from the margin by a narrow, smooth border. [Nonmuscular (synostosial) articulations occur between primibrachials 1 and 2 and secundibrachials 1 and 2 (Jäger, 1995). Klikushin (1987a) placed the genus in a new family, Shroshaecrinidae (order Cyrtocrinida, suborder Hyocrinina, superfamily Hyocrinacea), but Jäger (1995) placed it in the Millericrinidae on the basis of the unfused basals, Cyrtocrinida having at most a fused basal ring. Even though early cyrtocrinids such as *Ticinocrinus* Hess have distinct basals, *Shroshaecrinus* is herein regarded as a millericrinid in accordance with Simms (1989b) and Jäger (1995).] *Lower Jurassic (Sinemurian–Toarcian):* Eurasia.——Fig. 81,*1a–e*. **S. shroshaensis,* Pliensbachian, Caucasus, Russia; *a–c,* cup, *a*, lateral, *b*, proximal, *c*, distal, holotype, LGI JB-26-1, ×2; *d*, proximal column with basal circlet, LGI JB-26-3, ×5; *e*, facet of columnal, LGI JB-27-2, ×6 (Klikushin, 1987a).

Family APIOCRINITIDAE
d'Orbigny, 1840

[*nom. correct.* Rasmussen, 1978, p. 822, *pro* Apiocrinidae d'Orbigny, 1840 in 1840–1841, p. 1]

Cup very large, bowl to globe shaped, medium to high, very thick walled. Interradial plates variable in number, smaller plates may be concealed, wedged between other plates and reaching surface. Variable number of proximal columnals with increasing diameter form conical transition between cup and column. *Lower Jurassic–Lower Cretaceous.*

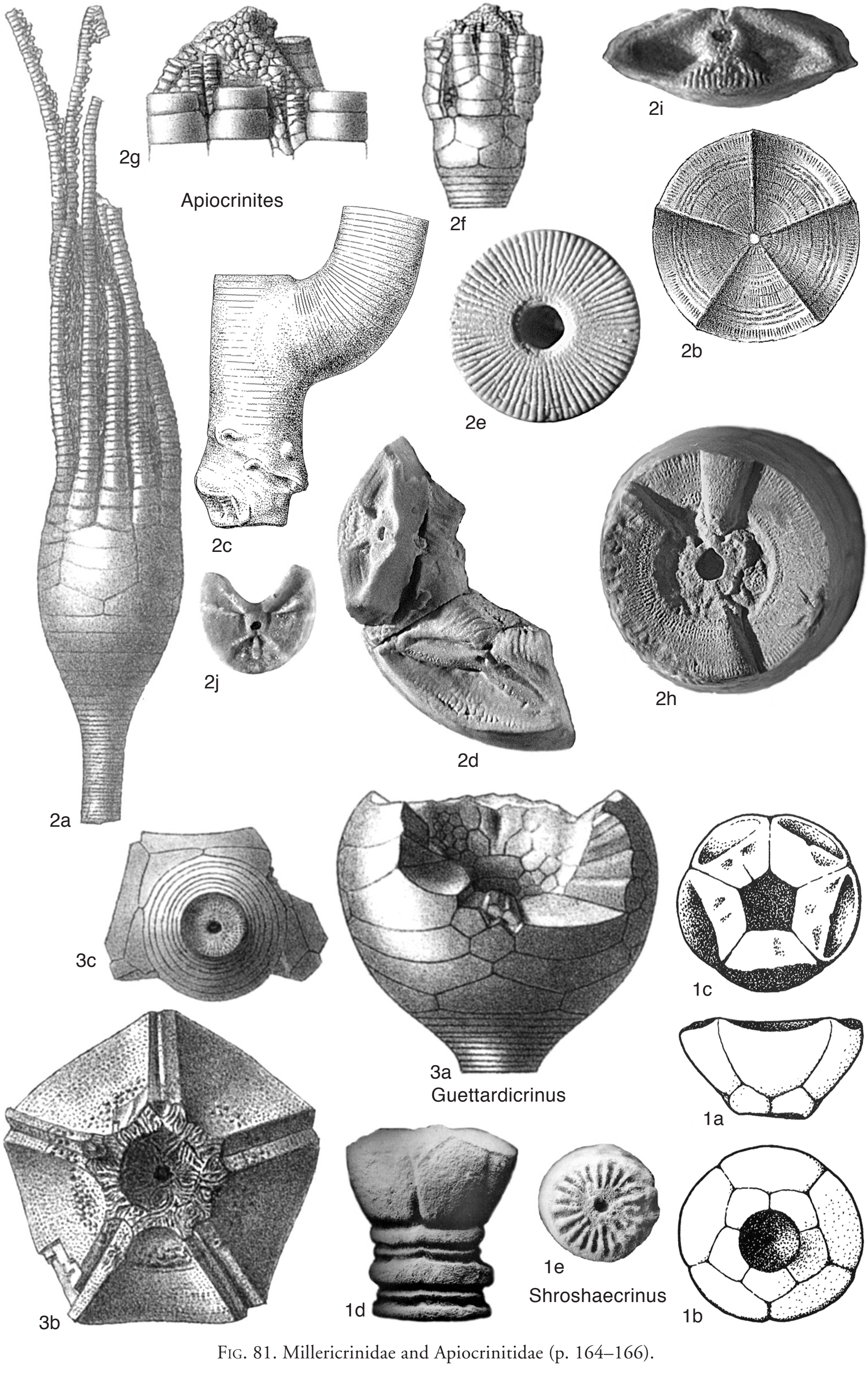

Fig. 81. Millericrinidae and Apiocrinitidae (p. 164–166).

Apiocrinites Miller, 1821, p. 17 [**A. rotundus*; SD d'Orbigny, 1840 in 1840–1841, p. 20; =*Encrinites parkinsoni* von Schlotheim, 1820, p. 332] [=*Apiocrinus* Agassiz, 1836, p. 195, *nom. van.*]. Cup typically globe or pear shaped to ovoid; greatest diameter at basal or radial circlet. Primibrachials meet laterally, with or without a few small, polygonal, interradial plates. Synarthry or synostosis with marginal crenulae between primibrachials 1 and 2, synarthry between secundibrachials 1 and 2. All or most secundibrachials free. Arms divided at primibrachial 2, and in some species, further divided once or twice with variable interval. First pinnule on secundibrachial 2. Proximal column of thin, discoidal columnals increasing gradually in diameter to form long, smoothly conical transition from column to cup. Proximal columnals typically with flat proximal articular facet and concave distal facet, leaving empty central space between columnals. Proximal facet of uppermost columnal with 5 radiating ridges separating facets facing basals. [By emendation, d'Orbigny (1840 in 1840–1841) left *A. rotundus* (=*A. parkinsoni*) as only the original species maintained in the restricted genus *Apiocrinus*. Several species generally referred to *Apiocrinites* have a hemispherical to almost spherical cup and a very short conical proximal column. In some species, only a single, 5-sided proximale with convex to pyramidal proximal facet included in the aboral side of the cup are known as in *Pomatocrinus*, but these have insufficiently known, presumed modified, and reduced articulations in the radials and proximal brachials. These species may perhaps belong to *Pomatocrinus* or may be intermediate in the evolution from *Pomatocrinus* toward *Guettardicrinus*.] *Lower Jurassic–Lower Cretaceous:* England, France, Germany, Hungary, Italy, Poland, Spain, Switzerland, Yugoslavia, Russia, Algeria, Mexico.——Fig. 81,*2a–b*. **A. parkinsoni* (von Schlotheim), Bathonian; *a,* crown, France, ×0.75; *b*, proximal view of topmost columnal with facets to basals, England, ×0.6 (de Loriol, 1882 in 1882–1889).——Fig. 81,*2c–j. A. roissyanus* d'Orbigny, 1841 in 1840–1841, France; *c,* branched column, Oxfordian, NMB M9607, ×0.8 (Hess, 1975); *d*, distal view of part of cup with facets of radial and primibrachial 1, Oxfordian, NMB M10610, ×1.6; *e*, facet of columnal from mesistele, Oxfordian, NMB M10571, ×3 (Hess, new); *f–g*, juvenile specimen, *f,* cup with proximal arms and tegmen, ×1, *g*, tegmen, Kimmeridgian, ×2.5 (de Loriol, 1887); *h*, distal view of top columnal and 2 reduced columnals, Oxfordian, NMB 2, ×1.5; *i*, proximal view of primibrachial 2 (synarthry), Oxfordian, NMB M10568, ×5; *j*, secundibrachial (syzygy), Oxfordian, NMB M10569, ×6 (Hess, new).

Guettardicrinus d'Orbigny, 1840 in 1840–1841, p. 14 [**G. dilatatus*; M] [=*Guettardocrinus* Bronn, 1851 in 1851–1856, p. 123, *nom. null.*]. Cup very large, as large as 76 mm in diameter, hemispherical to almost spherical. Uppermost columnal with low, conical proximal facet just reaching central cavity and with low ridges separating flat or slightly convex, feebly crenulate synostosial joint facets toward basals. Basals and radials rather low and wide. Radials and proximal brachials separated by several small, polygonal, interradial plates, variable in number. Brachials through second secundibrachials included in structure of cup, all stout and connected by modified, generally synostosial articulations with feeble granulation on joint faces. Proximal column of thin columnals increasing rapidly in diameter to form short, smoothly conical transition from column to cup. *Upper Jurassic (Oxfordian):* France, Switzerland.——Fig. 81,*3a–c*. **G. dilatatus,* Kimmeridgian, France; *a,* cup, lectotype herein, MNHN B11466, ×0.7; *b*, distal view of radial circlet, paralectotype, MNHN A25646, ×0.75; *c*, aboral view of proximal column with basals and radials, ×0.8 (de Loriol, 1882 in 1882–1889).

Family NEODADOCRINIDAE Hess, 2006

[Neodadocrinidae Hess, 2006, p. 47]

Cup conical, of variable height, composed of similarly sized, unfused basals and radials joined by flat synostoses. Radial cavity large and deep. Radials with wide adoral furrow; aboral edge of radial articular facet horizontal; adoral muscle fossae moderately encroaching adorally. Proximal columnals circular; symplectial facets with radiating crenulae. Synostosis between primibrachials 1 and 2 and secundibrachials 1 and 2. Holdfast unknown. [Hess (2006) proposed this family for the 2 species of *Neodadocrinus*, *N. tokayi* Manni & Nicosia and *N. brevis* Hess, and the genus *Pustulocrinus* Hess (2006). At first sight, the cup of *Neodadocrinus tokayi* is similar to that of the Triassic *Dadocrinus* von Meyer. Manni and Nicosia (1990a) established *Neodadocrinus* as a genus different from *Dadocrinus* on the basis of one axial canal on the radial articular facet (*Dadocrinus* has 2) and more inclined muscle fossae (subhorizontal in *Dadocrinus*). However, paired axial canals are not diagnostic of small Triassic crinoids (H. Hagdorn, personal communication, 2001). Manni and Nicosia (1990a) assigned *Neodadocrinus* to the Triassic family Dadocrinidae Lowenstam (considered by them to be millericrinids).

Subsequently, NICOSIA (1991) proposed a new order, Dadocrinida, for this family as well as Plicatocrinidae ZITTEL and Proholopodidae ŽITT. RASMUSSEN (1978), SIMMS (1988b), and KLIKUSHIN (1987c) had previously assigned Dadocrinidae to the order Millericrinida. *Neodadocrinus tokayi* shares with *Dadocrinus* the high, conical, dicyclic (or cryptodicyclic) cup (although *N. brevis* HESS has a lower, compact cup), but *Dadocrinus* has basals and radials connected by synostoses with deep ligament pits (see Fig. 14*a–b*). In contrast, the radials of *Neodadocrinus* are articulated to each other and to the basals by flat synostoses. Following HAGDORN (1996b), the Dadocrinidae are assigned to the Encrinida, in which juveniles and less specialized forms also have uniserial arms, similar cup structure, and comparable attachment disks with strongly crenulate columnal facets. The presence of a species of *Neodadocrinus* with a low cup suggests that cup height varies within the genus. Therefore, assignment of *Neodadocrinus* to the Triassic family Dadocrinidae is not followed, and *Neodadocrinus* is considered to be a primitive millericrinid.] *Lower Jurassic (Sinemurian–Pliensbachian).*

Neodadocrinus MANNI & NICOSIA, 1990a, p. 363 [**N. tokayi;* M]. Cup small, of variable height. Radial articular facet narrow, occupying entire width of adoral side; muscle fossae almost parallel to oral-aboral axis; one axial canal only. Primibrachials compact, joined by synostosis. [Columnals and secundibrachials are unknown. MANNI and NICOSIA (1990a) inferred the presence of an infrabasal circlet (fused infrabasals) from the nerve canals at the proximal surface of the basals of *N. tokayi*. Nerve canals are visible only on the distal surface in *N. brevis*, however, and there is no indication of an infrabasal circlet (HESS, 2006).] *Lower Jurassic (Sinemurian–Pliensbachian):* Switzerland, Turkey.——FIG. 82,*1a–b*. **N. tokayi*; reconstructed cup, *a,* lateral, *b,* distal, Turkey, ×7 (Manni & Nicosia, 1990a).——FIG. 82,*1c–h*. *N. brevis* HESS, Pliensbachian, Switzerland; *c,* cup, holotype, NMB M10152, ×8; *d*, adoral view of basal, syntype, NMB M10161, ×10; *e–h*, radial, *e*, proximal, *f,* aboral, *g*, adoral, *h*, distal, paratype, NMB M10156, ×8 (Hess, 2006).

Pustulocrinus HESS, 2006, p. 48 [**P. iguana*; M]. Cup low and wide. Pinnules mostly fused. Brachials and pinnulars with crest; all plates with strong, irregular pustules. *Lower Jurassic (Pliensbachian):* Switzerland.——FIG. 82,*2a–n*. **P. iguana*; *a–b,* cup, *a*, distal view of part of basal circlet on topmost columnal, *b*, proximal view of radial circlet, holotype, NMB M10493, ×5; *c–f*, radial, *c*, aboral, *d*, adoral, *e*, proximal, *f,* distal, paratype, NMB M10259, ×7.5; *g–i*, primibrachial 1, *g*, aboral, *h*, adoral, *i*, distal, paratype, NMB M10270, ×7.5; *j*, aboral view of primibrachial 2, syntype, NMB M10274, ×10; *k*, proximal view of secundibrachial 2, paratype, NMB M10280, ×10; *l–m*, secundibrachial, *l*, lateral, *m*, adoral, paratype, NMB M10288, ×7.5; *n*, pinnular, paratype, NMB M10298, ×10 (Hess, 2006).

Family BANGTOUPOCRINIDAE Stiller, 2000

[Bangtoupocrinidae STILLER, 2000, p. 39]

Long column of rather uniform, discoidal columnals without cirri. Holdfast discoidal to encrusting, consisting of several low columnals; latera and holdfast callus smooth or bearing tubercles to spines. Columnal facets with radial crenulae typically covering entire facet; culmina sometimes with longitudinal groove; culmina commonly bifurcated; additional crenulae may be inserted near margin; differently sculptured perilumen and/or narrow areola may be developed. Only column known. *Middle Triassic (Anisian).*

Subfamily BANGTOUPOCRININAE Stiller, 2000

[Bangtoupocrininae STILLER, 2000, p. 42]

Latera of columnals and surface of holdfast callus sculptured with tubercles to spines. Axial canal simple, lumen narrow. *Middle Triassic (Anisian).*

Bangtoupocrinus STILLER, 2000, p. 42 [**B. kokeni*; M; =*Entrochus rotiformis* KOKEN, 1900, p. 188, 212–214, pl. 10,*20–25*, *partim*, *non* pl. 10,*16–19,* which is *Qingyanocrinus kueichounensis* DUBATOLOVA & SHAO, 1959, p. 47]. Column long, cylindrical with rather uniform, discoidal columnals without cirri; latera with densely arranged, small tubercles to spines. Columnal articular facets with numerous radial crenulae typically covering entire facet; coarser culmina sometimes with longitudinal groove; culmina may bifurcate once or twice, and additional crenulae may be inserted; surface of culmina granulated; facets sometimes with circular, granulated perilumen with sculpture of crenulae modified. Holdfast discoidal to encrusting, of several low columnals typically covered by callous

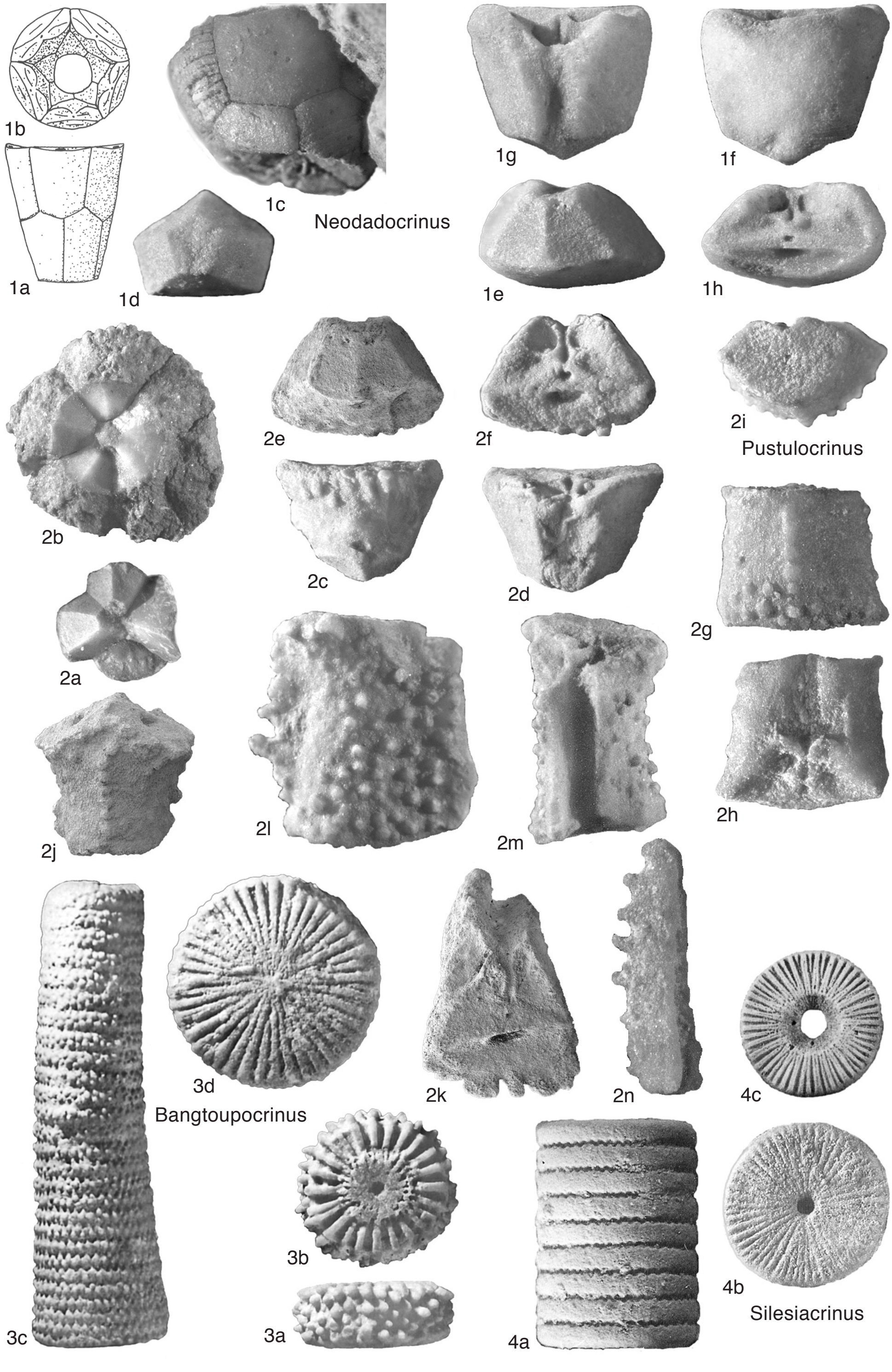

FIG. 82. Neodadocrinidae and Bangtoupocrinidae (p. 167–169).

crust; surface of holdfast callus studded with fine tubercles. *Middle Triassic (Anisian):* China (Qingyan, Guizhou Province).——Fig. 82,*3a–d*. **B. kokeni;* columnal, *a*, lateral, *b*, facet, paratype, NIGPAS B3B-1.Cr3.F83-4, ×5; *c–d*, column, Guizhou, holotype, NIGPAS B3B-1.Cr3.Fbt-3, *c*, lateral, ×2, *d*, facet, ×3 (Stiller, 2000).

Subfamily SILESIACRININAE Stiller, 2000

[Silesiacrininae Stiller, 2000, p. 47]

Latera of columnals and holdfast smooth. Axial canal simple or complex with lenticular spaces, lumen mostly wide, circular or weakly pentalobate. *Middle Triassic (Anisian).*

Silesiacrinus Hagdorn & Głuchowski, 1993, p. 175 [**Entrochus silesiacus* Beyrich, 1858, p. 46; OD]. Columnals low, circular, with straight to convex latera. Columnal articular facets multiradiate, culmina long, commonly with delicate, longitudinal groove; granular radial bands may occur on inner side; areola very narrow or lacking. Holdfast irregular discoidal, consisting of several columnals that may be partly fused. *Middle Triassic (Anisian):* Alps, Germany, Poland, Hungary, China.——Fig. 82,*4a–c*. **S. silesiacus* (Beyrich), Poland; *a–b,* pluricolumnal, *a*, lateral, *b*, facet, holotype, MNHB MB. E 713, ×2.5; *c*, facet of columnal, IGPT 1766/3, ×3 (Hagdorn, Głuchowski, & Boczarowski, 1996).

Family UNCERTAIN

Amaltheocrinus Klikushin, 1984, p. 79 [**Apiocrinites amalthei* Quenstedt, 1852, p. 612; SD Klikushin, 1984, p. 79]. Cup pear shaped, composed mostly of massive radials that may be fused; radial cavity deep. Basal circlet present or absent. Primibrachials thick walled, united by synostosis. Arms branching at least once beyond axillary primibrachial 2. Columnal articular facets covered peripherally with radiating ridges and centrally by weak knobs, short ridges, or ringlets. Attached by terminal disk. [Assignment to Millericrinida according to Simms (1990a); assignment to Cyclocrinidae by Klikushin (1984) and Jäger (1985, p. 78). Subsequently, Jäger (personal communication, 2002) considered *Amaltheocrinus* to belong to a separate family with characters of both Millericrinida and Cyrtocrinida. Assignment to Millericrinida is based on size, column length, and arm branching. Columnal facets are in part similar to those of Triassic forms such as *Qingyanocrinus*.] *Lower Jurassic:* Eurasia.——Fig. 83,*1a–m*. **A. amalthei* (Quenstedt), Pliensbachian, Germany; *a–b,* pluricolumnal, *a*, lateral, *b*, facet, NMB M10487, ×2 (Hess, new); *c*, columnal facet, NMB M10490, ×2 (Hess, 2008); *d–e*, primibrachial 1, *d*, adoral, *e*, distal, JME PL 1993/49, ×3; *f–g*, primibrachial 2, *f*, adoral, *g*, proximal, JME PL 1993/51, ×3; *h–i*, radial, *h*, aboral, *i*, adoral, JME PL 1993/34, ×2.6; *j–l*, radial circlet, *j*, lateral, *k*, proximal, *l*, distal, JME PL 1993/40, ×3; *m*, columnal facet, NMB M10492, ×2 (Jäger, 1993).

Carinacrinus Hess, 2006, p. 55 [**C. hagdorni*; M]. Cup unknown. Brachials triangular in cross section with smooth surface and aboral keel. Proximal and distal brachial articular facets at an angle to each other, either both muscular or one muscular and one synostosial. Large pinnule socket with fulcral ridge parallel to adoral furrow; no pinnule socket in approximately half the brachials with synostosial facet. Column unknown. *Lower Jurassic (Pliensbachian):* Switzerland.——Fig. 83,*2a–e*. **C. hagdorni*; *a–c,* secundibrachial, *a*, lateral, *b*, adoral, *c*, distal, holotype, NMB M10252, ×10; *d*, lateral view of secundibrachial, syntype, NMB M10250, ×10; *e*, proximal view of secundibrachial with synostosis, syntype, NMB M10251, ×10 (Hess, 2006).

Catinicrinus Hess, 2006, p. 56 [**C. jaegeri*; M]. Cup unknown. Primibrachials connected by synostosial facets. Saddle-shaped brachials with smooth surface, constricted body and large facets, with or without pinnule sockets. Brachial articular facets muscular, synostosial, or syzygial with 2 ridges arranged in a V shape. Distal brachials elongate, with articular facets at an angle to the ossicle and a protruding pinnule socket. Distal facets of many brachials with one muscle fossa on lappet articulating with spoon-shaped muscle fossa on proximal side of following brachial. Axils with proximal muscle fossae indicate arm branching distal to primibrachials. Column unknown. *Lower Jurassic (Pliensbachian):* Switzerland.——Fig. 83,*3a–h*. **C. jaegeri*; *a–c,* secundibrachial, *a*, aboral, *b*, adoral, *c*, distal, holotype, NMB M10312, ×10; *d–e*, secundibrachial, *d*, proximal (syzygy), *e*, adoral, paratype, NMB M10307, ×10; *f*, adoral view of distal secundibrachial, paratype, NMB M10316, ×10; *g*, aboral view of distal secundibrachial, paratype, NMB M10317, ×10; *h*, aboral view of primibrachial 1, paratype, NMB M10496, ×6 (Hess, 2006).

Rotacrinus Hess, 2006, p. 57 [**R. canalis*; M]. Cup unknown. Brachials disk shaped, with parallel facets and broad, adoral furrow bordered by sharp ridges; facets oblique and straight muscular, syzygial with 2 to 4 V-shaped or crosslike culmina, and synostosial with or without pinnule socket. Column unknown. *Lower Jurassic (Pliensbachian):* Switzerland.——Fig. 84,*1a–d*. **R. canalis*; *a–c,* epizygal secundibrachial, *a*, proximal, *b*, adoral, *c*, distal, holotype, NMB M10333, ×7; *d*, distal view of secundibrachial without pinnule socket, paratype, NMB M10337, ×7 (Hess, 2006).

Serracrinus Hess, 2006, p. 58 [**S. planus*; M]. Cup unknown. Brachials typically wide and low, rectangular to triangular in adoral or aboral view. Aboral surface with spines that increase in size laterally. Brachials with or without pinnule socket. Facets muscular and synostosial; muscular facets

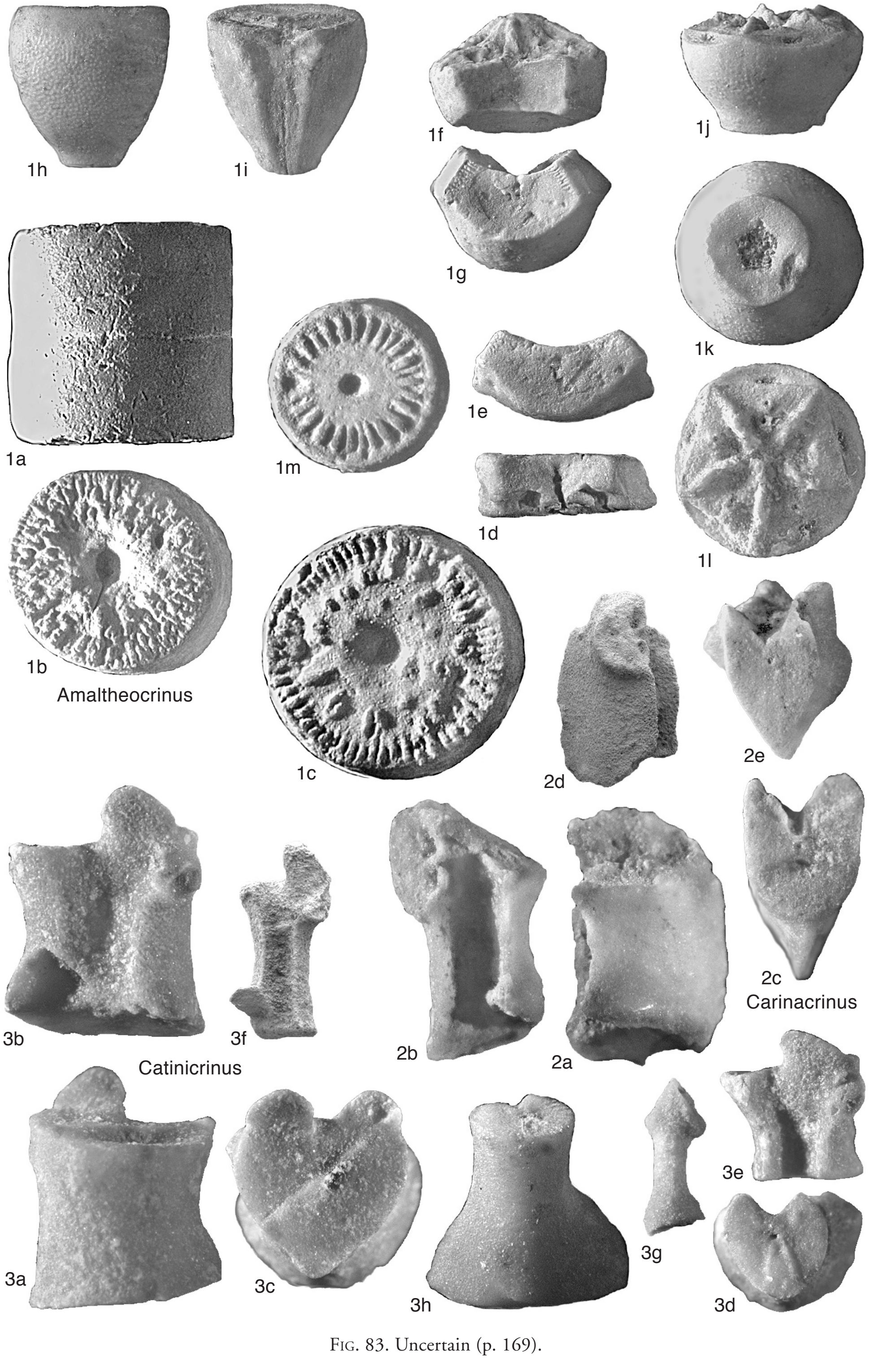

Fig. 83. Uncertain (p. 169).

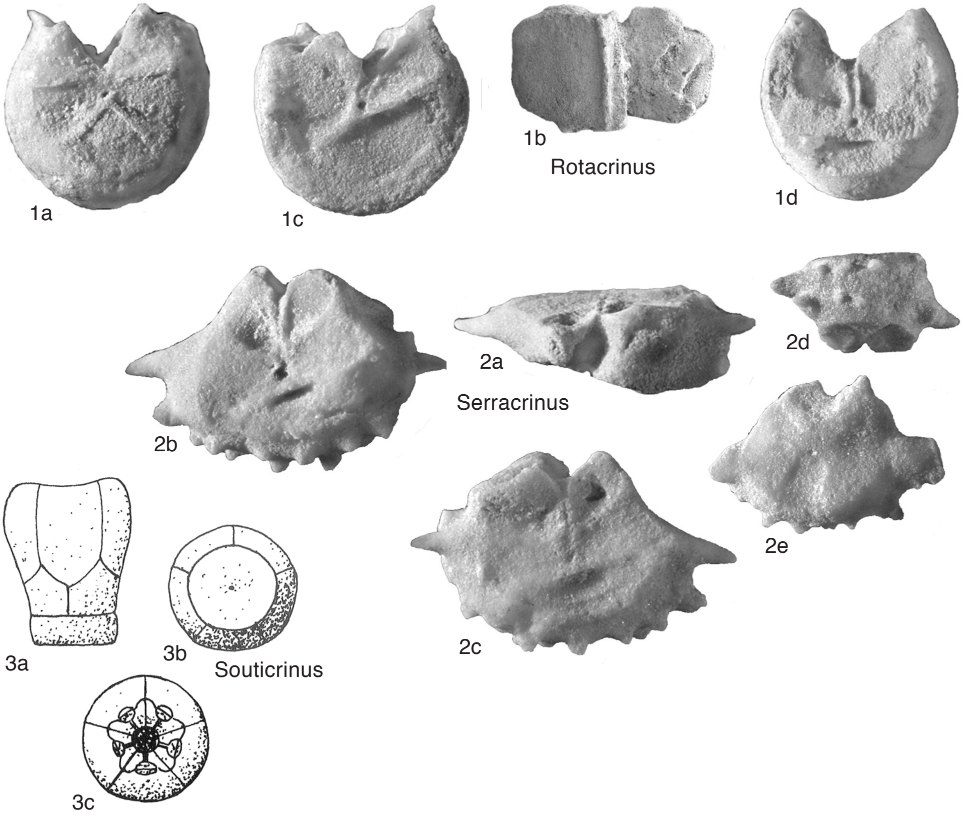

FIG. 84. Uncertain (p. 169–171).

with small, drop-shaped muscle fossae bordering adoral furrow. Column unknown. *Lower Jurassic (Pliensbachian):* Switzerland.——FIG. 84,*2a–e*. **S. planus*; *a–c,* secundibrachial, *a*, adoral, *b*, proximal, *c*, distal, holotype, NMB M10341, ×7; *d*, aboral view of secundibrachial, paratype, NMB M10347, ×7; *e*, proximal view of secundibrachial (synostosis), syntype, NMB M10349, ×10 (Hess, 2006).

Souticrinus NICOSIA, 1991, p. 398 [**S. farinacciae*; M]. Small compact cup with proximale, contiguous basals and radials. Radial cavity deep and narrow. Radial articular facet small, inward sloping; aboral ligament pit wide; adoral muscle fossae small. Column cylindrical. *Lower Jurassic (Sinemurian):* Turkey.——FIG. 84,*3a–c*. **S. farinacciae*; reconstructed cup, *a*, lateral, *b*, proximal, *c*, distal, ×3 (Nicosia, 1991).

HYOCRINIDA

HANS HESS

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Order HYOCRINIDA Rasmussen, 1978

[*nom. transl.* MIRONOV & SOROKINA, 1998b, p. 10, *ex* Hyocrinina RASMUSSEN, 1978, p. 826; *emend.,* HESS, herein, to exclude Guillecrinina]

Cup thin walled, hollow, formed by basals and radials; infrabasals absent; basals fused or with 1 to 3 sutures. Radials 5, separated by distinct sutures. Arms undivided, except in *Calamocrinus,* where the first division occurs between brachials 8 to 15, first division never at primibrachial 2. Arms branch exceptionally at brachial 4 in *Dumetocrinus* and *Gephyrocrinus*. Arms considerably narrower than radials, completely separated laterally; radial articular facet narrower than width of ossicle. Nonmuscular articulations smooth (synostosial), primibrachials 1 and 2 united by synostosis. First pinnule on brachials 2 to 6. Tegmen covered by small polygonal plates. Column homeomorphic, long, slender, without nodals or cirri. Columnal articulations typically symplectial proximally with radiating crenulae, grouped in more than 5 crenular units (except in *Laubiericrinus*, the only genus with pentamerous symplexies); symplexies sometimes with areolar depressions or piercings. Facets of distal columnals tending to reduced or densely arranged vermicular crenulae, commonly with juvenile symplectial pattern around lumen (see ROUX, 1980a, pl. 1,*5–6;* HOLLAND, GRIMMER, & WIEGMANN, 1991, fig. 40, 45; MIRONOV & SOROKINA, 1998b, pl. 4,*5–6;* ROUX & PAWSON, 1999, pl. 2,*9–10;* ROUX, 2004, fig. 3h–l). Attachment to substrate by expanded terminal disk, no radix. [RASMUSSEN (1978, p. 817) treated hyocrinids as a suborder of Millericrinida with which they share the cylindrical columnal devoid of cirri. However, hyocrinids have thin-walled, hollow cups, commonly with high radials that carry narrow, free arms. The supposed 5 distinct basals in *Calamocrinus*, which contributed to RASMUSSEN's (1978) and SIMMS's (1988b) assignment of hyocrinids to millericrinids is based on an erroneous interpretation: *Calamocrinus* never has more than 3 sutures in the commonly fused basal circlet (ROUX, 2004). The origin of hyocrinids remains obscure, although GISLÉN (1939) discussed a cyrtocrinid origin and postulated an affinity with Eudesicrinidae, in part because of the wide radial cavity. However, wide radial cavities of the Holopodidae and other stalkless cyrtocrinids cemented to the bottom result from the necessity to hide the soft parts under a protective arm cover, whereas hyocrinids, in addition to their long column, commonly house the viscera under a high tegmen, and arms that do not curl inward. Largely following GISLÉN's (1939) argument, AMÉZIANE and others (1999) and ROUX (2004) assigned the Hyocrinidae to the Cyrtocrinida. ROUX (1980a) placed the Hyocrinidae in the Cyrtocrinida based on a comparison of hyocrinid columnal facets and microstructure with those of *Cyclocrinus amalthei*, *Cyclocrinus hausmanni* (thought to belong to the Cyrtocrinida but now placed in *Amaltheocrinus*), and *Eugeniacrinites quenstedti*. However, cup and primibrachials of *Amaltheocrinus* are thick walled and, thus, quite different from those of hyocrinids. Cyrtocrinid columns are short and immovable. Herein, MIRONOV and SOROKINA (1998b) are followed in their treatment of hyocrinids as a separate order. However, their suborder Guillecrinina has been transferred to the Comatulida, and the remaining suborder Hyocrinina suppressed. A single fossil species, *Calamocrinus ilimanagei*, was described from the Danian of Greenland by RASMUSSEN (1972a). It is based on 3 small cylindrical columnals whose facets resemble those of extant hyocrinids. Unfortunately, no cup plates were found that could support this assignment, and the diagnostic value of such columnals appears to be questionable. The species was transferred by MIRONOV and SOROKINA (1998b) to *Cratecrinus (Excavocrinus)* of uncertain affinity.] *Holocene.*

Family HYOCRINIDAE Carpenter, 1884

[Hyocrinidae CARPENTER, 1884a, p. 217]

Characters as for order. *Holocene.*

Hyocrinids attach to rocky substrates by their encrusting disk. They live in cold, deep water on continental margins, rises, seamounts, and ferromanganese nodule fields in abyssal plains (ROUX & PAWSON, 1999); larger forms occur on slopes and seamounts and smaller ones on abyssal plains where food supply is limited. Restricted food supply may be one reason for their mostly delicate skeleton. They are mostly unbranched but display dense filtration fans by virtue of their long pinnules (Fig. 85,*1c;* ROUX, 1987, fig. 5c). With the exception of *Dumetocrinus antarcticus* and *Calamocrinus diomedae* (shallowest depth approximately 500 m), hyocrinids inhabit depths in excess of 700 m. Specimens are scarce in dredge and trawl samples, but deep-sea photographs have revealed several abundant, stalked crinoid populations, including hyocrinids on rocky current-swept substrates (ROUX, 1980b, 2002). Recently, knowledge of hyocrinids has progressed rapidly. ROUX, MESSING, and AMÉZIANE (2002) mentioned 18 species of living hyocrinids, only 8 of which were mentioned by ROUX (1980a); 13 have been described since 1998, mostly by MIRONOV and SOROKINA (1998b) and AMÉZIANE and ROUX (2011). MIRONOV and SOROKINA (1998b) erected 4 subfamilies in Hyocrinidae using the architecture of genital pinnules as one of the most important characters. Two of these subfamilies (Calamocrininae and Hyocrininae) had been proposed previously by A. M. CLARK (1973b), and the others (Dumetocrininae and Ptilocrininae) issued from changes and restrictions in the diagnosis of the genus *Ptilocrinus*. However, as with other stalked crinoids, the most important taxonomic character lies in the pattern of branching and arrangement of arm articulations (ROUX, 2004), especially in the proximal part. Stalked crinoid ontogeny has a complex mosaic of heterochronic development (AMÉZIANE & ROUX, 1994), providing a wide field of phenotypic variations at different taxonomic levels. Among hyocrinids, heterochronic gradients have been documented in *Hyocrinus foelli* ROUX & PAWSON, with wide intraspecific variations (ROUX & PAWSON, 1999), and in *Thalassocrinus* at the generic level (ROUX, 2002). A statistical evaluation of morphological variation has not been attempted, because numerous hyocrinid taxa are known from single specimens only, which prevented ROUX (2004) from defining intermediate taxonomic categories such as subfamilies and subgenera. However, he suggested close affinities among *Calamocrinus*, *Ptilocrinus,* and *Gephyrocrinus*, genera that were placed by MIRONOV and SOROKINA (1998b) in separate subfamilies. The following classification follows ROUX (2004) and AMÉZIANE and ROUX (2011).

Hyocrinus THOMSON, 1876, p. 47 [**H. bethellianus;* M]. Basals 3 or fused, forming a circlet without distinct sutures. Width of distal radial articular facet 33 to 44 percent of upper width of radial. No lateral spines or flattened projections on proximal brachials and pinnulars. Second and third nonmuscular articulations between brachials 3 and 4 and 5 and 6. First pinnule typically on brachial 6, rarely on 5. In middle part of arm, successive series of 2 or 3 brachials united by synostosis, never successive muscular articulations. Expansion of genital pinnules with one row of H-shaped plates, but shape of cover plates very variable and useful at species level only (ROUX, 2004, fig. 7). Cover plates consisting of 2 or 3 pairs corresponding to each pinnular. Tegmen typically low, sometimes inflated. Oral plates typically large, forming high oral cone where tegmen low. Anal cone low. Columnal symplexies with 6 to 10 crenular units of one crenula each, or more in larger species like *H. biscoitoi* (number of crenular units and crenulae unknown in *H. giganteus*). *Holocene:* Southern Ocean, Indian Ocean, Pacific Ocean (bathyal and abyssal).——FIG. 85,*1a–b.* **H. bethellianus; a,* proximal column and crown, Crozet Islands at approximately 3000 m, holotype, BMNH (18)85.3.30.31, ×1.7 (Thomson, 1876); *b,* adoral view of cup with tegmen, ×10 (Carpenter, 1884a, pl. 6,*4*).——FIG. 85,*1c. H. biscoitoi* ROUX, 2004; complete specimen, length of crown 25 cm, 35 pinnules on each side, East Pacific Rise at 2410 m, holotype, MNHN EcPh90 (Roux, 2004).——FIG.

85,*1d–e. H. cyanae* Bourseau & others, 1991; *d*, proximal column and base of crown, *e*, portion of mesistele, southwestern Pacific, MNHN EcPs244, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

Anachalypsicrinus A. M. Clark, 1973b, p. 269 [**A. nefertiti;* M]. Three basals with distinct sutures. Width of distal radial articular facet 40 to 50 percent of upper width of radial. Second nonmuscular articulation between brachials 4 and 5, third between brachials 6 and 7; nonmuscular articulations irregularly distributed along middle arm. Consecutive muscular articulations commonly 1 or 2, maximum 4. First pinnule on brachial 5. Expansion of genital pinnules with one row of H-shaped plates. Cover plates of 2.5 to 3.5 pairs corresponding to each pinnular. Tegmen low. Anal cone low. Oral cone large and high. Columnal symplexies with 9 to 12 crenular units of 1 to 5 crenulae each. *Holocene:* northern Atlantic Ocean (lower bathyal).——Fig. 86,*1a. *A. nefertiti;* proximal column and base of crown, northeastern Atlantic, holotype, BMNH 1972.12.5, ×1.5 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).——Fig. 86,*1b. A. atlanticus* (Roux, 1990); facet of distal columnal, Newfoundland at 1850–1875 m, holotype, NMNH ED-319, ×15 (Roux, 1990, under *Ptilocrinus*, species transferred to *Anachalypsicrinus* by Mironov & Sorokina, 1998b).

Belyaevicrinus Mironov & Sorokina, 1998b, p. 58 [**B. latipinnulus*; M]. Structure of cup unknown. Second nonmuscular articulation between brachials 4 and 5; middle part of arm with 2 or series of 3 brachials united by synostosis. Maximum number of consecutive muscular articulations 1. Brachials do not become narrower at inner margin of arms. First pinnule on brachial 6. Fewer than 10 (approximately 5) pinnules on one side of arm. Expansion of genital pinnules wide and well developed; 2 rows of genital plates on one side of pinnule. Interradial fossae of tegmen not equal in height; tegmen reaching brachial 3 in interrays BC and CD, but only brachial 1 in interray AE. Tegminal interradial plates tend to be arranged in median row. Columnal symplexies with 7 crenular units of 1 or 2 straight crenulae each. *Holocene:* Indian Ocean, Southern Ocean (abyssal).——Fig. 85,*2a–c. *B. latipinnulus*; *a*, highest part of tegmen at interradius BC, ×4, *b*, anal cone, ×4, *c*, proximal part of arm, Antarctica at approximately 5600 m, holotype, ZMM C-21, ×3 (Mironov & Sorokina, 1998b).

Calamocrinus Agassiz, 1890, p. 165, *emend.*, Roux, 2004, p. 606 [**C. diomedae*; M]. Basals fused or with a few inconspicuous sutures, aboral side of basal circlet flanged. Arms irregularly branching, first branching between brachials 8 to 15, additional branching more distally. Second synostosis between brachials 5 and 6. Maximum number of consecutive muscular articulations approximately 9. Distribution of nonmuscular articulations along middle arm irregular. First pinnule on brachial 4. Expansion of genital pinnules with numerous, imbricated, small plates, never in rows (Roux, 2004, fig. 7e). Tegmen inflated, with well-developed anal cone. Columnal symplexies with 7 to 16 crenular units of 1 to 4 crenulae, depending on columnal diameter. *Holocene:* eastern Pacific Ocean (bathyal).——Fig. 86,*2. *C. diomedae*; proximal column and base of crown, USNM E47881, ×2 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

Dumetocrinus Mironov & Sorokina, 1998a, p. 413 [**Ptilocrinus antarcticus* Bather, 1908, p. 296; SD Mironov & Sorokina, 1998a, p. 413]. Basals fused, aboral side of basal circlet flanged. Arms 5, exceptionally branching at brachial 4. Second nonmuscular articulation between brachials 5 and 6. Maximum number of consecutive muscular articulations 16. Middle portion of arm with brachials as wide as proximal brachials. First pinnule on brachial 4. Three rows of genital plates on one side of pinnule; the median row consisting of H-shaped plates. Large, laterally flattened projections on pinnulars. Tegmen inflated. Oral plates of moderate size. Anal cone slightly lower than oral cone. Tegminal plates connected with first 5 brachials. All or most proximal columnals compound. In mesistele, 11 or 12 crenular units of 1 or 2 crenulae each; in dististele, numerous (approximately 33) long crenulae weakly grouped into crenular units. *Holocene:* Southern Ocean (bathyal).——Fig. 86,*3. *D. antarcticus* (Bather); Southern Ocean at approximately 480 m, holotype, ×1.5 (Bather, 1908).

Feracrinus Mironov & Sorokina, 1998a, p. 410, *emend.*, Améziane & Roux, 2011, p. 138 [**F. aculeatus*; M] [=*Ptilocrinus* A. H. Clark, 1907b, p. 551 (type, *P. pinnatus,* M), *sensu lato, partim,* Roux, Messing, & Améziane, 2002, p. 822; =*Camaecrinus* Mironov & Sorokina, 1998b, p. 21, *nom. nov. pro Ailsacrinus* Mironov & Sorokina, 1998a, p. 404–405 (type, *Ailsacrinus peripterus* Mironov & Sorokina, 1998a, OD), *non* Taylor, 1983]. Basals fused or basal circlet with 1 to 3 sutures. Arms moderately narrow. Width of distal radial articular facet 74 to 81 percent of upper width of radial. Second nonmuscular articulation between brachials 5 and 6; synostoses occur regularly after brachial 7. Distal arm with fewer than 5 successive muscular articulations in juveniles and at most 22 in large adult specimens. First pinnule on brachial 4. Proximal part of genital pinnules with one row of lateral plates on each side, rarely joined by stereom bridges over gonad in H-shaped plates. Cover plates of distal pinnules with short, terminal, fingerlike projection; outer perpendicular spine or tubercle absent. Tegmen low to inflated. Oral plates of moderate size. Anal cone lower or higher than oral cone. Tegminal plates connected with brachials 1 to 4. Columnal symplexies with 6 to 10 crenular units of 1 to 3 crenulae each. [Améziane and Roux (2011) pointed out that *Feracrinus* and *Ailsacrinus* (the latter renamed *Camaecrinus* by Mironov & Sorokina, 1998b) are based on 3 specimens, each attributed to a different species.

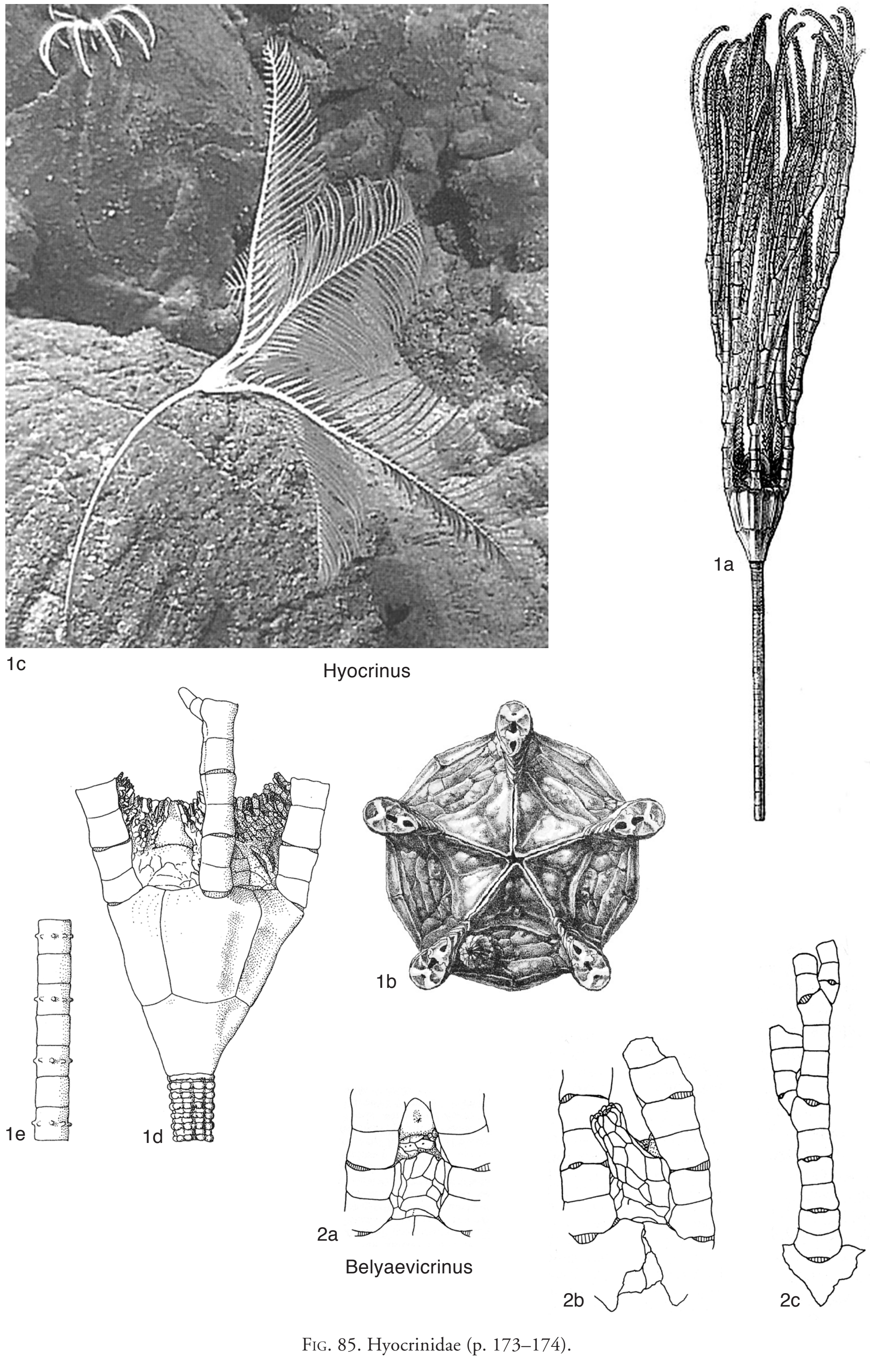

FIG. 85. Hyocrinidae (p. 173–174).

Camaecrinus peripterus and *Feracrinus aculeatus* are from the same station in the northern Pacific; the third, *Camaecrinus klikushini* (Mironov & Sorokina, 1998a), is from a neighboring area and the same depth. With relatively gracile arms, a tegmen dominated by oral plates, and distal columnals as high as wide, the relatively small holotype of *C. klikushini* appears to be a young, weakly sculptured individual. The holotype of *C. peripterus* is an older specimen in which the tegminal plates restrict extension of the oral cone; the arms are more robust, and all columnals are wider than high. The inflated tegmen and columnal symplexies with strongly irregular, hieroglyph-like crenular units indicate that the holotype of *F. aculeatus* is the oldest specimen. Main characters of genital pinnules, orals, and arm pattern are similar in the 3 specimens, except for variations in sculpturing. Thus, Améziane and Roux (2011) interpreted the 3 specimens as the ontogenic sequence of a single species, *F. aculeatus*.] *Holocene:* northern and southwestern Pacific Ocean (lower bathyal to upper abyssal).——Fig. 86,*4a–g*. **F. aculeatus*; *a–c, a,* cup, *b*, tegmen and proximal part of arms, *c*, anal cone, northern Pacific at 3200 m, holotype, ZMM C-13, ×1.5; *d–g*, holotype of *Camaecrinus peripterus* Mironov & Sorokina; *d*, cup, ×1.5, *e*, tegmen and proximal part of arm, ×1.5 *f*, proximal part of arm aboral, ×3, *g*, proximal part of arm adoral, northern Pacific at 3200 m, ZMM C-12, ×3 (Mironov & Sorokina, 1998b).

Gephyrocrinus Koehler & Bather, 1902, p. 68, *emend.*, Roux & Bohn, 2010, p. 429 [**G. grimaldii;* M]. Interbasal sutures absent, aboral border of basal circlet flanged. Arms 5, exceptionally branching at brachial 4. Lateral spines or flattened projections on proximal brachials and pinnulars absent. Second nonmuscular articulation between brachials 5 and 6, rarely 4 and 5. In middle and distal arm, regular pattern with successive brachial pairs united by synostosis and separated by a muscular articulation. Rarely, series of 3 brachials united by synostosis. First pinnule on brachial 4, rarely 5. Expansion of genital pinnules with numerous small plates, never in rows. Tegmen moderately inflated. Anal cone higher than oral cone. Columnal symplexies with 6 to 8 crenular units of 1 to 3 crenulae each. *Holocene:* northeastern Atlantic and Pacific Oceans (bathyal).——Fig. 86,*5a–b*. **G. grimaldii; a*, proximal column and base of crown; *b*, portion of mesistele, northern Atlantic, MNHN EcPs245, ×4 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

Laubiericrinus Roux, 2004, p. 598 [**L. pentagonalis*; M]. Three interbasal sutures. Width of distal radial articular facet 71 to 77 percent of upper width of radial. First pinnule on brachial 5. Second nonmuscular articulation between either brachials 3 and 4 or 4 and 5; beyond brachial 5, synostoses alternating with muscular articulations. Well-developed cylindrical anal cone shorter than oral cone. Proximal columnals weakly pentagonal; columnal symplexies with 5 crenular units of 1 (juvenile) to 3 (adult) crenulae. *Holocene:* southwestern Pacific Ocean (lower bathyal).——Fig. 87,*1a–c*. **L. pentagonalis,* North Fiji Rise at 2765 m, holotype, MNHN EcPs10269; *a*, holdfast, ×4; *b*, facet of proximal columnal, ×20; *c*, facet of distal columnal, ×20 (Roux, 2004).

Ptilocrinus A. H. Clark, 1907b, p. 551 [**P. pinnatus*; M]. Basals 3 or fused. Synostoses distributed irregularly in middle part of arm; maximum number of consecutive muscular articulations 17. Some brachials cuneate and not reaching inner margin of arm. First pinnule on brachial 4, rarely 5. More than 10 pinnules on each side of arm. Expansion of genital pinnules high or inconspicuous. Genital plates in 1 to 5 rows on one side of pinnule. Tegmen from moderate to high, interradial fields of tegmen equal in height. Proximal columnals commonly in one piece. Columnal facets with 6 to 10 crenular units of 1 to 3 crenulae each. [The genus was subdivided by Mironov and Sorokina (1998b) into 2 subgenera, *Ptilocrinus s. str.* with *P. pinnatus* as type species, and *Chambersaecrinus* Mironov & Sorokina (1998b, p. 52), with *P. brucei* Vaney (1908, pl. 24,*70*) as type species. Following Roux (2004), these subgenera are not used herein. A new species, *P. tasmaniaensis* Améziane & Roux (2011) is intermediate in several characters between the subgenera *Ptilocrinus* and *Chambersaecrinus*.] *Holocene:* Southern Ocean, northern Pacific Ocean (lower bathyal to abyssal).——Fig. 87,*2a*. **P. pinnatus*; proximal column and base of crown, MNHN EcPs237, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).——Fig. 87,*2b–d*. *P. brucei* Vaney; *b*, basal circlet with topmost column, *c*, proximal part of arm, *d*, middle part of arm, Southern Ocean at 4970 m, holotype, RSM 1921.143.1743, ×3 (Mironov & Sorokina, 1998b).

Thalassocrinus A. H. Clark, 1911a, p. 474 [**T. pontifer*; M]. Basals 3 or fused. The most frequent proximal arm pattern with second nonmuscular articulation between brachials 4 and 5, third synostosis between brachials 6 and 7, no series of 3 or more brachials united by synostoses before brachial 10. (In middle part of arm of *T. pontifer,* muscular articulations regularly follow pair of brachials joined by synostosis). First pinnule on brachial 5; each pinnular with 2 to 2.5 pairs of cover plates. Well-developed oral and anal cones. Number of tegminal plates greater than 10 in each interradius. Proximal columnals hexagonal or hexalobate, columnals of mesistele hexagonal. Symplexies with 6 or 7 crenular units of 1 to 3 crenulae each. [Median brachial formula, form of cover plates, and columnals of mesistele unknown in *T. depauperatus*. The genus was divided by Mironov and Sorokina (1998b) into 2 subgenera, *Thalassocrinus s. str.,* with *T. pontifer* as type species; and *Conferocrinus* Mironov & Sorokina (1998b, p. 39) with *T. depauperatus* Mironov & Sorokina (1998b, p. 39), as type species. As discussed by Roux (2002), *Conferocrinus* is probably a

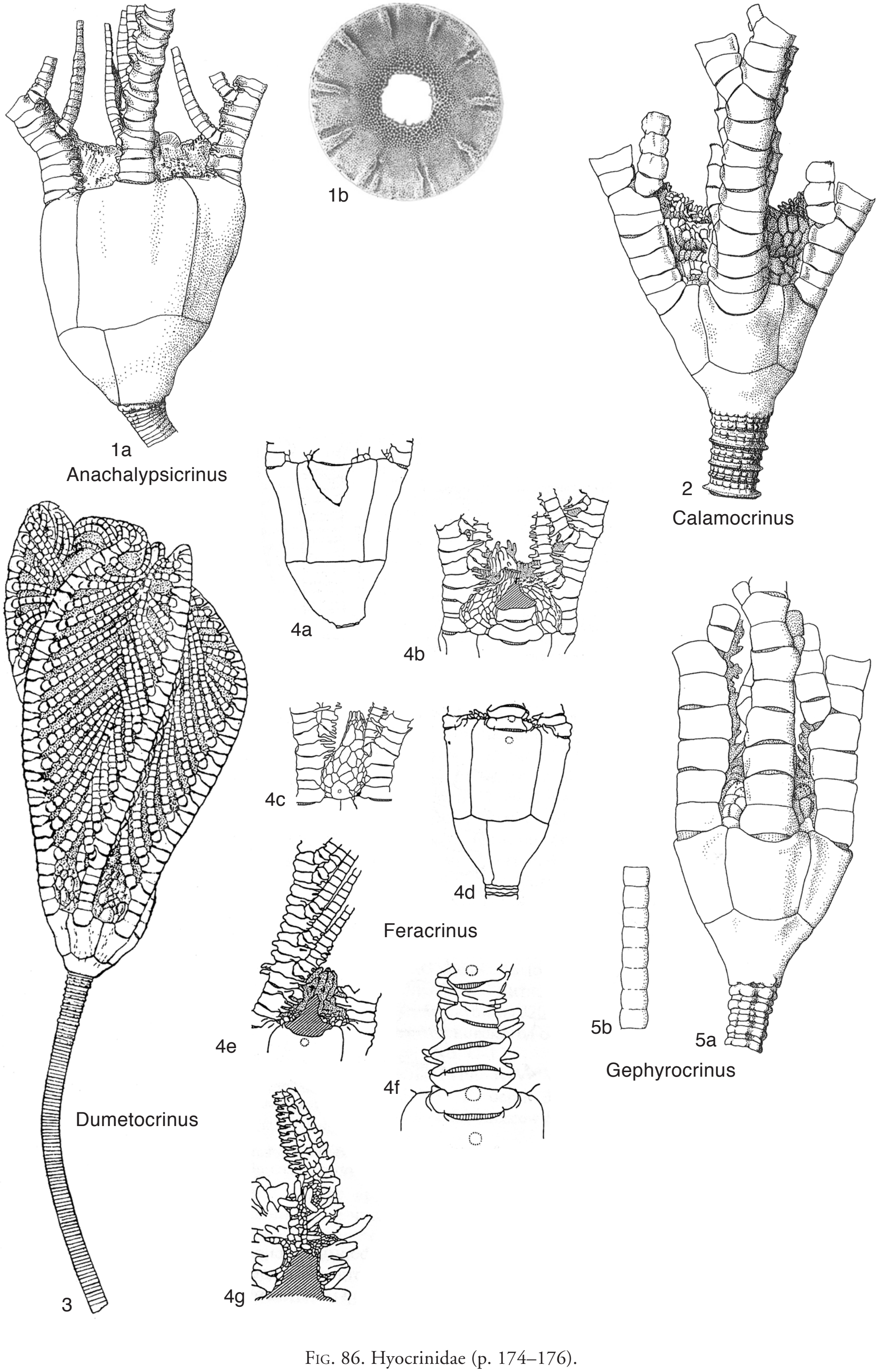

FIG. 86. Hyocrinidae (p. 174–176).

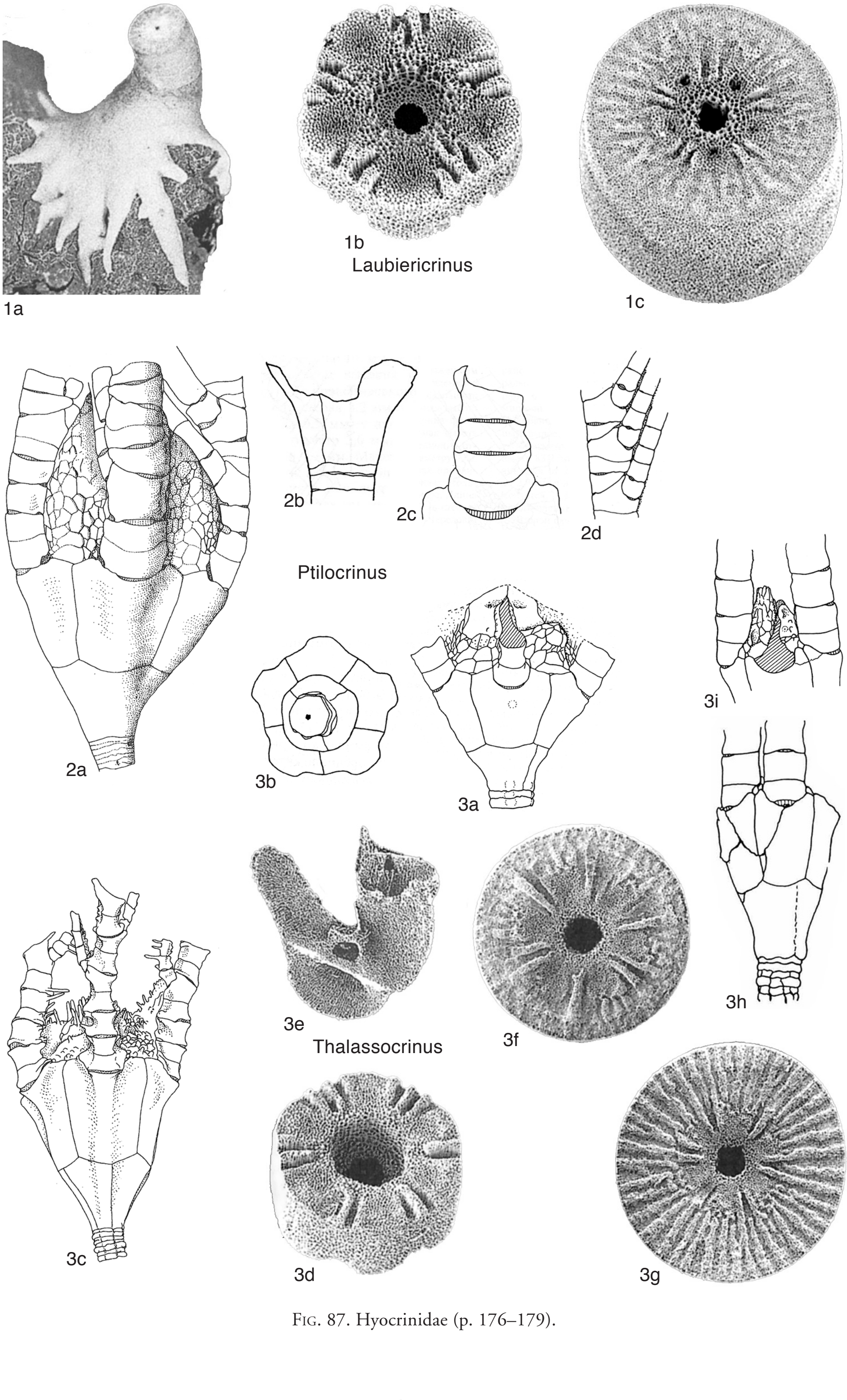

FIG. 87. Hyocrinidae (p. 176–179).

juvenile closer to *Hyocrinus* than to *Thalassocrinus*. Distinction of the 2 subgenera appears unjustified.] *Holocene:* western tropical and northeastern Pacific and eastern Indian Oceans (bathyal to abyssal).——FIG. 87,*3a–b*. **T. pontifer*; *a*, cup with tegmen and anal cone; *b*, cup from below to show sutures in basal circlet, western Pacific Ocean at 2272 m, holotype, USNM 27483, ×3 (Mironov & Sorokina, 1998b).——FIG. 87,*3c–g*. *T. alvinae* ROUX, 2002; *c*, proximal column and base of crown, ×4; *d*, facet of proximal columnal, ×20; *e*, distal view brachial with pinnule socket, Molucca Islands at 3100 m, holotype, USNM E36051, ×14 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*); *f*, columnal facet from mesistele; *g*, columnal facet from dististele, East Pacific Rise at 3500 m, paratype, USNM E36052, ×14 (Roux, 2002).——FIG. 87,*3h–i*. *T. depauperatus* (MIRONOV & SOROKINA); *h*, proximal column and base of crown; *i*, tegmen, eastern Indian Ocean at approximately 5100 m, holotype, ZMM C-16, ×2 (Mironov & Sorokina, 1998b).

CYRTOCRINIDA

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Order CYRTOCRINIDA Sieverts-Doreck, 1952

[Cyrtocrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952, p. 614]

Cup with or without proximale or distinct basals that may be hidden, cup may be elongated and columnlike. Column short; columnals, when present, cylindrical, without nodals and cirri, articulation symplectial to cryptosymplectial, immovable. Arms divided at primibrachial 1 or 2, no further division, except in *Neogymnocrinus*. Secundibrachials with muscular, rarely synostosial, articulations. Attachment by disk, where known, or cup attached directly to the substrate. [Classification of the Cyrtocrinida essentially follows that of JAEKEL (1891, 1892, 1907, 1918) and ARENDT (1974), expanded to include taxa described since then. The origins of cyrtocrinids are obscure, and they have so far not been reported from the Triassic. They radiated extensively in the Early Jurassic (HESS, 2006) and are perhaps the most diverse crinoid group in the Mesozoic. Most authors (e.g., SIMMS, 1988a) assumed that they represent a distinct offshoot from the millericrinids. In fact, the Early Jurassic phyllocrinid *Ticinocrinus* has 5 distinct, exposed basals; the cup is articulated with a symplectial facet to the column, but the radials are high, with facets for rudimentary arms sunken between interradial projections, a character not found in millericrinids. Both millericrinids and cyrtocrinids lack synarthrial columnal articulations; however, synarthrial and syzygial brachial articulation that occurs in millericrinids are unknown in cyrtocrinids. Thus, cyrtocrinid origins remain speculative; and these crinoids with so many strange-looking or even bizarre forms may not even represent a monophyletic clade. However, molecular analysis of 2 extant forms suggests that cyrtocrinids are monophyletic (ROUSE, JERMIN, & MESSING, 2006). In addition to the simplified body plan, cyrtocrinids have an extremely reduced nervous system (HEINZELLER, 1998).

Extant cyrtocrinids live on hardgrounds in bathyal environments (BOURSEAU & others, 1991; DONOVAN & JAKOBSEN, 2004), while the fossil representatives lived in relatively shallow (HESS & SPICHIGER, 2001; DONOVAN & JAKOBSEN, 2004) or deeper water (HESS, 2006; CHARBONNIER & others, 2007) and commonly also attached to solid objects. They occupied the lowest tier and are practically never preserved intact as fossils. Columns are mostly short or absent altogether. Cups are commonly composed of fused radials and have inclined radial articular facets (hence the name crooked crinoids). Arms are generally much reduced (except in Sclerocrinidae, Plicatocrinoidea, and Holopodidae) and may be concealed or coiled as a protective measure. This mode of life caused a highly variable morphology in many forms. Much of the knowledge of their anatomy may be deduced from the few extant forms, *Cyathidium* (known also from well-preserved fossils, see DONOVAN & JAKOBSEN, 2004), *Holopus*, *Neogymnocrinus* (a large form by cyrtocrinid standards), and *Proeudesicrinus*. Valuable reconstructions are due to JAEKEL (1907), ARENDT (1974), and PISERA and DZIK (1979). Exceptionally rich cyrtocrinid faunas are known from the Lower Jurassic of Arzo, Switzerland, with 17 species (HESS, 2006), and the Lower Cretaceous of Štramberk, Czech Republic, with 30 species (JAEKEL, 1891; ŽITT, 1974a, 1974b, 1975, 1978a, 1978b, 1979a, 1979b, 1983). Other important faunas are from the Lower Jurassic (Toarcian) of Calvados, France (DE LORIOL, 1882–1889), and central Italy (MANNI & NICOSIA, 1990b); the Lower Jurassic (Sinemurian–Pliensbachian) of Turkey (NICOSIA, 1991); the Middle Jurassic (Bathonian–Callovian) of Ardèche, France (DE LORIOL, 1882–1889; CHARBONNIER &

others, 2007); and the Upper Jurassic sponge facies (Oxfordian) of France, Germany, and Switzerland (Quenstedt, 1876; de Loriol, 1882–1889; Jaekel, 1892; Hess, 1975; Hess & Spichiger, 2001).] *Lower Jurassic (Sinemurian)–Holocene.*

Suborder CYRTOCRININA
Sieverts-Doreck, 1952

[*nom. transl.* Arendt, 1974, p. 84, *ex* Cyrtocrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952, p. 614]

Column present, with attachment disk. *Lower Jurassic (Sinemurian)–Holocene.*

Superfamily
EUGENIACRINITOIDEA
Roemer, 1855

[*nom. correct.* Hess, herein, *pro* Eugeniacrinitacea Arendt, 1968, p. 156, *nom. transl. ex* Roemer, 1855, in Bronn & Roemer, 1851–1856, p. 227]

Cup of 5 radials; basals absent except in *Nerocrinus*, *Ticinocrinus,* and possibly *Gutticrinus*. Pinnulars not fused. *Lower Jurassic (Pliensbachian)–Holocene.*

Family EUGENIACRINITIDAE
Roemer, 1855

[*nom. correct.* Rasmussen, 1978, p. 832, *ex* Eugeniacrinidae Roemer, 1855 in Bronn & Roemer, 1851–1856, p. 227]

Radials with broad and low articular facets. Primibrachials 1 and 2 articulated by synostosis. First primibrachial low, second primibrachial a high axillary. Arms small. *Middle Jurassic (Bathonian)–Lower Cretaceous (Valanginian).*

Eugeniacrinites Miller, 1821, p. 111 [**E. quinquangularis;* M; =*Encrinites cariophilites* von Schlotheim, 1813, p. 68, *ex Caryophyllitea* Walch, 1762, p. 80 and *caryophylli* Walch, 1769 in 1768–1773, p. 114; =*Encrinites cariophyllites* von Schlotheim, 1820, p. 332; =*E. caryophyllatus* Goldfuss, 1829 in 1826–1844, p. 163; =*Pentacrinus*? *paradoxus* Goldfuss, 1831 in 1826–1844, p. 200; =*Eugeniacrinus angulatus* d'Orbigny, 1850 in 1850–1852, p. 383; =*Eugeniacrinus impressus* d'Orbigny, 1850 in 1850–1852, p. 383] [=*Eugeniacrinus* Agassiz, 1836, p. 195, *nom. van.*; =*Eugeniocrinites* Agassiz, 1842–1846, p. 147, *nom. null.;* =*Eugeniocrinus* Agassiz, 1842–1846, p. 147, *nom. nov. pro Eugeniacrinus* Agassiz, 1836, p. 195, *nom. null.*]. Cup conical to funnel shaped, rarely nearly cylindrical. Radial articular facet steep, low, and wide, with small, aboral ligament fossa, deeply excavated interarticular fossae and low adoral muscle fossae, separated by ridge parallel to fulcral ridge. Articular facets separated by small interradial projections. Radial cavity wide and rather shallow. Aboral side of cup entirely occupied by almost flat, articular facet for column. First primibrachials very low. Axillary second primibrachials large, with compact, spearhead-shaped, median prolongation above small, lateral, articular facets for secundibrachials, and joined aborally by symplectial facets as protective lid over adoral side of cup when retracted. Arms small, may be coiled between second primibrachials. Columnals cylindrical to slightly conical, commonly high. Uppermost columnal with diameter equal to base of cup, commonly closely attached to cup. Articular facet of columnals with marginal granulation. [Wagner (1684) first recorded the type species under the name *Caryophyllos aromaticos*, as the petrified fruit of clove tree (*Eugenia caryophyllata*). Lhwyd (1699) referred it to the crinoids, and it has since been recorded under pre-Linnean names such as *Caryophyllitarum* (Rosinus, 1718) and *Caryophyllis* (Scheuchzer, 1752). The unavailable (unpublished, but distributed to a few people) name *Symphytocrinus caryophyllum* Koenig (1825) is based on this species.] *Middle Jurassic (Bathonian)–Lower Cretaceous (Valanginian):* Albania, Czech Republic, France, Germany, Hungary, Italy, Portugal, Romania, Slovakia, Switzerland, Russia.——Fig. 88,*1a–g*. **E. cariophilites* (von Schlotheim), Oxfordian; *a–b,* cup and column, *a*, lateral, *b*, lower facet, Germany, ×3; *c*, distal view of cup, Germany, ×3; *d–e*, primibrachial 2, *d*, aboral, *e*, lateral, Germany, ×4; *f*, adoral view of primibrachial 2, Germany, ×4 (Jaekel, 1891); *g*, reconstruction of closed crown, foremost primibrachials removed to show coiled arm, ×2.5 (Jaekel, 1907).

Lonchocrinus Jaekel, 1907, p. 297 [**Eugeniacrinus dumortieri* de Loriol, 1882 in 1882–1889, p. 132; M]. Axillary primibrachial 2 with long, spinelike process. [Jaekel (1907) established this genus on the basis of the previously described *Eugeniacrinus dumortieri* and an unnamed new species. De Loriol (1882 in 1882–1889, p. 134) left no doubt that the axillary brachials with spinelike process and the cups from the same localities belonged to the same species. Jaekel (1907, p. 298) tentatively assigned *Eugeniacrinus granulatus* Remeš, 1902 (p. 203, pl. 19,*3*), Valanginian, Štramberk, to the newly established genus; this species was renamed *E. remesi* by Biese (1937 in 1935–1937, p. 585) and designated type species of *Lonchocrinus* by Arendt (1974, p. 95). Pisera and Dzik (1979, p. 817) accepted this, although they pointed out that *E. remesi* Biese was based on a cup. de Loriol (1879 in 1877–1879, p. 230, pl. 19,*9–10*) described similar axillary brachials from the Upper Jurassic of Switzerland as radials of *Phyllocrinus gracilis* and referred similar brachials from the localities in Ardèche, France, to *Phyllocrinus fenestratus* (Dumortier, 1871) (de Loriol, 1882 in 1882–1889, p. 167, pl. 17,*9*). The cups of the type species, *L. dumortieri*, resemble

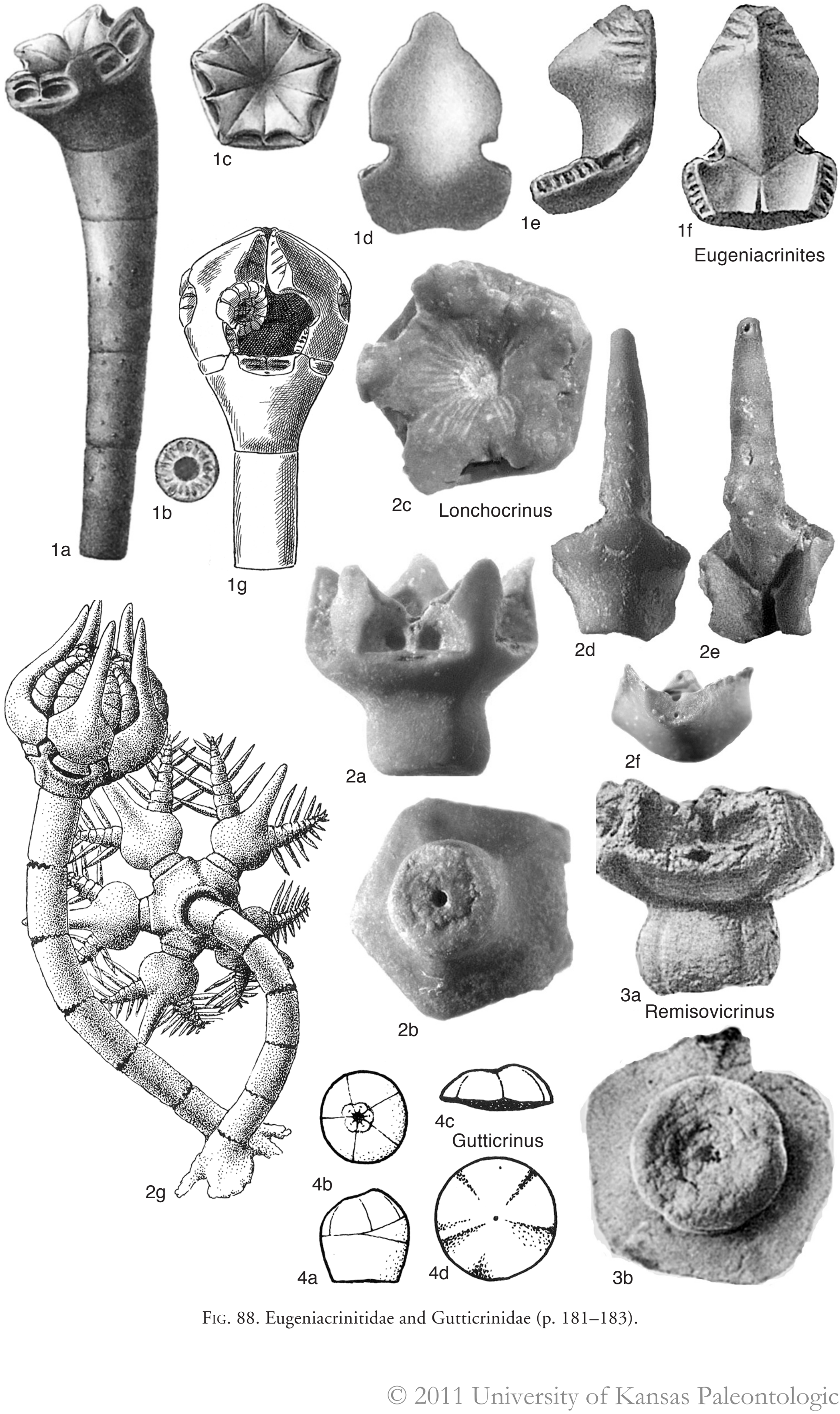

Fig. 88. Eugeniacrinitidae and Gutticrinidae (p. 181–183).

those of *Eugeniacrinites cariophilites* but have more pronounced interradial processes. Species with low cups and short interradial processes were also assigned to *Lonchocrinus* based on the common occurrence of the characteristic second primibrachial, e.g., *L. staszici* Pisera & Dzik (1979), Tithonian, Poland. In these forms, the cup has round interradial processes and a concave facet to the column. *L. staszici* has been synonymized with *L. pskaboirensis* Arendt (1974, p. 97) by Salamon, Zatoń, and Kazmierczak (2008, p. 561).] *Middle Jurassic (Bathonian)–Upper Jurassic (Tithonian):* Czech Republic, France, Germany, Hungary, Italy, Poland, Switzerland.——Fig. 88,*2a–f.* **L. dumortieri* (de Loriol); *a–c,* cup, *a*, lateral, *b*, proximal, *c*, distal, Bathonian, France, NMB M10572, ×5; *d–f*, primibrachial 2, *d*, aboral, *e*, adoral, *f*, proximal, Bathonian, France, NMB M10573, ×5 (Hess, new).——Fig. 88,*2g. L. staszici* Pisera & Dzik, 1979 (=*L. pskaboirensis* Arendt); reconstruction, Tithonian, Poland, ×2 (Pisera & Dzik, 1979).

Remisovicrinus Arendt, 1974, p. 100 [**R. taprakensis*; M]. Cup funnel shaped, with barrel-shaped lower part separated by a constriction from low and wide upper part. Radial articular facet large and wide, separated by narrow interradial projections. Articular facets almost parallel with oral-aboral axis; with inconspicuous aboral ligament fossa but distinct pit; large, deeply excavated adoral muscle fossae. Facet to column concave, with traces of marginal granulation or crenulae. Brachials and columnals unknown. [Assignment to Eugeniacrinitidae is tentative, because the distinctive axillary primibrachial 2 is unknown.] *Middle Jurassic (Callovian)–Upper Jurassic (Oxfordian):* Poland, Russia.——Fig. 88,*3a–b*. **R. taprakensis*; cup, *a*, lateral, *b*, proximal, Kimmeridgian, Russia, holotype, PIN 2280/30, ×4 (Arendt, 1974).

Family GUTTICRINIDAE Klikushin, 1987

[Gutticrinidae Klikushin, 1987a, p. 252]

Cup very small, bulbous, composed of a proximale or fused basal circlet and 5 radials with very small arm facets; facet to column pentaradiate and symplectial. Radial cavity very small. Brachials and columnals unknown. [Klikushin (1987a, p. 252) assigned this family to Bourgueticrinida on the basis of "columnal articula covered by weak, radiating ribs near their periphery." However, Klikushin (1987a, p. 253) also stated that "the column had not been identified." The ball-shaped cup with the tiny articular facets has a certain resemblance to fusiform bourgueticrinines, but these have distinct basals. There is no reason to assign this possibly juvenile Early Jurassic form to Bourgueticrinina, a suborder that is only known from the Upper Cretaceous to Holocene.] *Lower Jurassic (Pliensbachian).*

Gutticrinus Klikushin, 1987a, p. 252 [**G. guttiformis*; M]. Characters as for family. *Lower Jurassic (Pliensbachian):* Crimea, Caucasus.——Fig. 88,*4a–d*. **G. guttiformis*; *a–b,* cup, *a*, lateral, *b*, distal, Caucasus, holotype, LGI JB-28-1, ×2.5; *c–d*, radial circlet, *c*, lateral, *d*, proximal, Crimea, LGI JK-47, ×2.5 (Klikushin, 1987a).

Family HOYACRINIDAE Delogu & Nicosia, 1986

[Hoyacrinidae Delogu & Nicosia, 1986, p. 3]

Cup composed of 5 interradially bulging radials, star shaped in outline, interradial projections moderately high. Articular facet occupying approximately half the width of radial. Articular facet to column relatively small, concave, surrounded by collar. Brachials and columnals unknown. *Upper Jurassic (Kimmeridgian).*

Hoyacrinus Delogu & Nicosia, 1986, p. 3 [**H. sincerus*; M]. Characters as for family. *Upper Jurassic (Kimmeridgian):* Italy.——Fig. 89,*1a–c*. **H. sincerus*; *a–b*, cup, *a*, lateral, *b*, distal, paratype, UR NS 6/115, ×7 (Manni & Nicosia, 1994); *c*, proximal view of cup, paratype, UR NS 6/116, ×4 (Delogu & Nicosia, 1986).

Family PHYLLOCRINIDAE Jaekel, 1907

[Phyllocrinidae Jaekel, 1907, p. 274] [=Nerocrinidae Manni & Nicosia, 1999, p. 327]

Cup symmetrical, commonly pentalobate in outline. Radials with very small articular facets, sunken between more or less prominent interradial projections that may meet orally and fuse above the small arms. Axillary second primibrachial not high. Early forms with distinct basals that may be partly fused. Facet to column small, except in *Ticinocrinus*, generally deeply concave. *Lower Jurassic (Pliensbachian)–Lower Cretaceous (Valanginian).*

Phyllocrinus d'Orbigny, 1850 in 1850–1852, p. 110 [**P. malbosianus;* M]. Cup mostly small, interradial projections do not meet adorally. Distinct basals absent. Radial cavity narrow and deep, limited by horizontal radial notches between interradial processes, followed aborally by outward sloping

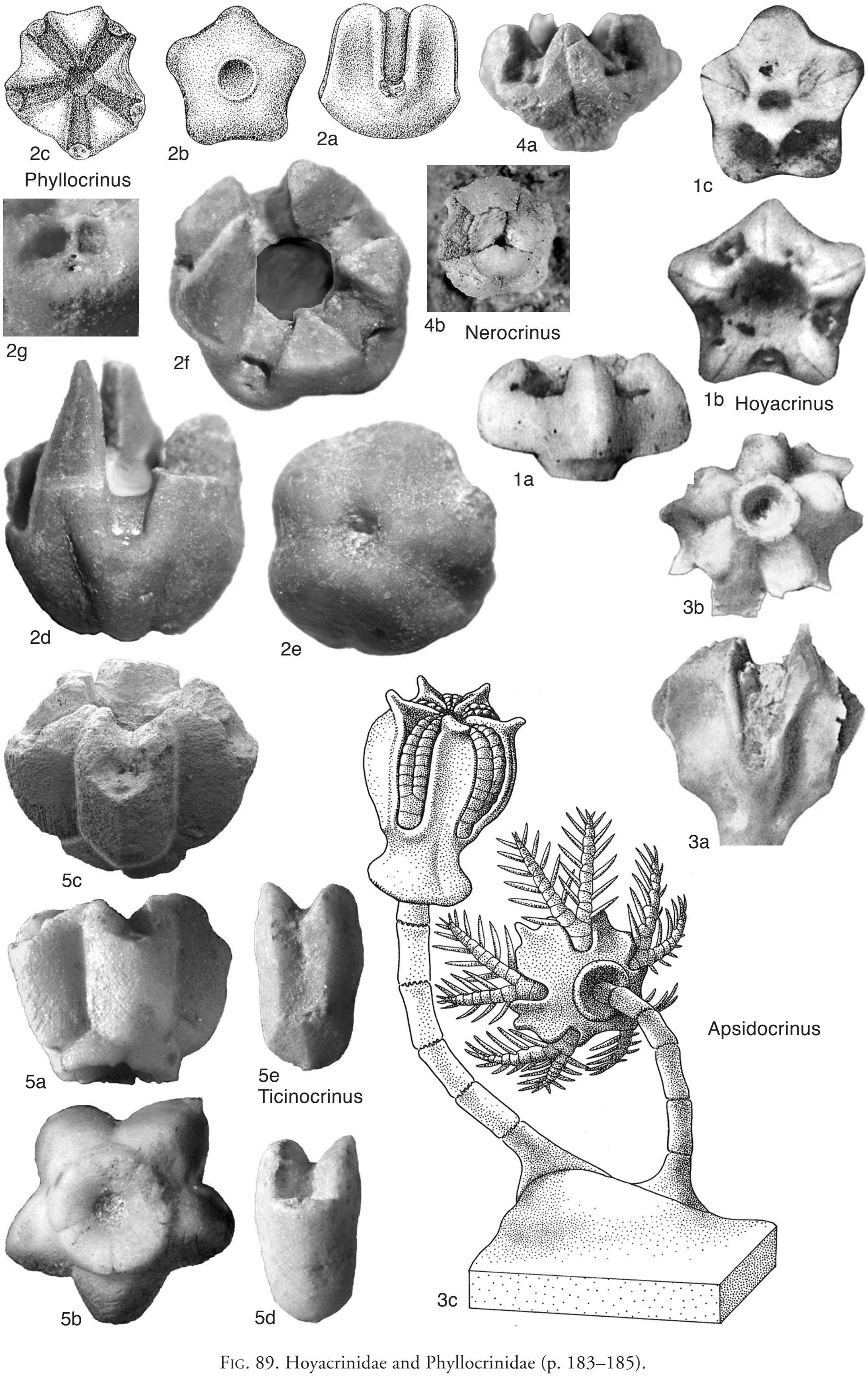

FIG. 89. Hoyacrinidae and Phyllocrinidae (p. 183–185).

radial articular facet; adoral muscle fossae circular and deep. Brachials and columnals unknown. [*Phyllocrinus* was subdivided into *Phyllocrinus s.s., Apsidocrinus*, and *Pyramidocrinus* by RASMUSSEN (1978, p. 835), but following ŽÍTT (1978a), *Apsidocrinus* is treated as a genus of its own.] *Middle Jurassic (Bajocian)–Lower Cretaceous (Barremian):* Albania, Austria, Czech Republic, France, Hungary, Italy, Poland, Romania, Switzerland, Russia, Slovakia, Crimea, New Zealand.——FIG. 89,*2a–c.* **P. malbosianus*; cup, *a*, lateral, *b*, proximal, *c*, distal, Neocomian, France, lectotype, repository unknown, ×2.5 (Rasmussen, 1961).——FIG. 89,*2d–g. P. fenestratus* DUMORTIER, 1871, topotype, Bathonian, France; *d–f,* cup, *d*, lateral, *e*, proximal, *f*, distal, NMB M10575, ×10; *g*, radial articular facet, NMB M10574, ×15 (Hess, new).

Apsidocrinus JAEKEL, 1907, p. 304 [**A. remesi*; M] [=*Pyramidocrinus* REMEŠ, 1912, p. 162 (type, *Phyllocrinus cyclamen* REMEŠ, 1902, p. 205, SD REMEŠ, 1912, p. 162)]. Cup large, with lobate basal part; interradial grooves prolonged into prominent interradial projections that are curved inward and bladelike at top, and may meet adorally. Brachials and columnals unknown. *Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Valanginian):* Czech Republic, Hungary, Italy, Turkey.——FIG. 89,*3a–b.* **A. remesi*; cup, *a*, lateral, *b,* proximal, Valanginian, Czech Republic, GIP 171/9, ×2.5 (Žítt, 1978a).——FIG. 89,*3c. A. moeschi* (ZITTEL in DE LORIOL, 1879 in 1877–1879); reconstruction, Tithonian, Poland, ×2 (Ausich & others, 1999; redrawn from Pisera & Dzik, 1979).

Nerocrinus MANNI & NICOSIA, 1999, p. 328 [**N. petri*; M]. Small cup composed of 3 distinct basals and 5 radials with small facets sunken between interradial projections. Radial cavity deep. Brachials and columnals unknown. [HESS (2006) did not accept the family Nerocrinidae (order Dadocrinida, suborder Cyrtocrinina, superfamily Eugeniacrinitoidea), proposed by MANNI and NICOSIA (1999), on the basis of the presence of the distinct basals. Reduction and fusion or absorption of basals is a relatively simple process that does not justify the creation of an additional higher taxon.] *Lower Jurassic (Pliensbachian):* Italy, Switzerland.——FIG. 89,*4a–b.* **N. petri,* Switzerland; *a,* lateral view of cup, NMB M10017, ×10; *b*, proximal view of cup, NMB M10019, ×10 (Hess, 2006).

Ticinocrinus HESS, 2006, p. 35 [**T. coronatus*; M]. Cup small, composed of a circlet of 5 distinct, low basals and 5 bulging, weakly keeled, high radials. Basals with symplectial facet to column and a concave central area. Radials with moderately high, blunt interradial projections; radial articular facet very small, sunken. Radial cavity deep. Brachials and columnals unknown. *Lower Jurassic (Pliensbachian):* Switzerland.——FIG. 89,*5a–e.* **T. coronatus*; *a–c,* cup, *a,* lateral, *b,* proximal, *c,* lateral-distal, holotype, NMB M10020, ×7.5; *d–e*, radial, *d,* aboral, *e,* adoral, paratype, NMB M10023, ×7.5 (Hess, 2006).

Family PROHOLOPODIDAE Žitt, 1974

[Proholopodidae ŽITT, 1974a, p. 28]

Cup funnel shaped, narrowing rapidly aborally, outline distally pentagonal, sides ornamented. Radial cavity large and deep, with distinct grooves. Radial articular facet narrow, not separated by interradial projections, with large muscle fossae and narrow aboral ligament fossa. Articular facet to column shallow. Brachials and columnals unknown. *Upper Jurassic (Tithonian)–Lower Cretaceous (Hauterivian).*

Proholopus JAEKEL, 1907, p. 292 [**Eugeniacrinus holopiformis* REMEŠ, 1902, p. 203; OD]. Characters as for family. *Upper Jurassic (Tithonian)–Lower Cretaceous (Hauterivian):* Crimea, Czech Republic, France, Hungary.——FIG. 90,*1a–b.* **P. holopiformis* (REMEŠ); cup with columnal, *a,* lateral, *b,* upper (distal), Hauterivian, Grenoble, France, UJF-ID.2138, ×2.5 (Rasmussen, 1961).

Family PSALIDOCRINIDAE Žitt, 1978

[Psalidocrinidae ŽITT, 1978a, p. 117]

Cup funnel shaped, proximally narrow, with nearly vertical sides and high, bladelike interradial processes that may meet adorally. Radial cavity large and deep. Radial articular facets large (as in *Eugeniacrinites*), sunken between high interradial processes (as in *Phyllocrinus*). Facet to column relatively large, flat to shallow concave. [ŽÍTT (1978a) erected this family following a suggestion by REMEŠ and BATHER (1913), who pointed out that the characteristics of *Psalidocrinus* make it difficult to place it in either Eugeniacrinitidae or Phyllocrinidae.] *Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Valanginian).*

Psalidocrinus REMEŠ in REMEŠ & BATHER, 1913, p. 347 [**P. remesi* BATHER in REMEŠ & BATHER, 1913, p. 352; OD]. Characters as for family. [According to ŽÍTT (1978a), *Eugeniacrinites strambergensis* REMEŠ (1912, p. 161) is a separate species.] *Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Valanginian):* Austria, Crimea, Czech Republic, Hungary, Italy, Poland.——FIG. 90,*2a–b.* **P. remesi* BATHER; *a–b,* cup, *a,* lateral, *b,* distal, Valanginian, Czech Republic, GIP 248/9, ×2.5 (Žítt, 1978a).——FIG. 90,*2c–h. P. armatus* (ZITTEL, 1870), *c–d,* Tithonian, Poland; cup, *c,* lateral, *d,* proximal, ×3; *e–g*, primibrachial 2, *e,* lateral, *f,* aboral, *g,* proximal, ×4.4

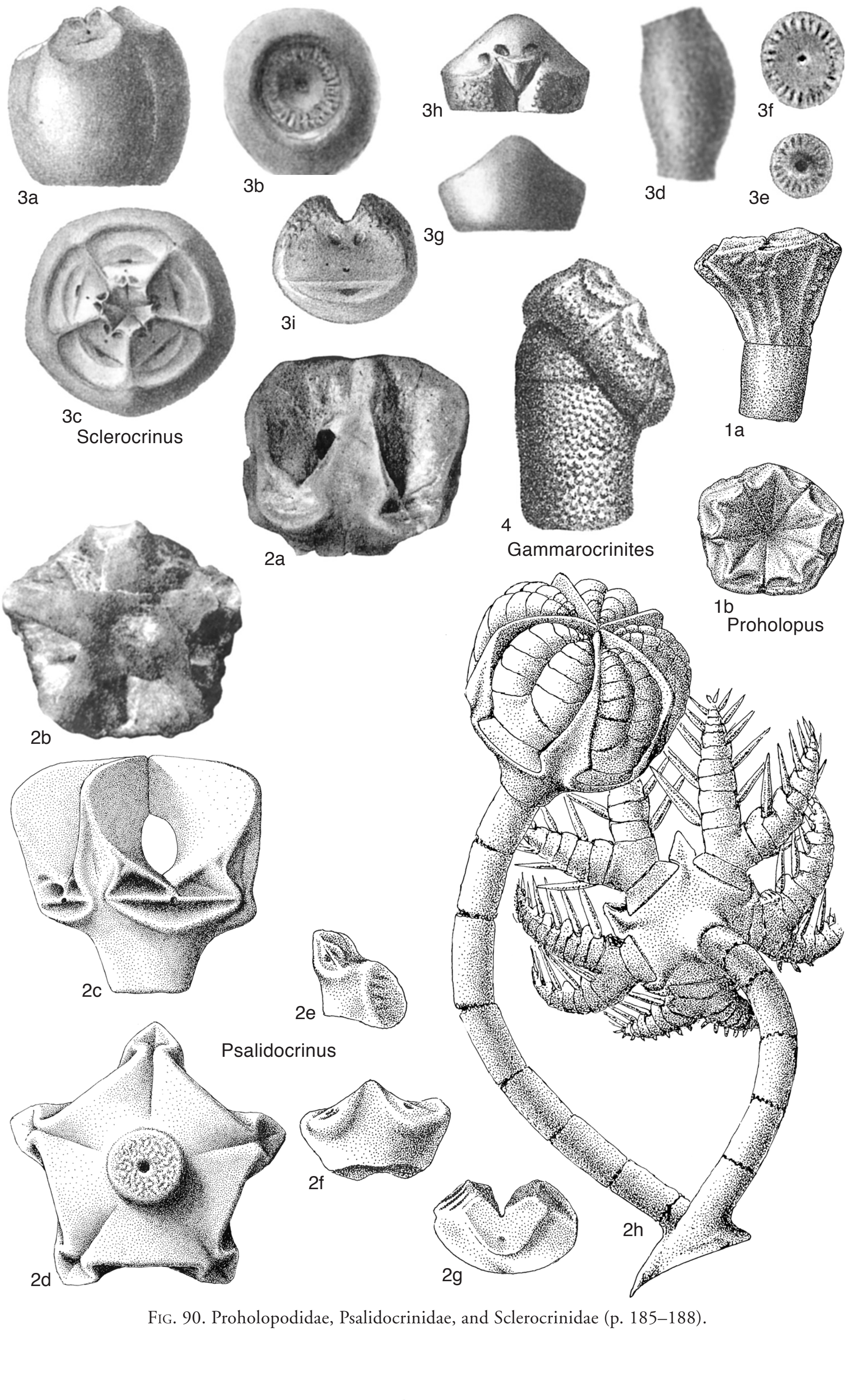

FIG. 90. Proholopodidae, Psalidocrinidae, and Sclerocrinidae (p. 185–188).

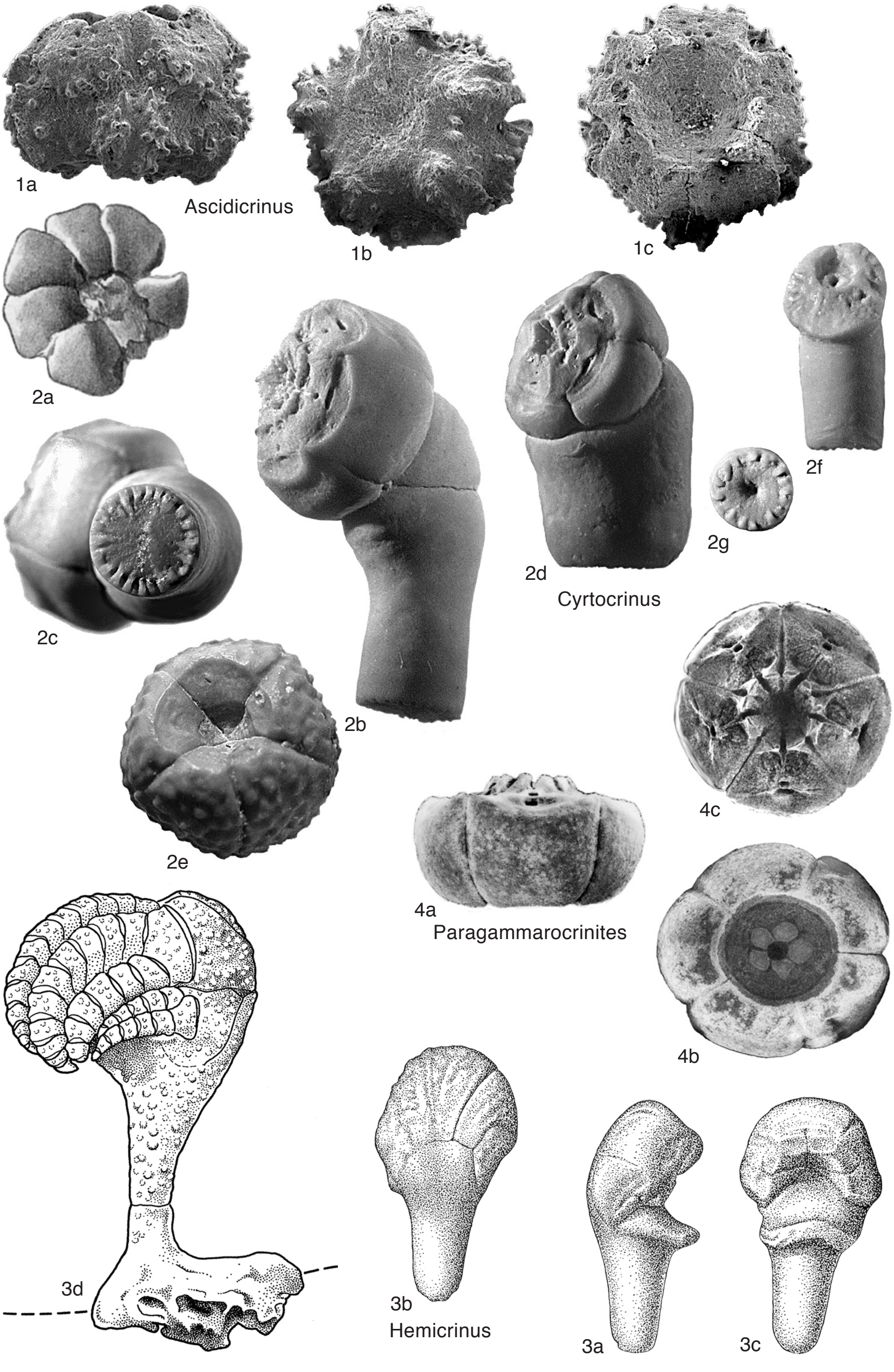

FIG. 91. Sclerocrinidae (p. 188–189).

(Pisera & Dzik, 1979); *h*, reconstruction, ×2.4 (Pisera & Dzik, 1979, fig. 9a).

Family SCLEROCRINIDAE Jaekel, 1918

[Sclerocrinidae Jaekel, 1918, p. 75] [=Hemicrinidae Rasmussen, 1961, p. 233; =Paragammarocrinitidae Jäger, 1982, p. 76]

Cup compact, commonly asymmetrical, highly variable and typically more or less oblique and attached in oblique position to column; cup may be fused with top columnal, and sutures may be indistinct. Small basals may be present. Radial cavity shallow, of variable diameter. Radials mostly without interradial projections. Facet to column concave, large, commonly with stunted columnals. Arms robust, may be reduced in number and size. Primibrachials 1 and 2 may be fused. Brachials may be bipinnulate (2 pinnules per brachial). Length of column variable. *Middle Jurassic (Bathonian)–Holocene.*

Sclerocrinus Jaekel, 1891, p. 621 [**S. strambergensis*; SD Rasmussen, 1961, p. 217]. Cup mostly round, extremely massive; radial articular facet rounded, sloping strongly outward, with very small muscle fossae; interradial processes low or lacking; radial cavity small. Facet to column large and deep, with differentiated inner part containing minute columnals. *Upper Jurassic (Oxfordian)–Lower Cretaceous (Valanginian):* Czech Republic, Hungary, Poland.——Fig. 90,*3a–i*. **S. strambergensis*, Valanginian, Czech Republic; *a,* lateral view of cup, lectotype, ×3; *b*, proximal view of cup, ×3; *c*, distal view of cup, ×3; *d–f*, distal columnal, *d,* lateral, *e,* lower, *f,* upper facet, ×2; *g–i*, fused primibrachials 1 and 2, *g,* aboral, *h,* adoral, *i,* proximal, ×6 (Jaekel, 1891).

Ascidicrinus Hess, Salamon, & Gorzelak, 2011, p. 124 [**A. armatus*; OD]. Cup rather low, bulging or lobed interradially, especially in proximal view, commonly ornamented; radial articular facets broad, not sunken; radial cavity relatively deep, variable in diameter; facet for the column deep. *Upper Jurassic (Tithonian):* Poland.——Fig. 91,*1a–c*. **A. armatus*, cup; *a,* lateral, *b,* aboral, *c,* adoral, holotype, GIUS 8-3577AaH, ×10 (Hess, Salamon, & Gorzelak, 2011).

Cyrtocrinus Jaekel, 1891, p. 602; *emend.,* Jaekel, 1907, p. 278 [**Eugeniacrinites nutans* Goldfuss, 1829 in 1826–1844, p. 164; SD Jaekel 1907, p. 281]. Cup compact, low, more or less oblique, with wide and deep concave base obliquely attached to top of column and distinctly overhanging uppermost columnal, which may be triangular in side view or rudimentary. Radial cavity small to moderately large, shallow. Radial articular facet large, almost flat, sloping outward, muscle fossae distinct, commonly small and deep. First primibrachial axillary, composed of completely or incompletely fused primibrachials 1 and 2. Secundibrachials stout, angular, ability to curl, rectangular or cuneate. Column short, with cylindrical columnals. Surface of cup, brachials, and columnals generally smooth but may be sculptured by granules. [Cups of *C. nutans* have great variation in height, sculpturing, radial cavity diameter, and inclination of radial facets to column axis (see also de Loriol, 1879 in 1877–1879, pl. 18,*29–52,* and de Loriol, 1882 in 1882–1889, p. 115). Specimens from a single locality are linked by intermediates, so that assignment to distinct species is not possible. For example, Hess and Spichiger (2001) reported a ratio of radial cavity diameter to cup diameter between 80 and 20 percent in specimens from the middle Oxfordian Birmenstorf Member of Holderbank, Switzerland; such variation corresponds to Quenstedt's (1876) "subspecies" *nutans apertus* and *nutans opertus*. Granular specimens, designated by Goldfuss (1826–1833 in 1826–1844) as *Eugeniacrinites compressus*, were assigned by Jaekel (1891, p. 626) to his genus *Sclerocrinus* and by Rasmussen (1978, p. 831) to *Gammarocrinites*. However, these may be merely variants or ecophenotypes of one species. The material from the Birmenstorf Member includes specimens with a radial articular facet at a right angle to the column axis caused by either a triangular or a bent top columnal; the radials and the cup also exhibit a tendency to fuse with the top columnal, suggesting that *Cyrtocrinus* is ancestral to *Hemicrinus*.] *Middle Jurassic (Bathonian)–Lower Cretaceous (Valanginian):* France, *Bathonian;* Albania, France, Germany, Switzerland, *Oxfordian–Tithonian;* Austria, Czech Republic, *Valanginian.*——Fig. 91,*2a–g*. **C. nutans* (Goldfuss), Oxfordian; *a,* coiled arm, Germany, ×4 (Jaekel, 1891); *b–c*, cup on triangular top columnal, *b,* oblique lateral, *c,* lower columnal facet, Switzerland, NMB M10578, ×5; *d*, cup obliquely attached to single columnal, Switzerland, NMB M10679, ×3; *e*, proximal view of granular cup, Switzerland, NMB M10576, ×4; *f–g*, top columnal, *f,* lateral, *g,* distal facet, Switzerland, NMB M10577, ×4 (Hess, new).

Gammarocrinites Quenstedt, 1858, p. 654 [**Eugeniacrinites compressus* Goldfuss, 1829 in 1826–1844, p. 164; SD Rasmussen, 1978, p. 831 (ICZN Opinion 2155, 2006)]. Cup low, compact, more or less oblique, with granular surface, radial cavity rather small. Facet to column wide, deep and concave. [As discussed under *Cyrtocrinus*, *Eugeniacrinites compressus* may be a ornamented form of *C. nutans*. Nevertheless, in rejecting an application to give *Sclerocrinus* precedence over *Gammarocrinites* (Hess, 2004), *Gammarocrinites* was placed in the Official List of Generic Names in Zoology (ICZN, 2006, Opinion 2155).] *Upper Jurassic (Oxfordian–Tithonian):* Austria, Crimea, France, Germany, Hungary, Italy, Poland, Switzerland.——Fig. 90,*4*. **G. compressus* (Goldfuss); cup with top columnal, Oxfordian, Germany, ×5 (Goldfuss, 1829 in 1826–1844).

Hemicrinus d'Orbigny, 1850 in 1850–1852, p. 90 [**H. astierianus;* M; =*Cyrtocrinus granulatus* Jaekel, 1891, p. 611]. Cup low and bowl shaped, more or less oblique or irregular, formed by 5 distinctly asymmetric radials, fused, generally at right angle to column part, with a slender, conical cylindrical or claviform proximal columnal; sutures commonly indistinct. Proximal columnal may be articulated directly to holdfast, which is similar to proximale, cylindrical to conical with irregularly expanded distal end attached to substrate. [In contrast to Rasmussen (1978, p. 831), Žitt (1983) distinguished *Torynocrinus* from *Hemicrinus* (based on a crystallographic study) on the basis of a spoon-shaped part of fused elongate radials and no column versus fused radials connected to a column part that articulates symplectially with the holdfast. Both have similar holdfast parts. This argument is followed herein even though recognition of fused radials only (as opposed to radials fused with top columnal) may be difficult in practice.] *Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Albian):* Crimea, Czech Republic, England, France, Hungary, Poland, Slovakia.——Fig. 91,*3a–d*. **H. astierianus*, Neocomian, France; *a–c,* cup, *a,* lateral, *b,* aboral, *c,* adoral, lectotype, MNHN B14793, ×2.5 (Rasmussen, 1961); *d*, reconstruction, ×3 (Ausich & others, 1999).

Neogymnocrinus Hess, 2006, p. 77 [**Gymnocrinus richeri* Bourseau, Améziane-Cominardi, & Roux, 1987, p. 595; OD]. Cup asymmetric, formed mostly by first primibrachials with closely fitting extensions that seal the adoral side of the cup. Radials rudimentary or fused with the proximal columnal. Crown strongly asymmetric, with some arms much shorter than others; branching and number of arms highly variable; primibrachial 1 or 2 axillary; further branching may occur to tetribrachial 13, and the first brachials of 3 consecutive brachitaxes may all be axillary. Primibrachial 1 and secundibrachial 1 united orally, enclosing radial furrow; arms may curl inward to form a compact fist. Brachials asymmetrical, more or less cuneate in aboral view, thicker part with pinnule socket and thinner part developed into winglike extension, coiled pinnules fitting into depression on the extension of the neighboring brachial; all brachial articulations muscular. Column composed of a granular or smooth proximal columnal of variable length, and a smooth, much shorter distal columnal attached to the substrate by a slightly expanded base. *Holocene:* southwestern tropical Pacific Ocean (bathyal).——Fig. 92,*1a–b*. **N. richeri* (Bourseau, Améziane-Cominardi, & Roux); *a,* intact specimen, New Caledonia at 470 m, holotype, MNHN Spec. No. 1 Chalcal 2, station DW 76, ×1.5 (D. Brabant, new); *b*, facet of proximal secundibrachial, MNHN spec. No. 12 Chalcal 2, station DW 76, ×6 (Bourseau & others, 1991).

Paragammarocrinites Jäger, 1982, p. 76 [**P. campanicus*; M]. Cup compact, without interradial projections, composed of 5 distinct radials; radial articular facet large, nearly horizontal; radial cavity small; underside of cup wide and deeply concave, with 5 small, hidden basals. [Jäger (1982, p. 76) proposed the family Paragammarocrinitidae for this form, based on the presence of vestigial basals but agrees with its assignment herein to the Sclerocrinidae (M. Jäger, personal communication, 2004).] *Upper Cretaceous (Campanian):* Germany.——Fig. 91,*4a–c*. **P. campanicus*; cup, *a,* lateral, *b,* proximal, *c,* distal, holotype, NLfB kca 37, ×6 (Jäger, 1982).

Pilocrinus Jaekel, 1907, p. 290 [**Eugeniacrinus moussoni* Desor, 1845, p. 220; M] [=*Gymnocrinus* de Loriol, 1879 in 1877–1879, p. 249 (type, *G. moeschi*, M), *nomen dubium,* Hess, 2006, p. 77]. Cup wide, almost cylindrical, slightly restricted at midheight; radial articular facets wide, outward sloping, separated by interradial projections; proximal side of cup with wide, deep concavity with rather large articular facet for column. Primibrachials 1 and 2 united by synostosis. Primibrachial 2 axillary with thickened sides, mostly united adorally and enclosing radial furrow. Secundibrachials commonly prolonged on one side but may also be united adorally. [A Lower Cretaceous occurrence is doubtful (Klikushin, 1996, p. 108), but Rasmussen (1975; 1978, fig. 559-3) figured a cup from the Upper Cretaceous (Campanian) of Germany. *Pilocrinus* has interradial projections; but radial articular facet, arms, and articulation to column correspond to other Sclerocrinidae. The name *Gymnocrinus* de Loriol, 1879 in 1877–1879, is a *nomen dubium*. Its type species, *G. moeschi* de Loriol, 1879 in 1877–1879, recognized as belonging to a previously described species in a valid genus (=*Pilocrinus moussoni* [Desor, 1845]), is invalid as a junior synonym (ICZN, 2009, Article 23) (Hess, 2006). Klikushin (1996) rejected the combination of the orally enclosed primibrachial 2 of "*G. moeschi*" with the cup of *Pilocrinus moussoni*. However, material from the middle Oxfordian of northern Switzerland includes a primibrachial 1 with a proximal muscular facet (Fig. 92,*2e*) matching the radial facet of the cup of *Pilocrinus moussoni* (Fig. 92,*2a*) and with a distal synostosial facet (Fig. 92,*2f*) matching the proximal facet of an orally open (Fig. 92,*2i*) or united (Fig. 92,*2g*) primibrachial 2.] *Upper Jurassic (Oxfordian):* Crimea, France, Germany, Hungary, Poland, Switzerland.——Fig. 92,*2a–i*. **P. moussoni* (Desor), Switzerland; *a,* cup, NMB M10580, ×5.5; *b*, proximal view of cup, NMB M10581, ×4; *c*, proximal view of cup with columnal, NMB M10582, ×4 (Hess, new); *d*, facet of columnal, NMB M9293, ×6 (Hess, 1975); *e–f*, primibrachial 1, *e,* proximal, *f,* distal, NMB M10528, ×5; *g–h*, primibrachial 2, *g,* proximal, *h,* distal, NMB M10529, ×5; *i*, proximal view of primibrachial 2, NMB M10530, ×5 (Hess, new).

Strambergocrinus Žitt, 1979b, p. 238 [**Cyrtocrinus remesi* Szörényi, 1959, p. 240; OD]. Cup club shaped to very low, attached to encrusting holdfast of variable height by highly concave to flat facet with narrow band of marginal crenulae (symplexy) that may rarely become cryptosymplectial. Distal side of cup more or less slanting, 2 to 5 articular

FIG. 92. Sclerocrinidae (p. 189).

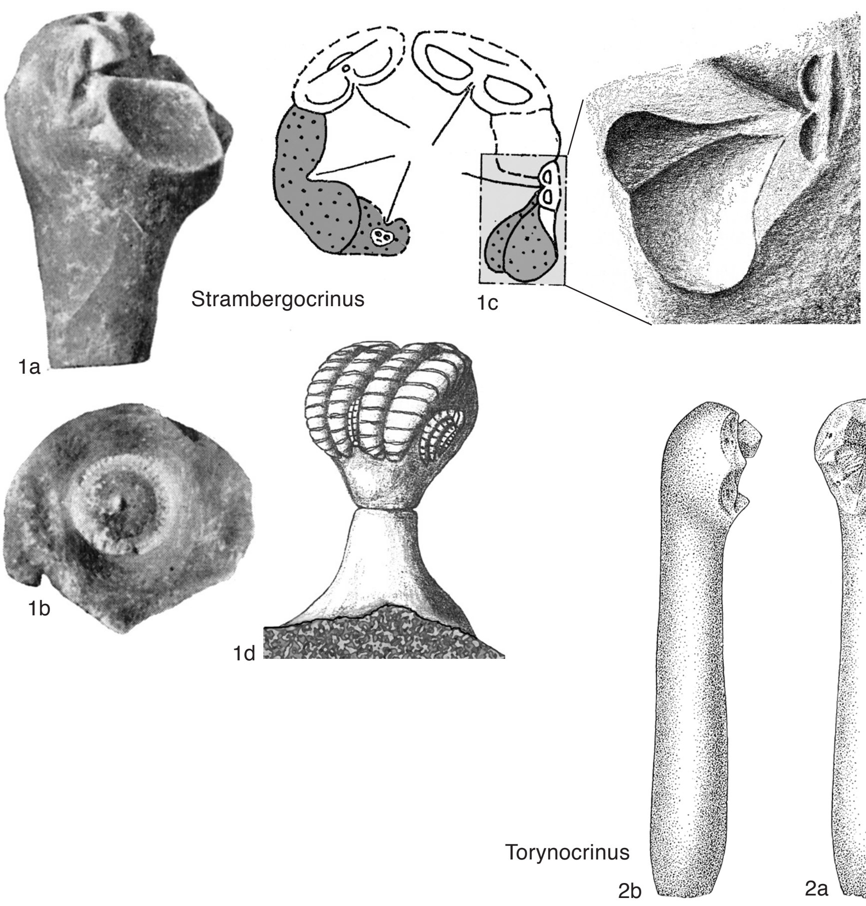

FIG. 93. Sclerocrinidae (p. 189–192).

facets for arms, unevenly developed, specimens with 2 to 3 facets approaching bilateral symmetry. Well-developed, large facets on elevated margin of cup, small, reduced facets adjacent to the large ones or on the opposite margin of cup between depressions supporting opposite arms. Arms short and stout, distal ends of larger arms leaning against flutes or fossae-like depressions on opposite side of radial cavity; lateral arms rudimentary, commonly articulated to minute lateral facets set directly on small adjacent depressions. [*Strambergocrinus* is similar to the Hemibrachiocrinidae (cup articulated to a holdfast), but Žitt (1979b) considered the 2 forms to be paraphyletic because of the presence of mostly symplectial articulation between the cup and holdfast in *Strambergocrinus*; in hemibrachiocrinids, cup and holdfast are invariably fused.] *Lower Cretaceous (Valanginian):* Czech Republic.——FIG. 93,*1a–d.* **S. remesi* (Szörényi); *a–b,* cup, *a,* lateral, *b,* proximal, SMO Z-2511/26. ×3.5 (Žítt, 1979b); *c*, distal view of cup, enlargement showing small, lateral facet with adjacent depressions for reception of arms, SMO Z-2511/17, ×5.3, ×10 (Žítt, 1979b); *d*, reconstruction, ×2 (Žítt, 1979b).

Torynocrinus Seeley, 1866, p. 174, *nom. nov. pro Koninckocrinus* Seeley, 1864, p. 277, *nom. nud.* [**T. canon*; M] [=*Torynocrinus (Collarocrinus)* Szörényi, 1959, p. 250 (type, *T. (C.) phialaeformis,* OD); =*Torynocrinus (Labiocrinus)* Szörényi, 1959, p. 250 (type, *T. (L.) labiatus,* OD)]. Cup composed of 5 more or less elongate asymmetric radials, forming a spoonlike element; sutures between radials partly visible, especially in adoral part. Radial articular facets more or less equal, forming right angle with column part of radials. Cup articulated directly to holdfast. [In spite of considerable individual variation in species of *Torynocrinus*, Szörényi (1959) divided this genus into 3 subgenera, 2 of them new, proposing 9 new species. Žitt (1983, p. 93, pl. 12,*4–5*) described a specimen of *Torynocrinus canon*, preserved in the Natural History Museum, London, as having a primibrachial with thickened sides united adorally and enclosing the radial furrow, similar to *Neogymnocrinus richeri* and "*Gymnocrinus moeschi*" (=*Pilocrinus moussoni). Torynocrinus* is obviously closely related to *Hemicrinus*, from which it seems to have developed by paedomorphosis (arrested column growth, followed by elongation and partial fusion of the radials). Specimens from the Albian Shenley Limestone have a circlet of 5 basals within the cup (Hess & Gale, 2010).] *Lower Cretaceous (Valanginian–Albian):* Czech Republic, England, Hungary, Slovakia.——Fig. 93,*2a–b*. **T. canon*; cup, *a,* adoral, *b,* lateral, Albian, England, holotype, CAMSM B.18178, ×1.25 (Rasmussen, 1961).

Family UNCERTAIN

Ancepsicrinus Salamon & Gorzelak, 2010, p. 876 [**A. parvus*; M]. Small, spoonlike crinoid with rosette-like, elongate cup, bilaterally symmetrical. Two radial articular facets on opposite axis of symmetry. Facet to column symplectial, with coarse crenulae. *Upper Jurassic (Tithonian):* Poland.——Fig. 94,*1a–b*. **A. parvus*, cup; *a,* adoral, *b,* aboral, holotype, GIUS 8-2850And/ApvH, ×10 (Salamon & Gorzelak, 2010).

Capsicocrinus Delogu & Nicosia, 1987, p. 158 [**C. souti*; M]. Cup comparatively large and massive, conical to bell shaped, composed of 5 radials with flat upper side and only small interradial processes; radial articular facet large and wide, filling most of the oral surface, corresponding central cavity very small. Two high primibrachials united by synostosis; primibrachial 2 axillary, unspecialized. Aboral nervous system with a single commissure. Column unknown. [Simms and others (1993, p. 504) assigned the genus to Eugeniacrinitidae, but the primibrachials differ from those of *Eugeniacrinites.* According to Delogu and Nicosia (1987), the type locality is Pliensbachian, but according to Nicosia (1991), it is Sinemurian.] *Lower Jurassic (Sinemurian–Pliensbachian):* Turkey.——Fig. 94,*2a–e*. **C. souti*; *a–c,* cup, *a,* lateral, *b,* proximal, *c,* distal, holotype, UR NS 6/153 ×2.3 (Nicosia, 1991); *d*, 2 radial articular facets, UR NS 6/155b, ×2.5 (Delogu & Nicosia, 1987); *e*, adoral view of radial, UR NS 6/155b, ×2.5 (Delogu & Nicosia, 1987).

Castaneacrinus Hess, 2006, p. 46 [**C. selliformis*; M]. Cup unknown. Brachials small, saddle shaped, aboral surface wrinkled; first primibrachial high, with distal synostosis; secundibrachials with only muscular facets and large pinnule sockets. Column unknown. *Lower Jurassic (Pliensbachian):* Switzerland.——Fig. 94,*3a–e*. **C. selliformis*; *a–b,* secundibrachial, *a,* oblique lateral, *b,* adoral, holotype, NMB M10147, ×10; *c–d*, primbrachial 1, *c,* aboral, *d,* adoral, paratype, NMB M10142, ×10; *e*, oblique distal view of secundibrachial, paratype, NMB M10144, ×20 (Hess, 2006).

Crataegocrinus Manni & Nicosia, 1985a, p. 137 [**C. toniellii;* M]. Cup relatively flat, composed of 5 low radials; articular facets semilunate and rather wide, interradial processes relatively low. Brachials and columnals unknown. [The low cup with outward bulging radial articular facet and moderate, rounded interradial processes is similar to *Lonchocrinus staszici,* Tithonian, Poland (Pisera & Dzik, 1979; see Fig. 88,*2g*).] *Middle Jurassic (Bajocian):* Italy.——Fig. 94,*4a–b*. **C. toniellii;* cup, *a,* lateral, *b,* proximal, holotype, UR NS 6/46, ×1.5 (Manni & Nicosia, 1985a).

Fischericrinus Castellana, Manni, & Nicosia, 1989, p. 74 [**F. sandrae*; M]. Radials with lateral median bulge increasing distally in thickness, with broad, outward sloping articular facet on top, leading to subtriangular cross section; interradial extensions moderately large; interradial sutures sunken. Primibrachial 2 axillary, high, with spinelike median process separating distal articular facets; crenulate lateral facets indicate that ossicles were joined laterally as enlargement of radial cavity. First primibrachials and columnals unknown. [*Fischericrinus* was assigned by the authors to Eugeniacrinitidae. It resembles some cups from the Lower Cretaceous described by Žítt (1974b) as *Eugeniacrinites zitteli* Jaekel. Unfortunately, the distinctive radial articular facets are not well preserved in the Italian material. The well-developed primibrachial 2 that the authors combined with the cups differs from that of *Eugeniacrinites cariophilites*.] *Middle Jurassic (Bajocian)–Upper Jurassic (Oxfordian):* Italy, *Bajocian;* Poland, *Callovian–Oxfordian.*——Fig. 94,*5a–c*. **F. sandrae*, Bajocian, Italy; *a,* lateral view of cup, paratype, UR NS 6/249, ×5 (Manni & Nicosia, 1994); *b*, proximal view of cup, UR NS 6/314, ×5; *c*, adoral view of second primibrachial, paratype, UR NS 6/316, ×6.5 (Castellana, Manni, & Nicosia, 1989).

Fusicrinus Hess, 2006, p. 45 [**F. simmsi;* M]. Cup unknown. Brachials high, spindle to crescent shaped, with very small articular facets, facets muscular or synostosial; ambulacral groove narrow, mostly with scalloped or corrugate margin for accommodation of cover plates; pinnule sockets absent. Columnals unknown. *Lower Jurassic (Pliensbachian):* Switzerland.——Fig. 94,*6a–d*. **F. simmsi*; *a–b,* primibrachial 1, *a,* adoral, *b,* proximal, holotype, NMB M10133, ×10; *c*, adoral view of primibrachial 2, paratype, NMB M10139, ×6; *d*, oblique lateral view of secundibrachial, paratype, NMB M10138, ×10 (Hess, 2006).

Ninocrinus Castellana, Manni, & Nicosia, 1990, p. 18 [**N. parvulus*; M]. Cup small. Radial articular facet small, outward sloping; interradial projections high and thin, subtriangular in cross section. Radial cavity wide and deep. Brachials and columnals unknown. [This genus should be classified in family Uncertain, according to the authors. It resembles *Fischericrinus*, with which it may be congeneric, in bearing a radial facet on a median bulge, and it resembles *Phyllocrinus* in the high interradial projections.] *Middle Jurassic (Bajocian):* Italy.——Fig. 94,*7*. **N. parvulus*; cup, holotype, UR NS 6/452, ×10 (Castellana, Manni, & Nicosia, 1990).

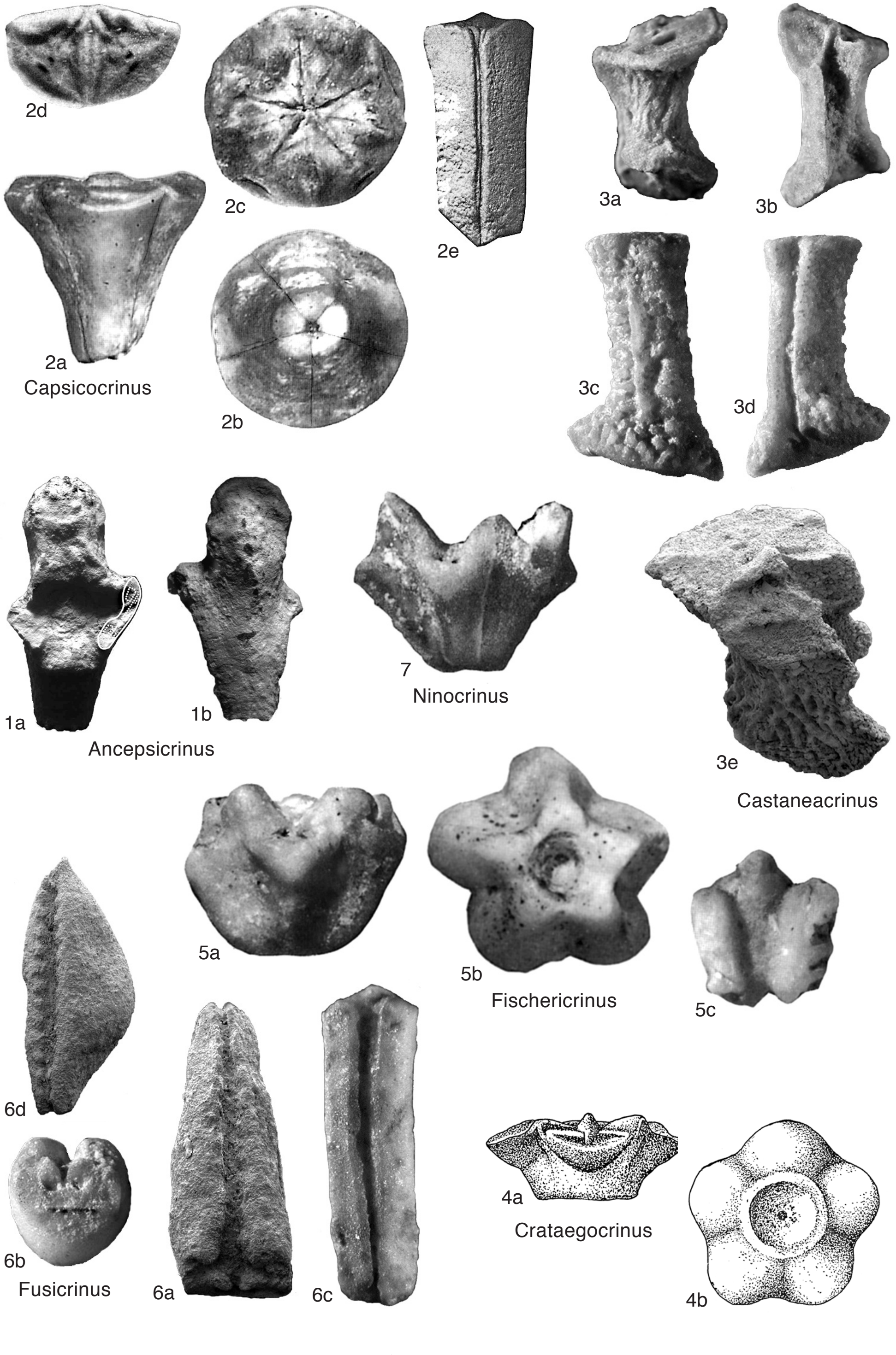

FIG. 94. Uncertain (p. 192).

Superfamily PLICATOCRINOIDEA Zittel, 1879

[*nom. correct.* HESS, herein, *pro* Plicatocrinacea ARENDT, 1968, p. 156, *nom. transl. ex* Plicatocrinidae ZITTEL, 1879 in 1876–1880, p. 346, 387]

Cup consisting of fused basal element and circlet of radials, variable in number from 3 to 8, commonly 4 or 6. Primibrachials 1 and 2 fused to axillary that carries unbranched arms, articulated by synostosis in Lower Jurassic *Plicatocrinus sulzkirchenensis* and in *Sacariacrinus*, and muscular articulation in *Praetetracrinus*. Muscular articulation between brachials. Pinnules (where known) fused, except in *Praetetracrinus*; a few synostosial articulations may occur in proximal pinnules; fused pinnules forming long spines or slightly curved rods, V-shaped in section with large and wide ambulacral furrow. Column presumably short, never fused with cup; attachment unknown. *Lower Jurassic (Sinemurian)–Lower Cretaceous (Valanginian).*

Family PLICATOCRINIDAE Zittel, 1879

[Plicatocrinidae ZITTEL, 1879 in 1876–1880, p. 346, 387; *emend.*, JAEKEL, 1892, p. 620; *emend.*, NICOSIA, 1991, p. 394]

Radials thin walled in *Plicatocrinus*, thicker in *Sacariacrinus*. [The family was originally established by ZITTEL (1879 in 1876–1880) to include *Plicatocrinus* and *Hyocrinus*. Subsequently, *Hyocrinus* was transferred by CARPENTER (1884a, p. 217) to a new family, Hyocrinidae; and *Tetracrinus* was transferred by JAEKEL (1892) from Eugeniacrinitidae to Plicatocrinidae. *Tetracrinus* was assigned by NICOSIA (1991, p. 395) to a family of its own. The affinity of Plicatocrinidae to Hyocrinidae was discussed by JAEKEL (1892) and GISLÉN (1939).] *Lower Jurassic (upper Sinemurian)–Upper Jurassic (Tithonian).*

Plicatocrinus MÜNSTER, 1839, p. 89 [**P. hexagonus*; SD SIEVERTS-DORECK, 1964b, p. 135]. Cup conical, more or less stellate in section with rounded radial ridges and interradial embayments; composed of 4 to 8, generally 6, thin-walled radials attached to a bowl- or funnel-shaped basal element; radial cavity wide and deep. Radial articular facet crescent shaped, generally occupying less than full width of radial plate. Primibrachials 1 and 2 commonly fused, but articulated by synostosis in Lower Jurassic *P. sulzkirchenensis* JÄGER (1993). [MÜNSTER (1839) introduced this genus in combination with 2 new species, *P. hexagonus* and *P. pentagonus*; DE LORIOL (1879 in 1877–1879, p. 246) and JAEKEL (1892, p. 640) considered *P. pentagonus* a synonym of *P. hexagonus*, and SIEVERTS-DORECK (1964b, p. 133) recorded *P. hexagonus* as the type.] *Lower Jurassic (Pliensbachian)–Upper Jurassic (Tithonian):* England, Germany, France, Poland, Switzerland.——FIG. 95,*1a–e*. **P. hexagonus*, Oxfordian; *a,* cup, Germany, ×4; *b–c*, radial, *b,* adoral, *c,* distal, Germany, ×4 (Jaekel, 1892); *d–e*, basal circlet, *d,* proximal, *e,* distal, Switzerland, NMB M10583, ×6 (Hess, new).——FIG. 95,*1f*. *P. fraasi* ZITTEL, 1882; intact crown, Tithonian, Germany, holotype, SMNS 64262, ×2 (Zittel, 1882).

Sacariacrinus NICOSIA, 1991, p. 394, 403 [**S. altineri*; OD]. Cup slightly conical and circular in section, with high radials, no interradial embayments. Basal circlet compact. Number of radials in cup probably variable, 5 or 6; radial cavity restricted. Radial articular facet rounded trapezoidal to elliptical, occupying full width of radial plate. Synostosis between primibrachials 1 and 2. [From the type locality in Turkey, only isolated radials and a basal circlet were described. From Switzerland, primibrachials were also described (HESS, 2006). According to NICOSIA (1991), *Eugeniacrinites deslongchampsi* DE LORIOL (1882–1889, p. 89, pl. 10) belongs to *Sacariacrinus* and not to *Quenstedticrinus,* as proposed by KLIKUSHIN (1987a) and adopted herein. However, JÄGER (1985, p. 80, 90; 1993, p. 76) assigned *Eugeniacrinites deslongchampsi* to *Amaltheocrinus* cf. *amalthei*.] *Lower Jurassic (upper Sinemurian–Toarcian):* Turkey, Switzerland.——FIG. 95,*2a–j*. **S. altineri*; *a–c,* reconstructed cup, *a,* lateral, *b,* proximal, *c,* distal, Turkey, ×10 (Nicosia, 1991); *d–e*, basal circlet, *d,* proximal, *e,* distal, Pliensbachian, Switzerland, NMB M10497, ×8; *f–g*, radial, *f,* adoral, *g,* distal, Pliensbachian, Switzerland, NMB M10065, ×8; *h–j*, primibrachial 1, *h,* adoral, *i,* proximal, *j,* distal, Pliensbachian, Switzerland, NMB M10072, ×8 (Hess, 2006).

Family TETRACRINIDAE Nicosia, 1991

[Tetracrinidae NICOSIA, 1991, p. 406; *emend.*, HESS, herein]

Cups composed of stout basal circlet or columnal-like basal element and mostly stout radials of variable number and height. Radial cavity moderately wide, continuing in shallow central depression in basal element; or small, extending to at most half the radial height in higher cups. Radial articular facet wide. Primibrachials 1 and 2 fused or articu-

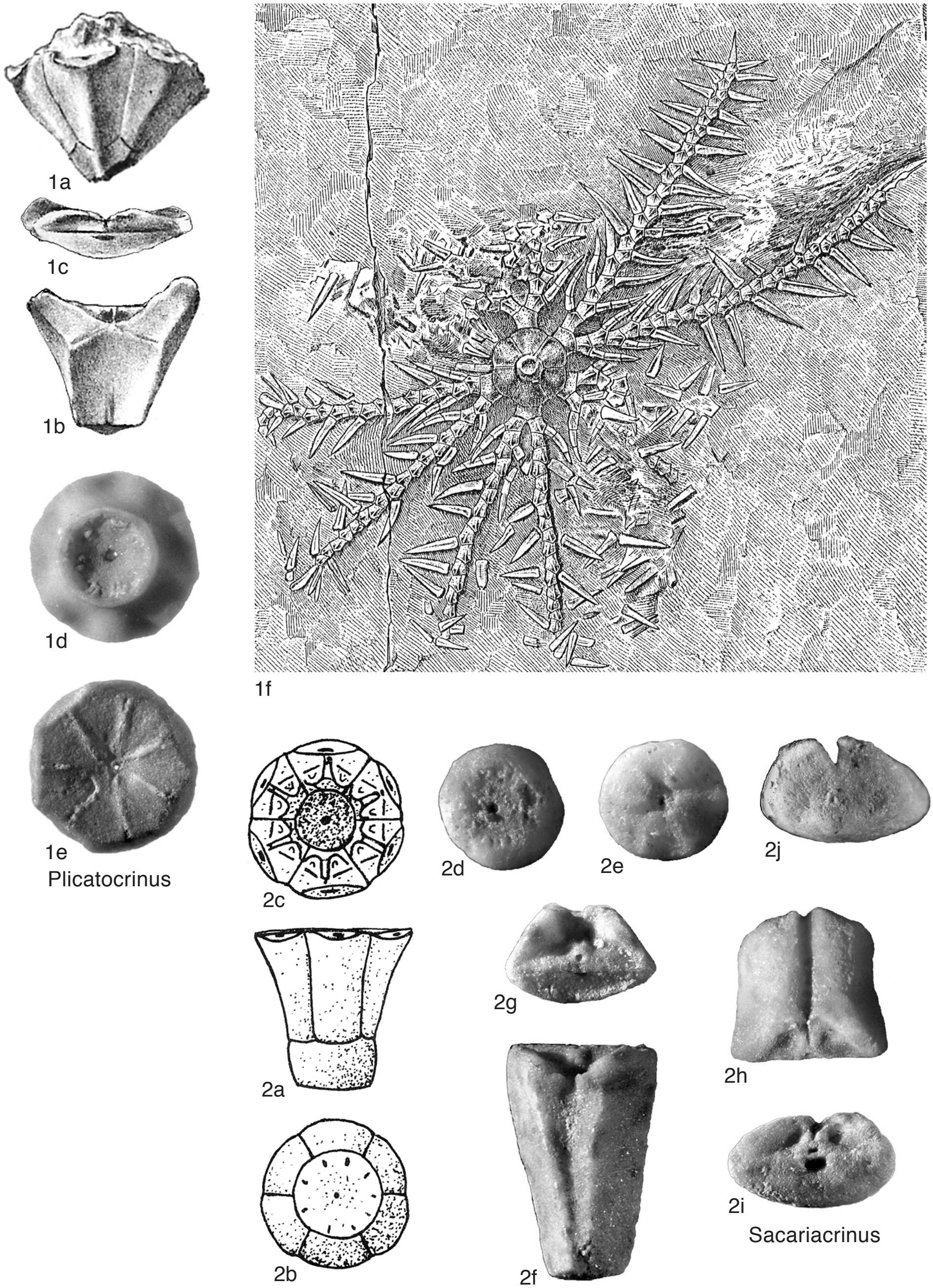

FIG. 95. Plicatocrinidae (p. 194).

lated by synostosis, in *Praetetracrinus* also by muscular articulation. Secundibrachials with only muscular articulations. Columnals cylindrical or lenticular to barrel shaped, with radiating marginal crenulae that may be arranged in groups corresponding to the number of the radials. [The family Tetracrinidae was proposed by NICOSIA

(1991) for *Tetracrinus* and the 2 Liassic genera *Shroshaecrinus* KLIKUSHIN and *Quenstedticrinus* KLIKUSHIN, and he assigned the family to the suborder Eudesicrinina MANNI & NICOSIA (1990b). Herein, *Quenstedticrinus* is considered to belong in a separate family of Cyrtocrinina (Quenstedticrinidae KLIKUSHIN), and *Shroshaecrinus* is considered to belong to Millericrinida.] *Lower Jurassic (Sinemurian)–Lower Cretaceous (Valanginian).*

Tetracrinus MÜNSTER, 1839, p. 88 [**Eugeniacrinites moniliformis* MÜNSTER in GOLDFUSS, 1829 in 1826–1844, p. 165; M]. Cup low, compact, with 3 to 6, commonly 4, radials, separated by a constriction and suture from compact basal element, which may be discoidal, lenticular, barrel shaped, or low subconical, resembling a columnal. Radial cavity moderate, continued in shallow central depression in basal element, generally less than half diameter of cup. Radial articular facet large and broad, occupying entire distal edge of cup and meeting along interradial sutures. Primibrachials 1 and 2 fused. Columnal articular facets with few crenulae or ridges, commonly in 4 groups. *Middle Jurassic (?Aalenian), Upper Jurassic (Oxfordian)–Lower Cretaceous (Valanginian):* Czech Republic, France, Germany, Poland, Switzerland.——FIG. 96,*1a–h*. **T. moniliformis* (MÜNSTER), Oxfordian; *a–b,* top columnal with basal and radial circlets, *a,* lateral, *b,* distal, Germany, ×4 (Jaekel, 1892); *c,* proximal view of basal circlet, Switzerland, NMB M10775, ×8; *d,* distal view of basal circlet, Switzerland, NMB M10774, ×8; *e,* aboral view of radial, Switzerland, NMB M10743, ×8; *f,* adoral view of fused primibrachials 1 and 2, Switzerland, NMB M10740, ×8; *g,* distal view of secundibrachial with pinnule socket, Switzerland, NMB M10742, ×10; *h,* fused pinnule, Switzerland, NMB M10753, ×8 (Hess, 1975).

Arzocrinus HESS, 2006, p. 44 [**A. lenticularis*; M]. Cup composed of 4 or 5 radials. Radials with smooth, exposed surface, concave in side view; proximal facet small, triangular, symplectial; radial cavity narrow. Arms unknown. Column composed of nodals without cirri and internodals alternating in diameter and height. Columnals circular, lenticular, or cushionlike; proximal columnals weakly pentagonal. One columnal facet concave, the other convex; facets restricted to half or two-thirds of total diameter except in very low, proximal columnals. Lumen narrow, areola smooth; crenulae strong, straight or somewhat irregular, restricted to peripheral ring. [*Arzocrinus* was tentatively assigned by HESS (2006) to Tetracrinidae because the profile and the facets of the columnals resemble those of *Tetracrinus moniliformis*.] *Lower Jurassic (Pliensbachian):* Switzerland.——FIG. 96,*2a–c*. **A. lenticularis*; pluricolumnal of 2, *a,* lateral, *b,* distal, *c,* proximal, holotype, NMB M10132, ×5 (Hess, 2006).

Bilecicrinus MANNI & NICOSIA, 1990a, p. 367 [**B. anatolicus*; M]. Cup moderately high, generally oblique, with 4 or 5 unequal radials, in case of 4 radials, the largest mostly with 2 facets, no interradial projections. Radial cavity small, extending to at most half the radial height. Cup attached to wedge-shaped aboral or basal element or top columnal. Synostosis between primibrachials 1 and 2. Secundibrachials with only muscular articulations; large pinnule sockets at right angle to distal facet. Columnals barrel shaped to cylindrical; facets symplectial with uniform, marginal crenulae. Surface of all types of ossicles covered with uniform granules. [*Bilecicrinus anatolicus* was characterized by MANNI and NICOSIA (1990a) as the only known crinoid with 4 radials, one of which with 2 radial facets, presumably the result of 2 fused radials. Cups of the Turkish species typically have one radial with 2 facets, but NICOSIA (1991, p. 414) also mentioned a cup composed of 4 radials with only one facet each. *Bilecicrinus* was assigned by NICOSIA (1991) to Eudesicrinidae BATHER (emended by MANNI & NICOSIA, 1990b), a family of essentially stalkless forms with the cup attached to the substrate by an expanded base (so-called dorsal element). No columnals with a granular surface that could be assigned to *Bilecicrinus anatolicus* were recorded by MANNI and NICOSIA (1990a) and NICOSIA (1991); however, such columnals were assigned to the closely related species *B. arenosus* by HESS (2006), who also described distinctive secundibrachials assumed to belong to this species.] *Lower Jurassic (Sinemurian–Pliensbachian):* Switzerland, Turkey.——FIG. 96,*3a–b*. **B. anatolicus*; cup, *a,* lateral, *b,* proximal, Turkey, UR NS 6/239, ×8 (Nicosia, 1991).——FIG. 96,*3c–k*. *B. arenosus* HESS, 2006, Pliensbachian, Switzerland; *c–e,* radial with 2 facets, *c,* aboral, *d,* oblique aboral-distal view of facets, *e,* adoral, paratype, NMB M10097, ×10; *f–h,* primibrachial 1, *f,* aboral, *g,* adoral, *h,* proximal, paratype, NMB M10013, ×8; *i,* aboral view of primibrachial 2, syntype, NMB M10107, ×10; *j,* proximal view of primibrachial 2, syntype, NMB M10106, ×10; *k,* oblique distal view of secundibrachial with large pinnule socket, syntype, NMB M10113, ×10 (Hess, 2006).

Praetetracrinus JÄGER, 1995, p. 12 [**P. doreckae;* OD]. Cup composed of mostly 4 relatively thin, high radials and a low basal circlet; diameter comparable to column. First and second primibrachials thin, articulated by synostosis or muscular articulation. First pinnule on secundibrachial 2, pinnulars not fused. Column probably rather high, ratio of columnal diameter to height very variable; articular facets with few crenulae commonly in 4 groups. *Lower Jurassic (Toarcian)–Middle Jurassic (Aalenian):* Germany, England.——FIG. 96,*4a–e*. **P. doreckae*, Toarcian, Germany; *a–b,* basal circlet, *a,* proximal, *b,* distal, syntype, SMNS 62568/39, ×13; *c–d,* pluricolumnal, *c,* lateral, *d,* facet, holotype, SMNS 62568/1, ×13; *e,* adoral view of radial, syntype, SMNS 62568/42, ×13 (Jäger, 1995).

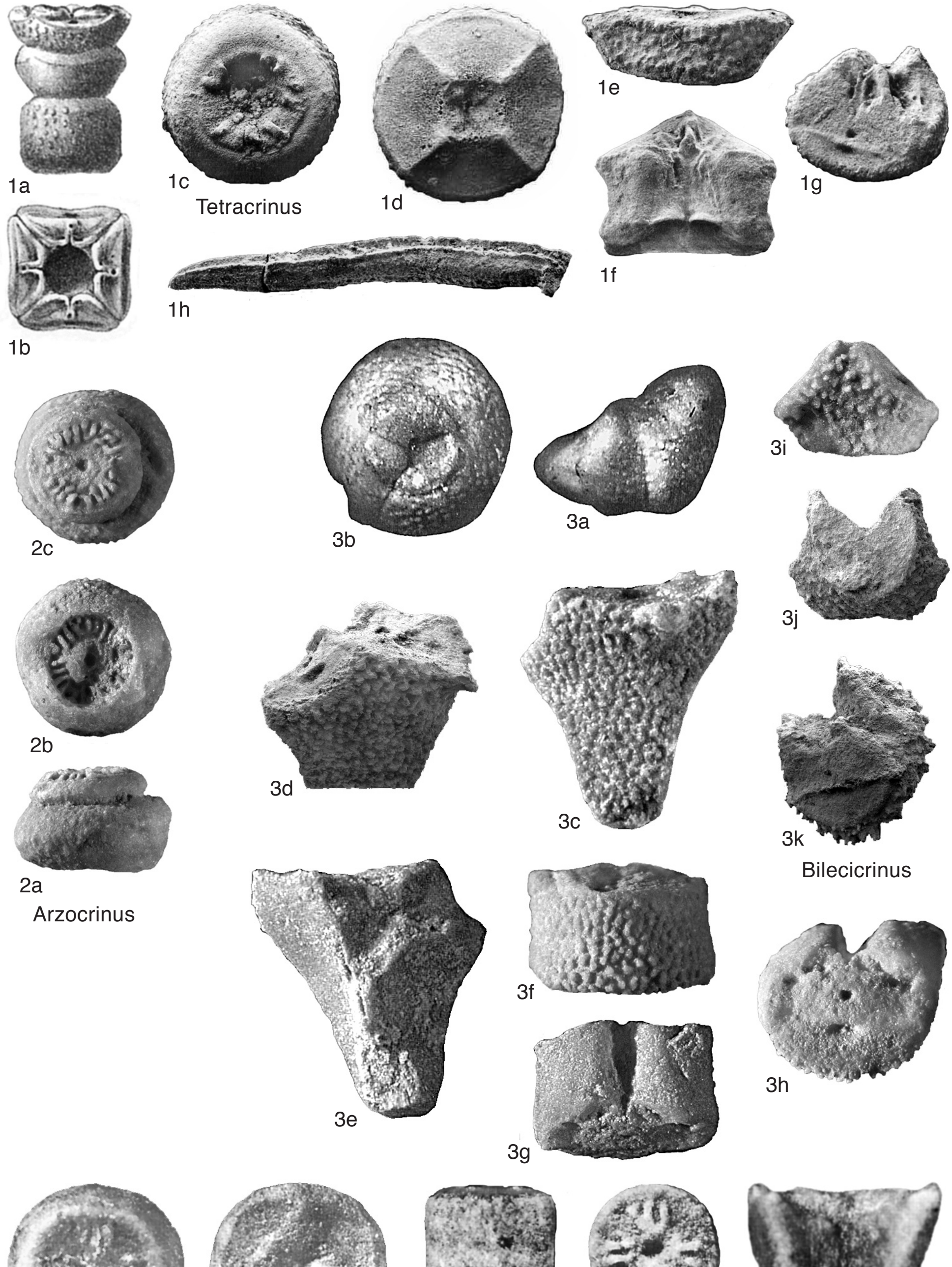

FIG. 96. Tetracrinidae (p. 196).

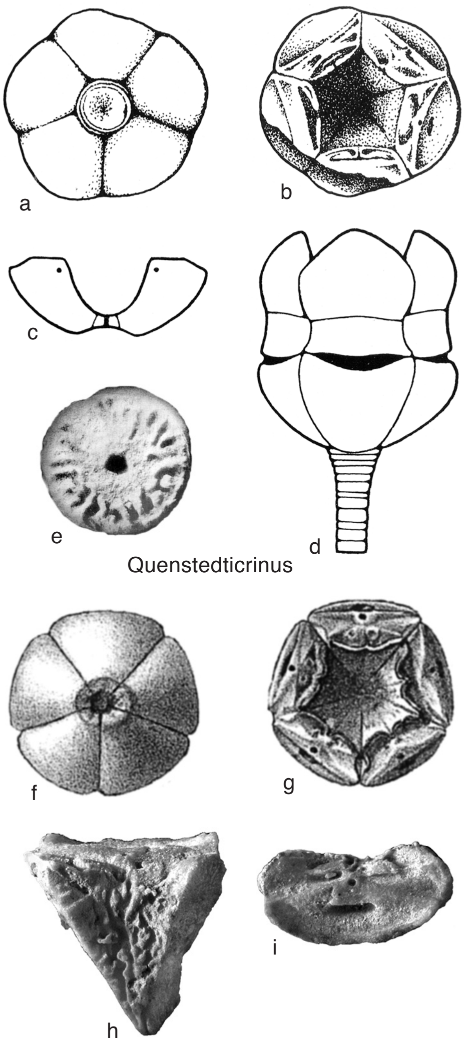

FIG. 97. Quenstedticrinidae (p. 198).

Family QUENSTEDTICRINIDAE
Klikushin, 1987

[Quenstedticrinidae Klikushin, 1987a, p. 245]

Cup wide, conical, composed of 5 large, distinct radials of similar size and cryptic basal circlet within the radial circlet; deep concave facet to column. Synostosis between primibrachials 1 and 2. Column slender, cylindrical, sharply separated from cup. Columnal facets with irregular, radiating crenulae. *Lower Jurassic (Pliensbachian–Toarcian).*

Quenstedticrinus Klikushin, 1987a, p. 245 [**Q. quenstedti*; OD]. Characters as for family. [Klikushin (1987a, p. 245) erected the family Quenstedticrinidae for this genus, but recognized it as clearly allied with *Plicatocrinus*, differing primarily in the cryptic nature of the basal circlet and the pentaradial symmetry of the cup. It may perhaps be a sister group to *Plicatocrinus* (Simms, 1989a, p. 92).] *Lower Jurassic (Pliensbachian–Toarcian):* Eurasia.——Fig. 97*a–e*. **Q. quenstedti*, Pliensbachian, Caucasus, Russia; *a–b,* cup, *a,* proximal, *b,* distal, holotype, LGI JB-2-1, ×2, *c*, section through basal circlet and 2 radials, ×2; *d*, reconstruction of proximal column and cup with primibrachials, ×2; *e*, columnal facet, LGI JB-2-1, ×6 (Klikushin, 1987a).——Fig. 97*f–i*. *Q. deslongchampsi* (de Loriol, 1882 in 1882–1889); *f–g,* cup, *f,* proximal, *g,* distal, Toarcian, France, ×2.5 (de Loriol, 1882 in 1882–1889); *h–i*, radial, *h,* adoral, *i,* distal, Pliensbachian, Switzerland, NMB M10078, ×5 (Hess, 2006).

Suborder HOLOPODINA
Arendt, 1974

[Holopodina Arendt, 1974, p. 150]

Cup with radials and base (so-called dorsal element) attached directly to substrate. Generally no articular facet between cup and base. In some forms, radials strongly elongate and fused with basals, or radials and basals connected by synostosis. Commonly one radial articular facet more developed. Some arms may be reduced or obliterated. [In this suborder are grouped essentially stalkless, mostly compact forms whose cups are fused with a base that is attached to the substrate; forms whose radials articulate synostosially with the base or a basal circlet, radials and basals may be elongated, columnlike; and forms with symplectial articulation at the aboral end of the cup, indicating the presence of a column. These features suggest that Holopodina may be a paraphyletic group.] *Lower Jurassic (Pliensbachian)–Holocene.*

Family HOLOPODIDAE Zittel, 1879

[*nom. correct*. Bather, 1899, p. 923, *ex* Holopidae Zittel, 1879 in 1876–1880, p. 346; *emend.*, Améziane & others, 1999, p. 440] [incl. Cyathidiocrinidae and Holopocrinidae Roemer, 1855, in Bronn & Roemer, 1851–1856, p. 226]

Cup composed of fused radials attached by slightly extended base to substrate without articulation or column. Radial

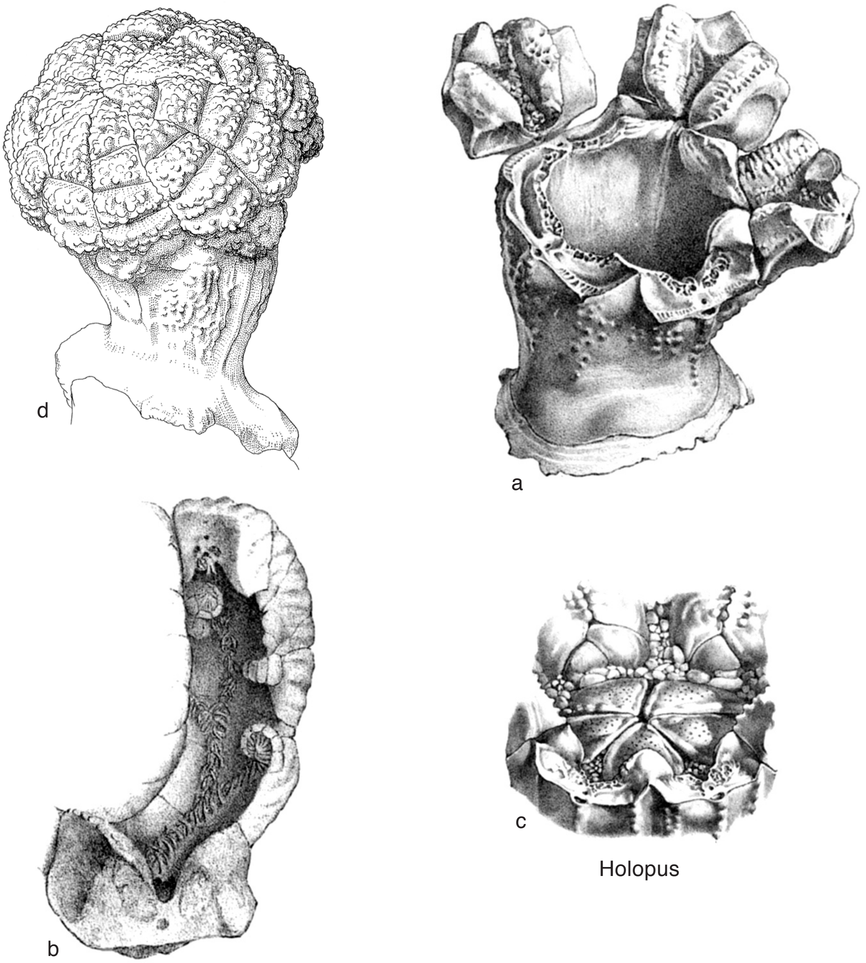

FIG. 98. Holopodidae (p. 199–201).

cavity mostly wide and deep, radial articular facet narrow. Arms divided at primibrachial 1 or the axillary primibrachial generally interpreted as fused primibrachials 1 and 2. Proximal brachials commonly stout and tumid. All brachial articulations muscular, and all secundibrachials with pinnule. Arms when retracted or coiled form cover over adoral side of cup. Distinct triangular and perforated oral plates. No chambered organ or aboral nerve center. *Upper Jurassic (Tithonian)–Holocene.*

Holopus d'Orbigny, 1837, p. 1 [**H. rangii*; M]. Cup tubular, more or less irregular, commonly with radial ridges or rows of tubercles. Upper edge more or less 5-sided. Radial articular facet rather large, sloping slightly outward; interarticular ligament fossae large. Radials and arms different in size, more or less distinctly arranged as group of 3 larger arms and group of 2 smaller arms. Arms 10, stout, coiled inward, forming fistlike cover over adoral surface; each branch with as many as 25 to 30 brachials forming spiral and meeting laterally as cover over adoral side of cup when retracted. Proximal 3 to 10 secundibrachials large, succeeded by distinctly smaller brachials. Some brachials may be irregular, commonly smaller, and triangular to fit within cover. *Paleogene (?Paleocene), Holocene:* Italy, *?Paleocene*; western tropical Atlantic Ocean, southwestern tropical Pacific Ocean (bathyal), *Holocene.*——FIG. 98*a–c.* **H. rangii*, Holocene; *a,* adoral view of cup and 3 primibrachials, ×3; *b*, adoral view of arm

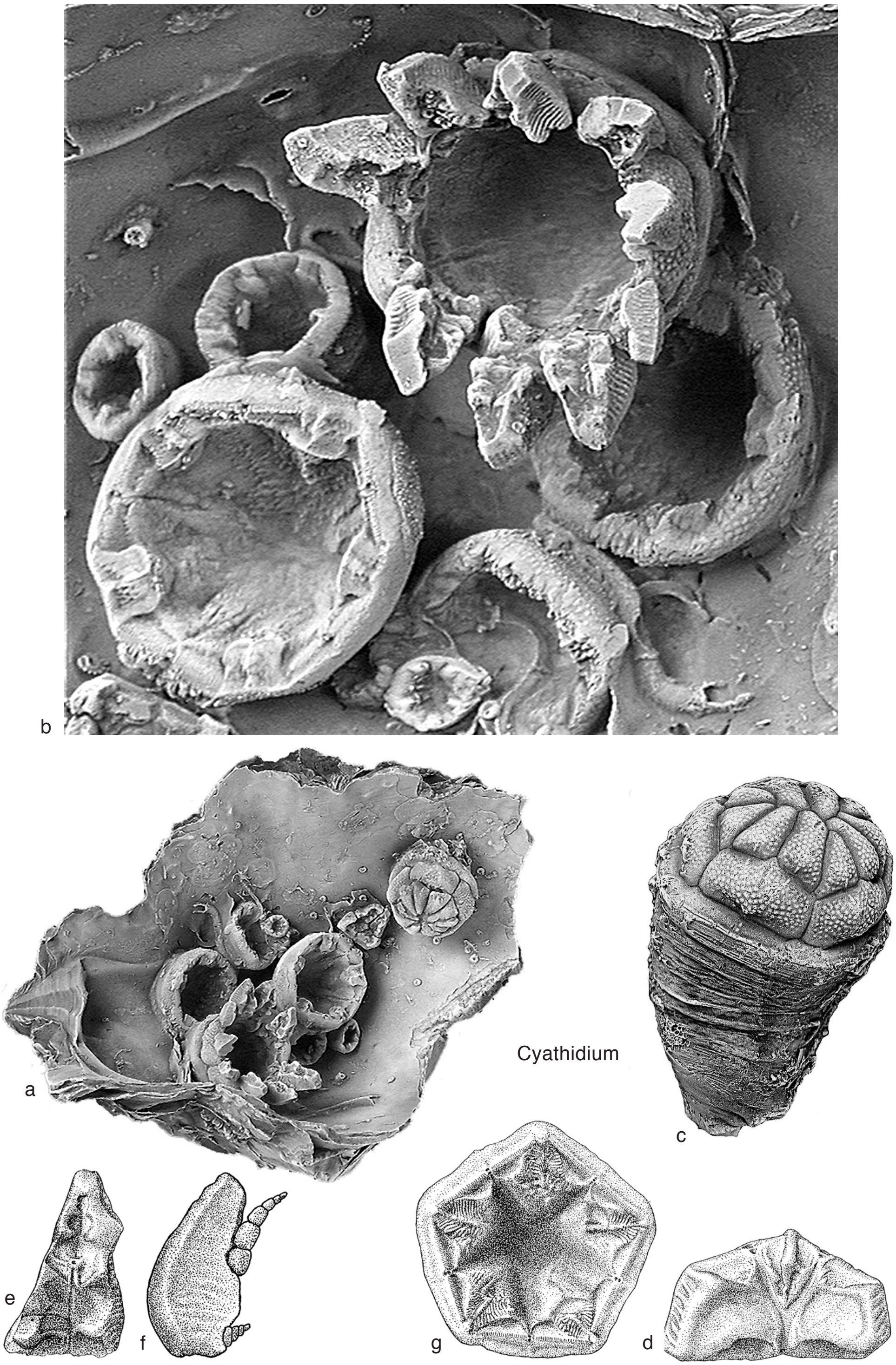

FIG. 99. Holopodidae (p. 201).

on axillary, ×4; *c*, adoral view of cup and tegmen with oral plates, ×3 (P. H. Carpenter, 1884a).——FIG. 98*d*. *H. alidis* BOURSEAU & others (1991); intact specimen, Holocene, MNHN EcPs41, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

Cyathidium STEENSTRUP, 1847b, p. 150 [**C. holopus*; M; *Cyathidium* is described on p. 150 in article without title, *Cyathidium holopus* is listed without description on p. 119] [=*Micropocrinus* MICHELIN, 1851, p. 93 (type, *M. gastaldii*, M); =*Pseudocupressocrinus* VALETTE in LAMBERT & VALETTE, 1934, p. 59 (type, *P. senessei*, M)]. Entire animal reduced to a convex cap or rounded cone of variable height. First primibrachial (and sometimes also secundibrachial) series forming pentagonal vault closing over adoral surface. Arms reduced, not visible when coiled inward. Upper edge of cup more or less 5-sided, occupied by low and wide articulations for arms, meeting interradially or just separated by very small projections at interradial edge, continued and enlarged inward; in adults, forming thickened interradial structures in the radial cavity. Radial articular facet with straight, crenulate fulcral ridge, narrow and very deep aboral ligament pit; no distinct interarticular ligament fossae, adoral muscle fossae inward sloping. Neural canal of radials superficial or exposed. Arms composed of a proximal and a distal series of brachials; proximal series with 2 primibrachials that may be fused and are axillary, with first 10 secundibrachials forming protective vault over adoral side of cup and coiled distal brachials series. Stout first primibrachial and first secundibrachial meet laterally in flat joint facets with pattern of curved furrows. Adoral surface of first secundibrachial with narrow median ambulacral furrow to more or less inward directed articulation for small succeeding brachial, and side furrow to articulation of first pinnule near proximal, abradial edge of plate. Secundibrachial 2 and succeeding secundibrachials small, corresponding to coiled part of arm. [*Micropocrinus* was never figured and not described in detail, but the specimen was identified by JAEKEL (1891, p. 621) and RASMUSSEN (1961, p. 239). The fossil community of *C. holopus* and pycnodontine oysters from the Danian of Fakse (DONOVAN & JAKOBSEN, 2004) is mirrored in an extant assemblage of large, deep-sea *Neopycnodonte* oysters and *Cyathidium foresti* (WISSHAK & others, 2009). The living forms occur upside down underneath bedrock overhangs at a depth of approximately 500 m, where they are protected from background sedimentation and possibly predators.] *Upper Jurassic (Tithonian)–Holocene:* Austria, Czech Republic, Denmark, France, Germany, Italy, Netherlands, Sweden, *Tithonian–Miocene*; northern mid-Atlantic seamounts, northwestern tropical Atlantic Ocean, southwestern tropical Indian Ocean (bathyal), *Holocene*.——FIG. 99*a–f*. **C. holopus*, Danian, Denmark; *a–b,* cluster of cups on oyster, *a,* whole specimen, ×1, *b,* adoral view of cups and proximal arms in presumed feeding position, MGUH 26762, ×4; *c*, intact specimen, FGM, ×3 (Donovan & Jakobsen, 2004); *d*, adoral view of axillary primibrachial, MGUH 8977, ×4 (Rasmussen, 1961); *e–f*, secundibrachial 1, *e,* adoral, *f,* lateral with first pinnule and succeeding brachials added, MGUH 8978, ×4 (Rasmussen, 1978).——FIG. 99*g*. *C. senessei* (VALETTE); distal view of cup, Santonian, France, lectotype, Lambert coll., ×2 (Rasmussen, 1961).

Family COTYLEDERMATIDAE Wright, 1876

[*nom. correct.* RASMUSSEN 1978, p. 836, *ex* Cotyledermidae WRIGHT, 1876, p. 94; *emend.*, MANNI & NICOSIA, 1990b, p. 87]

Cup low, thin walled, with or without circlet of basals. Radial cavity wide, extending into basal element of variable height. Radial articular facet narrow, with small aboral ligament pit, but no distinct interarticular ligament fossae; adoral muscle fossae very small. Two primibrachials connected by muscular articulation. Secundibrachials thin, with only muscular articulation. *Lower Jurassic (Pliensbachian–Toarcian).*

Cotylederma QUENSTEDT, 1852, p. 631 [**C. lineati* QUENSTEDT, 1858, p. 161; SD QUENSTEDT, 1858, p. 161] [=*Cotyloderma* DE LORIOL, 1879 in 1877–1879, p. 249, *nom. null.*; =*Cotylecrinus* DE LORIOL 1882 in 1882–1889, p. 188, *nom. van.*]. Cup flat, bowl shaped or shield shaped to cylindrical, only slightly oblique. *Lower Jurassic (Pliensbachian–Toarcian):* England, France, Germany, Italy, Switzerland, Bulgaria, Turkey.——FIG. 100,*1a*. **C. lineati* QUENSTEDT; attachment elements on ammonite, Pliensbachian, Germany, SMNS 29674, ×5 (Sieverts, 1932b).——FIG. 100,*1b–e*. *C. docens* DESLONGCHAMPS in DESLONGCHAMPS & DESLONGCHAMPS, 1858, Toarcian, France; *b–c,* radial circlet on attachment element, *b,* lateral, *c,* distal, ×4; *d*, adoral view of primibrachial 1, ×4; *e*, adoral view of primibrachial 2, ×4 (de Loriol, 1882 in 1882–1889).——FIG. 100,*1f–j*. *C. inaequalis* HESS, 2006, Pliensbachian, Switzerland; *f–g,* radial, *f,* oblique aboral-distal, *g,* proximal, syntype, NMB M10041, ×7; *h–i*, primibrachial 1, *h,* aboral, *i,* proximal, paratype, NMB M10050, ×7; *j*, adoral view of primibrachial 2, paratype, NMB M10052, ×7 (Hess, 2006).

Paracotylederma MANNI & NICOSIA, 1990b, p. 88 [**P. gracile;* OD]. Cup conical, composed of thin radials with narrow facets and thin basals; radial cavity deep and wide, with opening to unknown basal element. *Lower Jurassic (Toarcian):* Italy.——FIG. 100,*2a–c*. **P. gracile*; reconstructed cup, *a,* lateral, *b,* proximal, *c,* distal, ×4 (Manni & Nicosia, 1987).

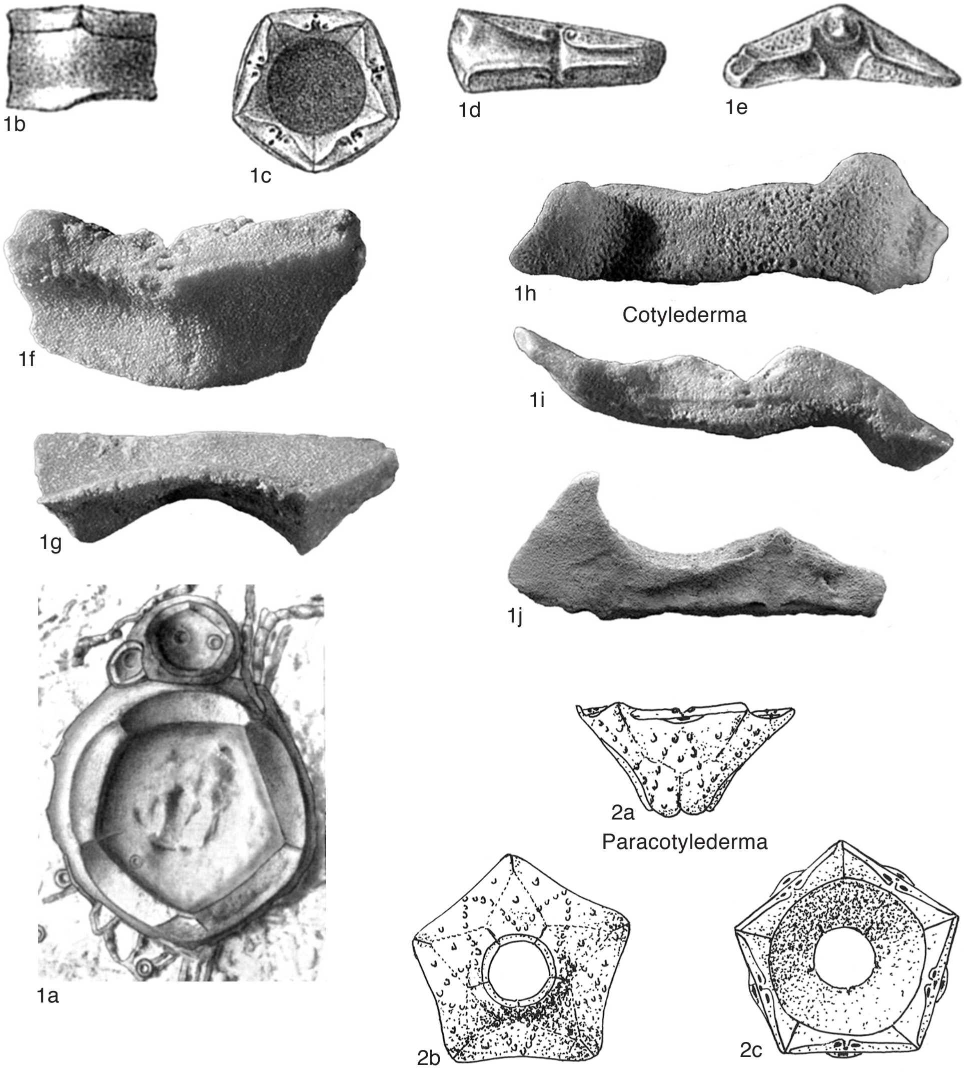

FIG. 100. Cotyledermatidae (p. 201).

Family EUDESICRINIDAE Bather, 1899

[Eudesicrinidae Bather, 1899, p. 923, *emend.*, Hess, herein, to exclude *Cotylederma* and to include *Dolichocrinus*] [=Cotyledermidae Wright, 1876, p. 94, *recte* Cotyledermatidae, *partim*]

Cup thick walled, with 5 radials separated by distinct sutures, one radial commonly considerably larger than others, radial articular facet inclined. Two primibrachials connected by muscular or synostosial articulation, primibrachial 2 axillary. [The family was emended by Manni and Nicosia (1990b, p. 82) to include *Bilecicrinus* and *Dinardocrinus*, but *Bilecicrinus* is herein assigned to Tetracrinidae. The extant *Proeudesicrinus* with radials connected to a columnal or basal element by a symplectial facet is provisionally assigned to this family.] *Lower Jurassic (Pliensbachian)–Holocene.*

Eudesicrinus de Loriol, 1882 in 1882–1889, p. 99 [**Plicatocrinus mayalis* Deslongchamps in Deslongchamps & Deslongchamps, 1858, p. 171; M]. Cup typically oblique, low to moderately high. Radial cavity narrow to rather large, in some specimens reaching basal element. Facet of cup to basal element concave and synostosial. Basal element of

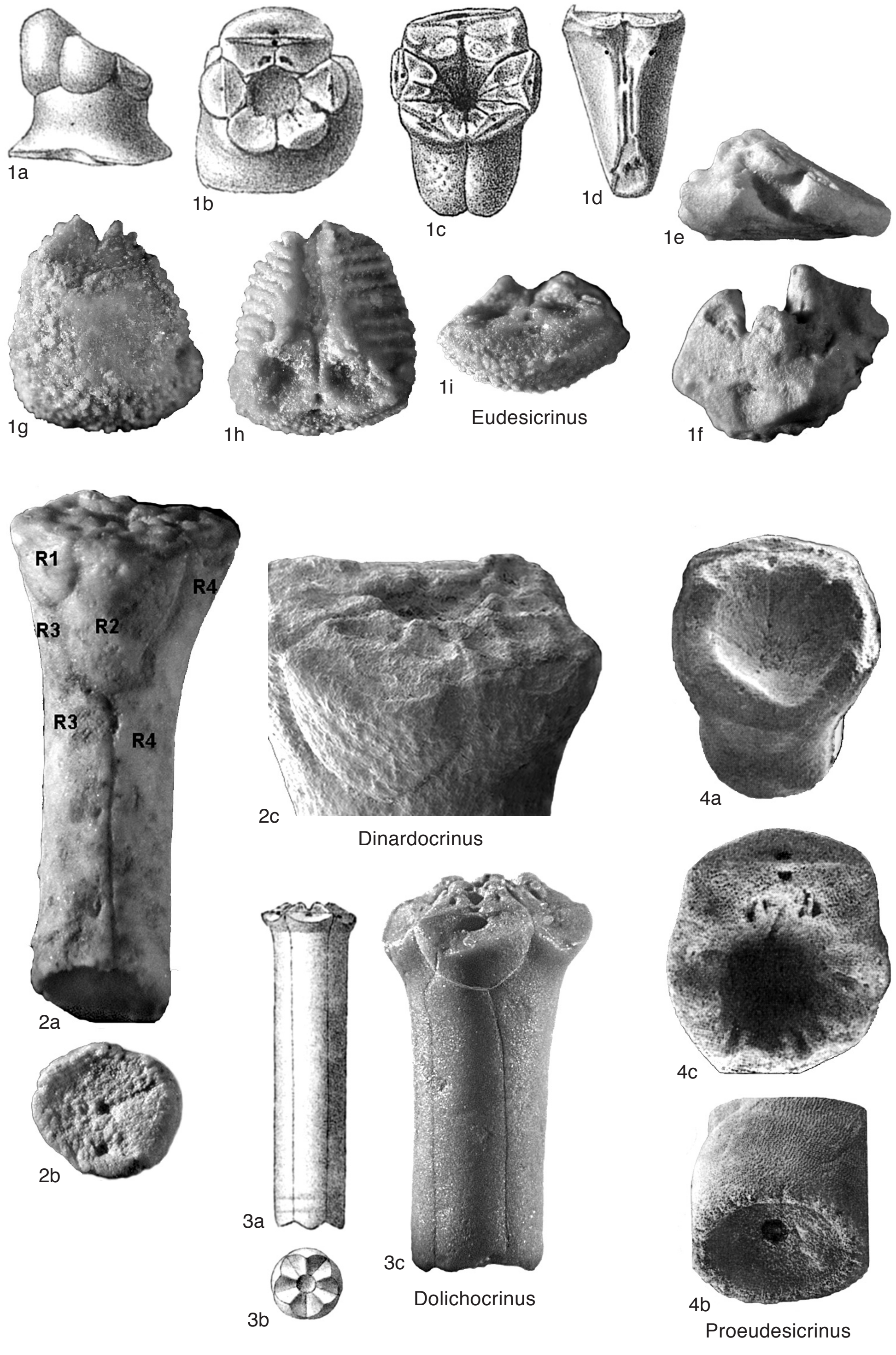

FIG. 101. Eudesicrinidae (p. 202–204).

variable height and shape. Primibrachials stout, meeting laterally in corrugate sides; articulation between primibrachials 1 and 2 muscular and broad in *E. mayalis*; oblique synostosial, small and circular in *E. cuneatus* Hess (2006). Secundibrachials stout, commonly cuneate, with muscular articulation and large pinnule socket. *Lower Jurassic (Pliensbachian–Toarcian), Upper Jurassic (?Tithonian):* England, France, Germany, Italy, Poland, Switzerland, Turkey.——Fig. 101,*1a–f*. **E. mayalis* (Deslongchamps), Toarcian, France; *a–b,* cup on attachment disk, *a,* lateral, *b,* distal, ×5; *c*, oblique distal view of cup, ×2.5; *d*, adoral view of radial, ×3 (de Loriol, 1882 in 1882–1889); *e–f*, secundibrachial, *e,* adoral, *f,* distal, topotype, NMB M10470, ×7 (Hess, 2006).——Fig. 101,*1g–i. E. cuneatus* Hess, 2006; primibrachial 1, *g,* aboral, *h,* adoral, *i,* proximal, Pliensbachian, Switzerland, holotype, NMB M10036, ×10 (Hess, 2006).

Dinardocrinus Manni & Nicosia, 1990b, p. 83 [**D. tiburtinus*; OD]. Cup strongly elongate, composed of radials of extremely different length, proximal end (facet to column) concave. Radial cavity narrow, rather shallow. Brachials and attachment unknown. *Lower Jurassic (Pliensbachian–Toarcian):* Italy, Switzerland.——Fig. 101,*2a–c*. **D. tiburtinus*, Pliensbachian, Switzerland, NMB M10029; cup with 2 occluded radials R1 and R2, *a,* lateral, *R1–R4,* individual radials; *b,* facet to column, ×5, *c,* oblique distal, ×7.5 (Hess, 2006).

Dolichocrinus de Loriol, 1891, p. 130 [**Eugeniacrinus aberrans* de Loriol, 1882 in 1882–1889, p. 148; M] [=*Tetanocrinus* Jaekel, 1891, p. 628, obj.]. Cup elongate columnlike, composed of mostly high radials that may preserve joint facets toward a basal circlet; radials rarely low and connected to high basals leading to twisted sutures. Radial articular facets large, outward sloping, of equal size. Radial cavity narrow, prolonged into columnlike part of radial and basal circlets. Brachials and attachment unknown. [Rasmussen (1978, p. 926) considered *Dolichocrinus* a *nomen dubium* of uncertain order and family. It was transferred from Cyrtocrinida to Millericrinida by Jaekel (1907, p. 291), where indication of a basal circlet was found. A topotype specimen from the Bathonian, La Clapouze, Ardèche, France (Fig. 101,*3c*), has one low radial connected to a high basal by synostosis, whereas the other radials are high. Therefore, the columnlike cup may be composed of fused radials and basals. Elongate cups also occur in other cyrtocrinids such as *Dinardocrinus* and *Hemicrinus*.] *Middle Jurassic (Bathonian)–Upper Jurassic (Tithonian):* Crimea, France, ?Poland, Portugal.——Fig. 101,*3a–c*. **D. aberrans* (de Loriol); *a–b,* cup, *a,* lateral, *b,* proximal, Portugal, ×5 (de Loriol, 1891); *c,* cup with occluded radial, Bathonian, France, topotype, NMB M10584, ×7 (Hess, new).

Proeudesicrinus Améziane-Cominardi & Bourseau in Améziane-Cominardi & others, 1990, p. 119 [**P. lifouensis*; M]. Cup compact, with deep radial cavity, lower portion a fused cylinder (perhaps basals, or basals plus uppermost columnal); radials wide and high, with lateral sutures visible but no clear basal sutures. Four narrow and one wider radial articular facet. Lower facet of cup with lateral crenulae for attachment to unknown columnal or basal element. Brachials unknown. *Holocene:* New Caledonia at 960 m.——Fig. 101,*4a–c*. **P. lifouensis*; *a,* oblique distal view of cup, holotype, MNHN EcPs39, ×7; *b*, facet of cup to column, syntype, MNHN EcPs39, ×15; *c*, distal view of cup, syntype, MNHN EcPs39, ×15 (Améziane-Cominardi & others, 1990).

Family HEMIBRACHIOCRINIDAE Arendt, 1968

[Hemibrachiocrinidae Arendt, 1968, p. 156]

Cup compact, thick walled, generally elliptical in outline, composed of commonly fused radials that are fused with slightly expanded base of irregular shape, depending on the substrate. Radial cavity mostly large. Radial articular facets varying from 1 to 5, with large muscle fossae (smaller in *Brachiomonocrinus*) and weak ligament fossae. Arms reduced, supported by depressions on the opposite side of the cup, developed to a variable degree. Arms divided at primibrachial 1, or undivided. Arms short, forming cover over adoral side of cup when retracted, tip of arms leaning on opposite edge of cup. [The number of articular facets varies between 1 (*Brachiomonocrinus* Arendt, 1974) and 2 (*Dibrachiocrinus* Arendt, 1968) or 3 (*Hemibrachiocrinus* Arendt, 1968). In view of the high variabiliy of these crinoids, Žitt (1979a) considered *Hemibrachiocrinus* and *Dibrachiocrinus* to belong to the same genus, a view that is followed herein. Reduction of articular facets seems to be part of a continuum starting from 5 in juvenile specimens as demonstrated by Arendt (1974, pl. 34,*4–5*) for *Hemibrachiocrinus manesterensis* and ending in *Brachiomonocrinus*. Thus, all hemibrachiocrinids may belong to a single genus, as suggested by Žitt (1979a).] *Lower Cretaceous (Valanginian–Barremian).*

Hemibrachiocrinus Arendt, 1968, p. 156 [**H. manesterensis*; M] [=*Dibrachiocrinus* Arendt, 1968, p. 156 (type, *D. biassalaensis*, M)]. Edge of cup of adult specimens with 2 or 3 large articular facets, opposite arms atrophied. Middle portion of arm with stout, axillary primibrachial 1. *Lower Cretaceous (Valanginian–Barremian):* Crimea, Czech Republic.——Fig. 102,*1a–c*. **H. manesterensis*,

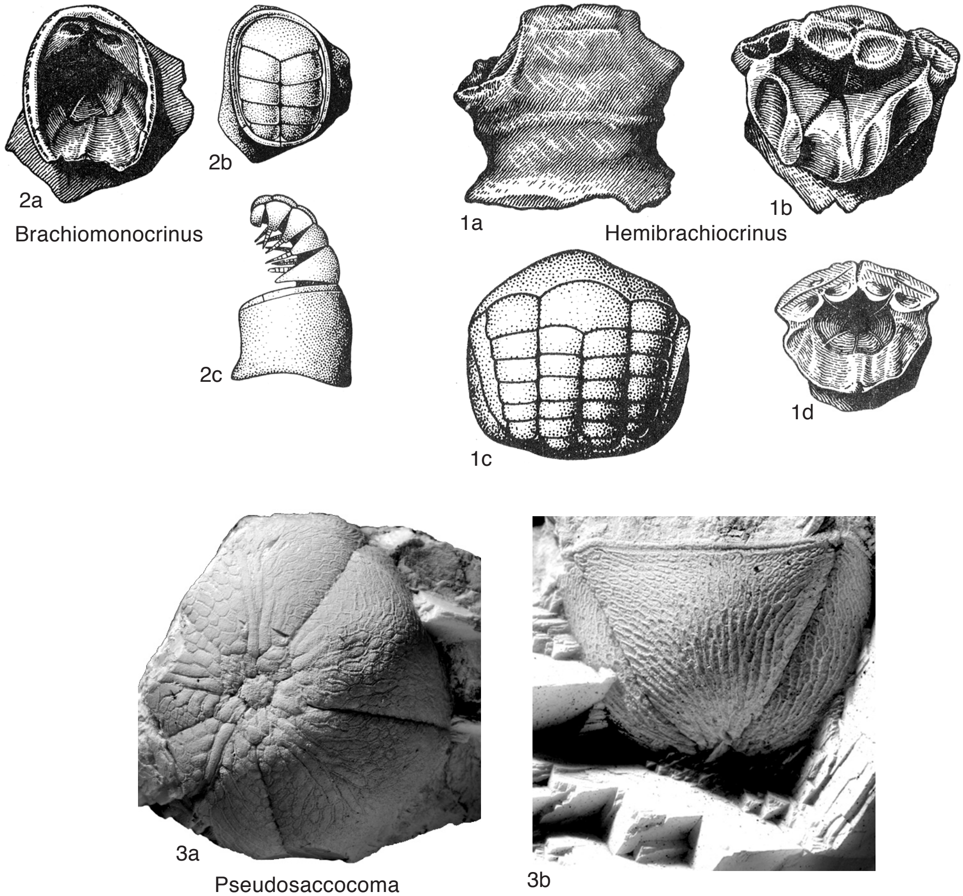

FIG. 102. Hemibrachiocrinidae and Pseudosaccocomidae (p. 204–206).

Barremian, Crimea; *a–b,* cup, *a,* lateral, *b,* distal, holotype, PIN 2278/11, ×4; *c,* reconstruction, ×4 (Arendt, 1974).——FIG. 102,*1d. H. solovjevi* (ARENDT, 1974); distal view of cup, Barremian, Crimea, PIN 2278/1, ×6 (Arendt, 1974).

Brachiomonocrinus ARENDT, 1974, p. 159 [**B. simplex*; M]. Cup with narrow ridge, more or less elliptical in outline. Single, large radial articular facet in narrow end of edge. *Lower Cretaceous (Valanginian–Barremian):* Crimea, Czech Republic.——FIG. 102,*2a–c.* **B. simplex*, Crimea; *a,* distal view of cup, holotype, PIN 2278/170, ×6; *b,* reconstruction, distal view, ×6; *c,* reconstruction, lateral view, ×6 (Arendt, 1974).

Family PSEUDOSACCOCOMIDAE Patrulius, 1956

[Pseudosaccocomidae PATRULIUS, 1956, p. 187]

Cup bowl shaped, composed of 5 thick-walled, rugose radials; cup cryptodicyclic with 5 basals that may be irregularly developed or fused into centrale; rarely, tiny infrabasals are present, but these are mostly fused into small centrale. Radial cavity wide, radials with wide articular facets. Cup fused with massive basal element of variable shape and size, surface sculpture of cup only visible after separation from basal element. [Cup and base (*Hüllkörper* of BACHMAYER, 1958; ballast ossicle of SEILACHER & MACCLINTOCK, 2005) invariably are embedded in a hard calcareous matrix. They may be separated to show the distinctive rugose surface, but the lower side of the base is never exposed. BACHMAYER (1958, p. 43) proposed the subfamily Pseudosaccocominae of the family Saccocomidae for

Pseudosaccocoma, and this was followed by RASMUSSEN (1961, p. 392; 1978, p. 926) with PATRULIUS (1956) as the author of the subfamily. KÄSTLE (1982) rejected a relationship of *Pseudosaccocoma* with *Saccocoma* and, thus, assignment to the Roveacrinida; and he considered the form to be related to *Isocrinus*. Based on the dendritic surface of the cup impressed onto the base, SEILACHER and MACCLINTOCK (2005, p. 235) discussed a possible homology of the base to a comatulid centrodorsal, but they also considered a sessile form such as *Cotylederma* as a stepping-stone stage to a secondary, soft-bottom dweller, with the expanded proximal columnal anchoring the animal. The irregular base, fused with the cup, and the wide radial cavity suggest placement in Holopodina.] *Upper Jurassic (Tithonian)–Lower Cretaceous (Aptian).*

Pseudosaccocoma REMEŠ, 1905, p. 62 [**P. strambergensis*; M]. Characters as for family. [*P. doreckianum* BACHMAYER (1958, p. 48), Tithonian limestone, Ernstbrunn (Austria), *P. araurica* YIN (1931, p. 161), Tithonian, France, and *P. japonica* KOBAYASHI (1935, p. 72), Tithonian, Japan, are considered to be ecophenotypes of a single species.] *Upper Jurassic (Tithonian)–Lower Cretaceous (Aptian):* Austria, France, Germany, Italy, Czech Republic, Japan.——FIG. 102,*3a–b*. **P. strambergensis*, Tithonian, Austria; *a,* aboral view of cup, NHMW 2008z0278/0012, ×2; *b*, lateral view of cup, NHMW 2008z0278/0011, ×2.5 (Schumacher, new).

ROVEACRINIDA

HANS HESS

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Order ROVEACRINIDA Sieverts-Doreck, 1953

[Roveacrinida SIEVERTS-DORECK in UBAGHS, 1953, p. 763]

Small, mostly pelagic stalkless forms with delicate skeleton. Cup composed of radials and discrete or more or less vestigial or fused basals that may be surmounted and overgrown by the mostly ornamented radials; some specimens with centrale; most Triassic forms with aboral projection. Two primibrachials. Primibrachial 2 axillary, 10 dichotomous arms with side branches. Articulation of brachials muscular and cryptosynarthrial. Articulation between primibrachials 1 and 2 and secundibrachials 1 and 2 strongly sloping cryptosynarthries. Flanges on radials and brachials common. Arms not developed in *Applinocrinus*. [The roveacrinids include the Triassic Somphocrinidae, the Jurassic Saccocomidae, and the Cretaceous Roveacrinidae, families whose relationship to each other and to other crinoid groups is unclear, according to SIMMS (1990b) and SIMMS and others (1993). However, these families are linked by the synapomorphy of strongly sloping cryptosynarthries in the proximal part of the arms, a feature that is also shared by the Triassic Axicrinidae, added to the Roveacrinida herein. Whereas the roveacrinids were mostly pelagic, some forms appear to have been benthic, at least during part of their life (HESS, 2002), suggesting that sloping cryptosynarthries were not merely the result of a pelagic lifestyle. *Saccocoma tenella,* a large form by roveacrinid standards, is the only known roveacrinid preserved intact with arms attached. Its morphology, unique to roveacrinids, indicates a special method for food collection, for which HESS and ETTER (2011) proposed the pulsating funnel model (see also HESS, 2010).] *Middle Triassic (Ladinian)–Lower Paleogene (Danian).*

Family ROVEACRINIDAE Peck, 1943

[Roveacrinidae PECK, 1943, p. 461; *emend.*, RASMUSSEN, 1961, p. 360]

Cup with double body cavity in most forms, composed of radials that have overgrown, small, discrete basals, forming an upper (oral) cavity above the basals and a secondary, mostly closed, and globose lower (aboral) cavity below the basals. Cup sculptured by spines, ridges, wings, and flanges; similar sculpturing on brachials. [RASMUSSEN (1978, p. 921) subdivided the Roveacrinidae into the subfamilies Roveacrininae PECK, 1943, and Somphocrininae PECK, 1978. Following SIMMS and others (1993), they are treated, herein, as separate families. SCHNEIDER (1989, 1995) suggested that development of the lower, aboral cavity during growth increased the capacity of gases and lower density fluids and, thus, compensated for the increased weight of the animal. He speculated that gas and/or fluid exchange between the 2 cavities may have enabled vertical movement without muscle activity; see also JAGT (2005).] *Lower Cretaceous (Hauterivian)–Lower Paleogene (Danian).*

Roveacrinus DOUGLAS, 1908, p. 358 [**R. alatus;* OD] [=*Drepanocrinus* JAEKEL, 1918, p. 72 (type, *D. sessilis,* OD)]. Cup with small semicircular arm facets and 5 undivided radial ridges extending from proximal portion of arm facets to aboral apex and sometimes beyond as an aboral spine; distal part of radial ridges may also bear spines, wings, or flanges. Basals absent in some species or distinct in others, and some species with additional circlet of tiny ossicles (cryptodicyclic cup); if present, basal circlet in radial cavity connected to the upper rim of the proximal part of the cup and separating the 2 cavities (see Fig. 5,*6*). [As discussed by SCHNEIDER (1987, 1989), development of basals is highly variable in *Roveacrinus*; cups are cryptodicyclic, monocyclic, or lack basals altogether.] *Lower Cretaceous (Hauterivian)–Lower Paleogene (Danian):* Spain, Algeria, Angola, Brazil, *Hauterivian, Albian*; Tunisia, *Albian–Cenomanian*; Germany, USA (Texas), Morocco, Turkey, *Cenomanian*; England, *Cenomanian–Coniacian*; Turkey, Syria, *Cenomanian–Turonian*; Crimea, Spain, Africa, Brazil, *Turonian;* Poland, *Danian.*——FIG. 103,*1a–b.* **R. alatus;* cup, *a,* lateral, *b,* distal, Coniacian, England, holotype, BMNH E45704,

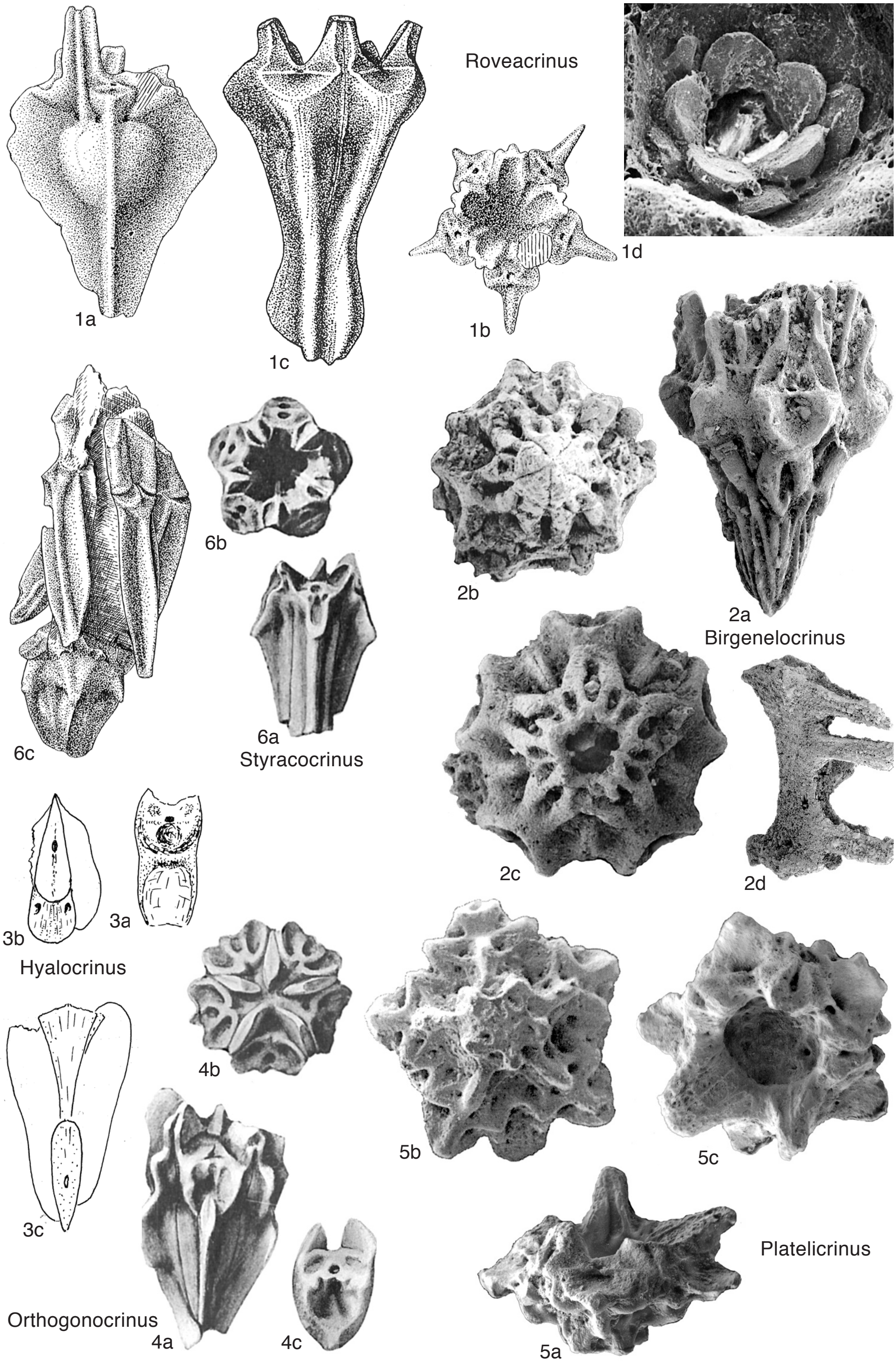


FIG. 103. Roveacrinidae (p. 207–211).

×15 (Rasmussen, 1961).——FIG. 103,*1c. R. communis* DOUGLAS; cup, Cenomanian, Germany, IPB (specimen missing), ×15 (Sieverts-Doreck, 1933b, as *Drepanocrinus sessilis* JAEKEL, 1918).——FIG. 103,*1d. R. occultus* SCHNEIDER, 1987; adoral view of radial cavity with 2 circlets of platelets, Cenomanian, Germany, holotype, Schneider Coll. Düsseldorf, ×50 (Schneider, 1987).

Birgenelocrinus JAGT, 1999a, p. 148 [**B. degraafi*; M]. Cup high, conical, strongly sculptured. Radials large, elongate with prominent interradial extensions and well-developed, nearly flat and almost vertical articular facets. Basals small, compact, forming aboral end and enclosing an aboral cavity. Secundibrachials with keeled aboral surfaces, deep ambulacral grooves, and paired, prominent flanges near both ends. *Upper Cretaceous (Maastrichtian):* Netherlands.——FIG. 103,*2a–d*. **B. degraafi*; *a,* lateral view of cup, paratype, NHMM MB 506-15j, ×30; *b*, aboral view of cup, paratype, NHMM JJ 9543a, ×30; *c*, distal view of cup, paratype, NHMM MB 506-15h, ×30; *d*, lateral view of brachial, NHMM MB 506-15c, ×35 (Jagt, 1999a).

Discocrinus PECK, 1943, p. 474 [**D. catastomus*; OD]. Cup low, without prominent wings or spines, large facets for arms located on outer sides of radials and almost parallel to aboral-adoral axis. [According to RASMUSSEN (1961, p. 387; 1978, p. 922), growth of radials below basals was incomplete, leading to the aboral cavity being open at the base. However, *Discocrinus integer* HESS (in HESS & GALE, 2010) from the Albian of England has an intact cup closed at the base, indicating that an open lower cavity is due to breakage or preservation, rather than to incomplete growth.] *Lower Cretaceous (Albian)–Upper Cretaceous (Cenomanian):* USA (Texas), England, *Albian;* England, *Cenomanian.*——FIG. 104,*1a–b*. **D. catastomus*, Albian, Texas; *a,* cup, paratype, UM E-13-5; *b*, distal view of cup, holotype, UM E-13-4, ×20 (Peck, 1943).

Hyalocrinus DESTOMBES, 1985, p. 10 [**H. bulliensis*; M]. Radials and brachials consisting largely of vitreous, transparent expansions, those on brachials in form of lateral wings. *Lower Cretaceous (Albian):* France.——FIG. 103,*3a–c*. **H. bulliensis*; *a,* aboral view of radial, holotype, MHNH; *b*, aboral view of primibrachial 1, paratype, MHNH; *c*, adoral view of primibrachial 2, paratype, MHNH, ×20 (Destombes, 1985).

Orthogonocrinus PECK, 1943, p. 464 [**O. apertus*; OD]. Cup more or less conical with undivided vertical radial ridges. Facets for arms well developed, occupying most of distal surface and parts of sides of radials, making almost right angle turn at transverse ridge. Arms unknown. *Lower Cretaceous (Albian)–Upper Cretaceous (Coniacian):* USA (Texas), *Albian–Cenomanian*; Czech Republic, *Turonian*; England, France, Germany, *Cenomanian–Coniacian*.——FIG. 103,*4a–c*. **O. apertus*, Albian, Texas; *a,* cup, paratype, UM E-21-4, ×20; *b–c*, cup, *b,* aboral, *c,* radial articular facet, holotype, UM E-21-5, ×20 (Peck, 1943).

Platelicrinus DESTOMBES & BRETON, 2001, p. 38 [**P. campaniensis*; M]. Cup with 5 unequal interradial processes, one considerably larger than the others. *Upper Cretaceous (Campanian):* France.——FIG. 103,*5a–c*. **P. campaniensis*; cup, *a,* lateral, *b,* aboral, *c,* distal, holotype, MHNH 9019, ×15 (Destombes & Breton, 2001).

Plotocrinus PECK, 1943, p. 469 [**P. hemisphericus*; OD]. Cup hemispherical with large arm facets; radial sculpturing consisting of either simple vertical ridges or simple ridges flanked along their distal half by additional ridges. Spines, wings, or horizontal flanges not developed. *Lower Cretaceous (Albian):* USA (Texas).——FIG. 104,*2a–d*. **P. hemisphericus; a–b,* cup, *a,* lateral, *b,* distal, holotype, UM E-10-2; *c*, adoral view of primibrachial 1, UM E-10-5; *d*, aboral view of primibrachial 1, UM HTL 35, ×15 (Peck, 1943).

Poecilocrinus PECK, 1943, p. 471 [**P. dispandus*; OD]. Cup with a prominent horizontal wing on each radial, sometimes fused around the cup, or each radial with curved, bowl-shaped wing with the opening of the concavity outward or downward. Radial ridge from wing to aboral apex. Radial articular facet outward sloping and connected with the wings by short lateral ridges. Interradial processes rather short and stout. *Lower Cretaceous (Albian)–Upper Cretaceous (Cenomanian):* USA (Texas).——FIG. 104,*3a–d*. **P. dispandus,* Albian; *a,* lateral view of cup, holotype, UM E-19-5; *b*, distal view of cup, paratype, UM E-19-4, ×15 (Peck, 1943); *c*, aboral-distal view of primibrachial 1, USNM 220404, ×20; *d*, reconstruction, ×4 (Scott & others, 1977).

Roveacrinoides RASMUSSEN, 1971, p. 287 [**R. nudus*; OD]. Similar to *Roveacrinus* but with small aboral cavity containing enclosed basal circlet, leaving only small opening to adoral cavity; adoral part of cup bowl shaped, similar to *Saccocoma*, without pronounced radial wings. [Genus established by RASMUSSEN (1971) based on basal circlet not being overgrown by radials and thus forming the aboral cavity. As demonstrated by SCHNEIDER (1987, p. 201), the basals are within the aboral cavity, which is formed by the radials.] *Upper Cretaceous (Turonian):* England, Germany.——FIG. 104,*4a–b*. **R. nudus,* England, cup; *a,* oblique aboral, *b,* distal, holotype, CAMSM B.97380, ×20 (Rasmussen, 1971).

Styracocrinus PECK, 1955, p. 1022 [**Drepanocrinus peracutus* PECK, 1943, p. 463; OD]. Cup small, elongate conical; radial articular facet triangular or semicircular in shape, sloping outward and downward at an angle from horizontal, slightly greater outside traverse ridge than inside; aboral ligament fossa steeply inclined, high, and very narrow. Axillary primibrachial 2 high and slender with narrow median ridge and thin lateral flanges. *Lower Cretaceous (Albian)–Upper Cretaceous (Cenomanian):* USA (Texas), Poland, *Albian–Cenomanian;* England, *Cenomanian*.——FIG. 103,*6a–c*. **S. peracutus* (PECK); *a,* cup, Albian, Texas, holotype, UM E-23-3, ×20; *b*, distal view of cup, Albian,

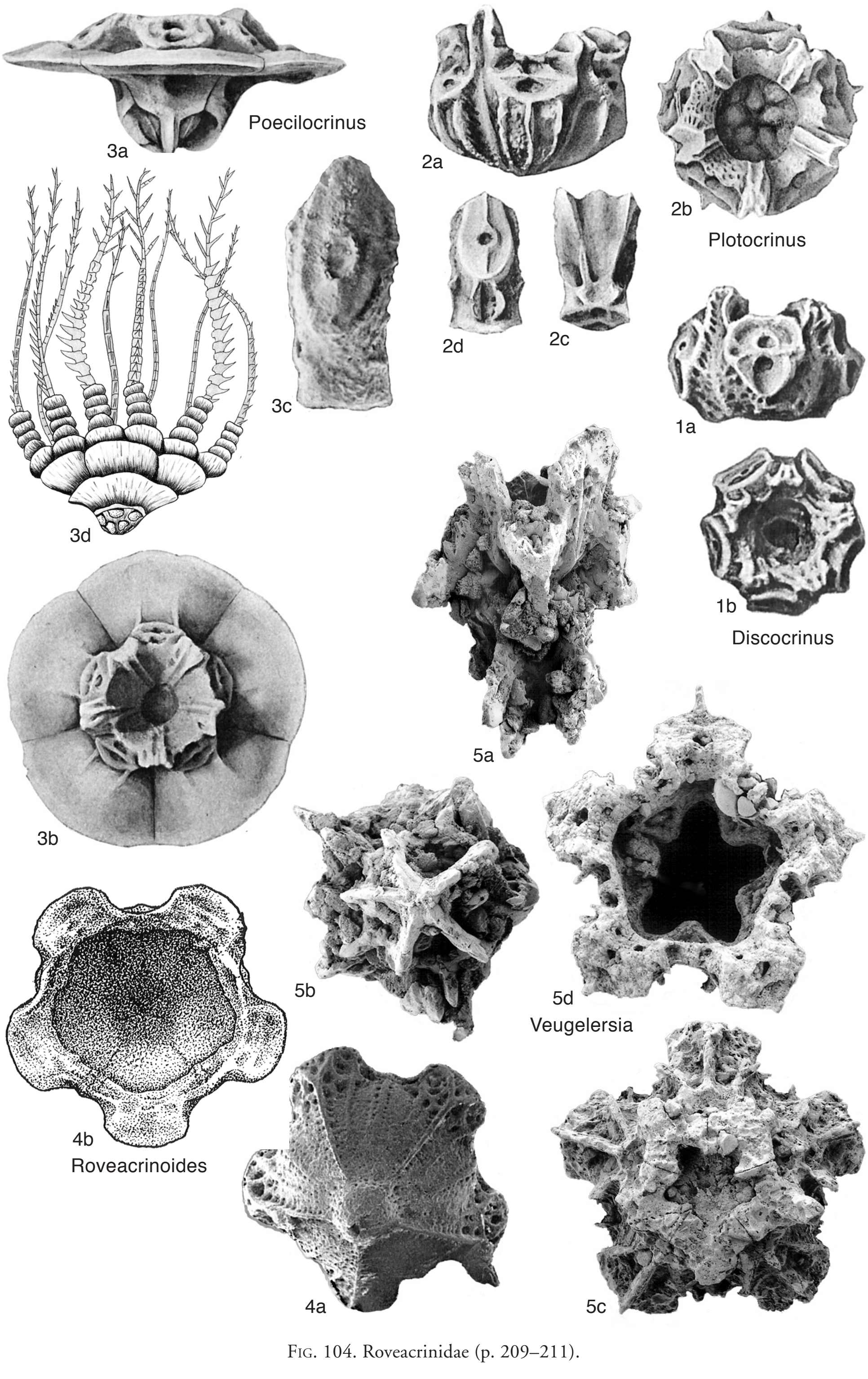


FIG. 104. Roveacrinidae (p. 209–211).

Texas, UM E-22-4, ×20 (Peck, 1943); *c*, cup with brachials, Cenomanian, England, BMNH E45862, ×15 (Rasmussen, 1961).

Veugelersia JAGT, 1999a, p. 150 [**V. diana*; M]. Cup broadly conical. Radials with prominent interradial flanges united into stellate base, and high, distally rounded and perforate interradial extensions; articular facets oblique with distal, flangelike continuation; bottom of body cavity formed by stellate basal ring. *Upper Cretaceous (Campanian–Maastrichtian):* Netherlands, France.——FIG. 104,*5a–d*. **V. diana*, Maastrichtian, Netherlands; *a,* lateral view of cup, holotype, NHMM MB 517-1a; *b*, aboral view of cup, paratype, NHMM MB 517-1b; *c*, aboral view of upper part of cup with basal ring, paratype, NHMM MB 865-17a; *d*, distal view of cup, paratype, NHMM MB 865-17b, ×30 (Jagt, 1999a).

Family AXICRINIDAE Hess, new family

[Axicrinidae HESS, herein] [type genus, *Axicrinus* KRISTAN-TOLLMANN, 1977, p. 195]

Cup smooth, with high, contiguous basals. Radials and primibrachials compact, without flanges or spines. Muscle fossae of radials, second primibrachial and secundibrachials large, prolonged in high processes. Arms with side branches or pinnules. [The sloping cryptosynarthries between primibrachials 1 and 2 and secundibrachials 1 and 2 as well as the nature of the muscle fossae indicate that this form belongs to the Roveacrinida, but the presence of well-developed basals is unique in this order. In addition, the ossicles are rather compact. KRISTAN-TOLLMANN (1977) thought that *Axicrinus* probably represented a new family but did not name it.] *Upper Triassic (Carnian).*

Axicrinus KRISTAN-TOLLMANN, 1977, p. 195 [**A. alexandri*; M]. Characters as for family. *Upper Triassic (Carnian):* Italy.——FIG. 105*a–e*. **A. alexandri*; *a,* oblique aboral-distal view of radial, holotype, Kr-To V 79; *b*, oblique adoral-proximal view of radial, Kr-To collection; *c*, aboral view of primibrachial 1, Kr-To collection; *d*, aboral view of primibrachial 2, Kr-To collection, ×15; *e*, lateral view of 2 secundibrachials with socket for pinnule or side branch, Kr-To collection, ×20 (Kristan-Tollmann, 1977).

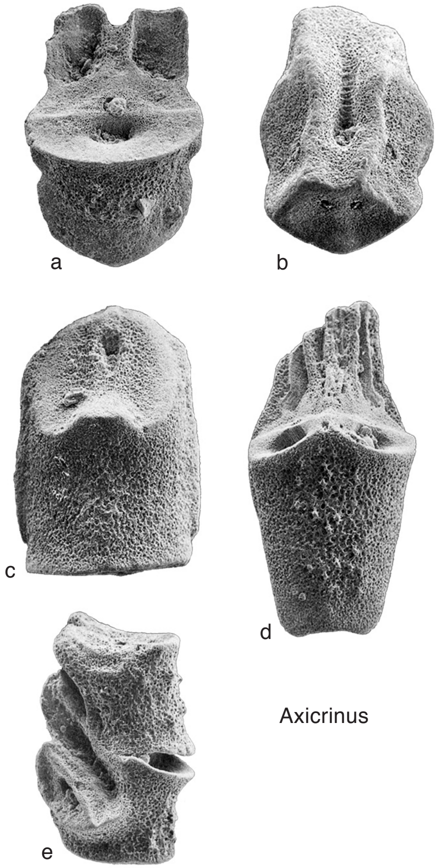


FIG. 105. Axicrinidae (p. 211).

Family SACCOCOMIDAE d'Orbigny, 1852

[Saccocomidae D'ORBIGNY, 1852 in 1850–1852, p. 137]

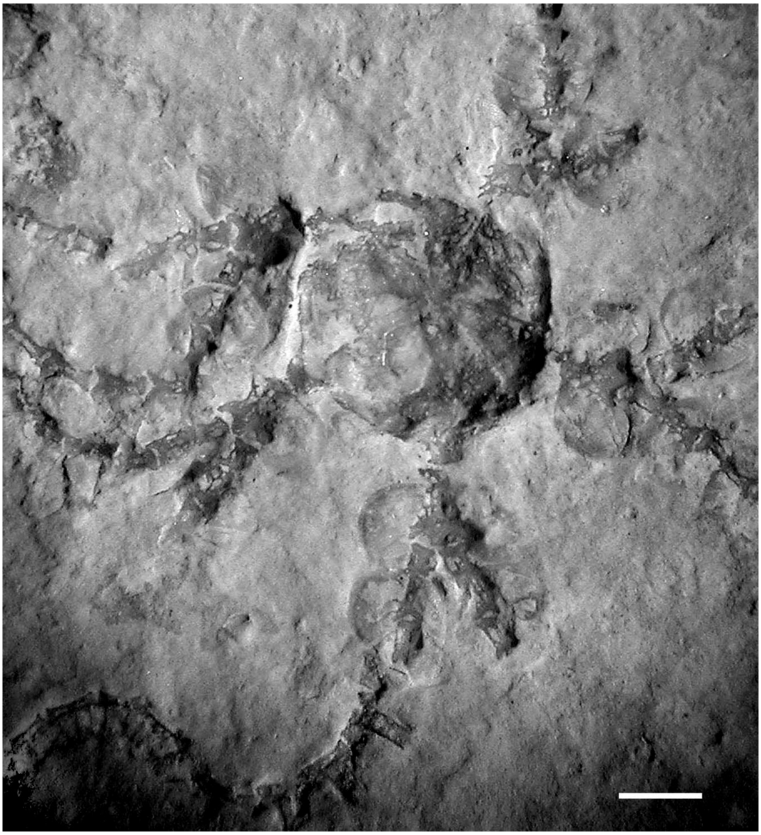
Cup bowl shaped, composed of radials that may be thick walled in early forms. Basals small or vestigial; minute central piece may be present but mostly fused with basals. *Upper Jurassic–Upper Cretaceous.*

Subfamily SACCOCOMINAE d'Orbigny, 1852

[*nom. transl.* BACHMAYER, 1958, p. 43, *ex* Saccocomidae D'ORBIGNY, 1852 in 1850–1852, p. 137]

Cup open on adoral side, composed of spherical radials that may be thick walled in early forms; minute central piece may be present. Arms well developed. Radials and brachials in advanced forms with lightened skeleton, flanges, and wings; some forms with spines on the cup. *Middle Jurassic (Callovian)–Lower Cretaceous (Albian).*

Saccocoma AGASSIZ, 1836, p. 193 [**Comatula tenella* GOLDFUSS, 1831 in 1826–1844, p. 204, pl. 62,*1;*



Saccocoma

FIG. 106. Saccocomidae (p. 211–213).

SD HESS, 1999c, p. 218; =*Comatula pectinata* GOLDFUSS, 1831 in 1826–1844, p. 205; =*Comatula filiformis* GOLDFUSS, 1831 in 1826–1844, p. 205] [=*Saccosoma* D'ORBIGNY, 1850 in 1850–1852, p. 381, *error pro Saccocoma* AGASSIZ, 1836; =*Eothrix* LOMBARD, 1945, p. 163 (type, *E. alpina*, *partim*, OD); =*Lombardia* BRONNIMANN, 1955, p. 44, (type, *L. arachnoidea*, OD)]. Cup a hemisphere or open bowl with deep radial cavity, very thin walled, surface covered with network of anastomosing ribs that reinforce area beneath articular facets where antlerlike processes may be present. Knob of fused basals and centrale mostly indistinct. Radial articular facet with small aboral part and elongate muscle fossae articulating with V-shaped muscle fossae on first primibrachial. Primibrachial 1 with low exposed aboral side, no lateral wings. Axillary primibrachial 2 and some of the secundibrachials with dishlike lateral wings, the more distal brachials with paired vertical adoral processes in the type species. Arms may branch distally. [JAEKEL, 1918, p. 92, assigned *Comatula filiformis* GOLDFUSS, 1831 in 1826–1844, to *Saccocoma* AGASSIZ, and he proposed *Saccoma* JAEKEL, a new genus, for *Comatula tenella* GOLDFUSS, 1831 in 1826–1844. *Eothrix alpina* was described by LOMBARD, 1945, from thin sections, thought to belong to algae. BRONNIMANN (1955) described similar thin sections from the Tithonian of Cuba and renamed the remains *Lombardia*, establishing three species (*L. arachnoidea*, *L. perplexa*, and *L. angulata*). VERNIORY (1954, 1956) recognized that the fossils in the thin sections are brachials of *Saccocoma,* and BRONNIMANN's three species corresponded to sections made under different angles.] *Middle Jurassic (Callovian)–Lower Cretaceous (Albian):* Austria, Germany, France, Italy, Poland, western Atlantic Ocean sediments, Cuba, Japan, *Callovian–Tithonian*; Germany, *Albian*.——FIG. 106. **S. tenella* (GOLDFUSS); cup and proximal arms, Tithonian, Germany, lectotype, IPB Goldfuss 423, ×10 (Hess, 2002).——FIG. 107*a–e*. **S. tenella* (GOLDFUSS); *a*, middle part of arm with adoral processes; *b*, distal part of arm with three side

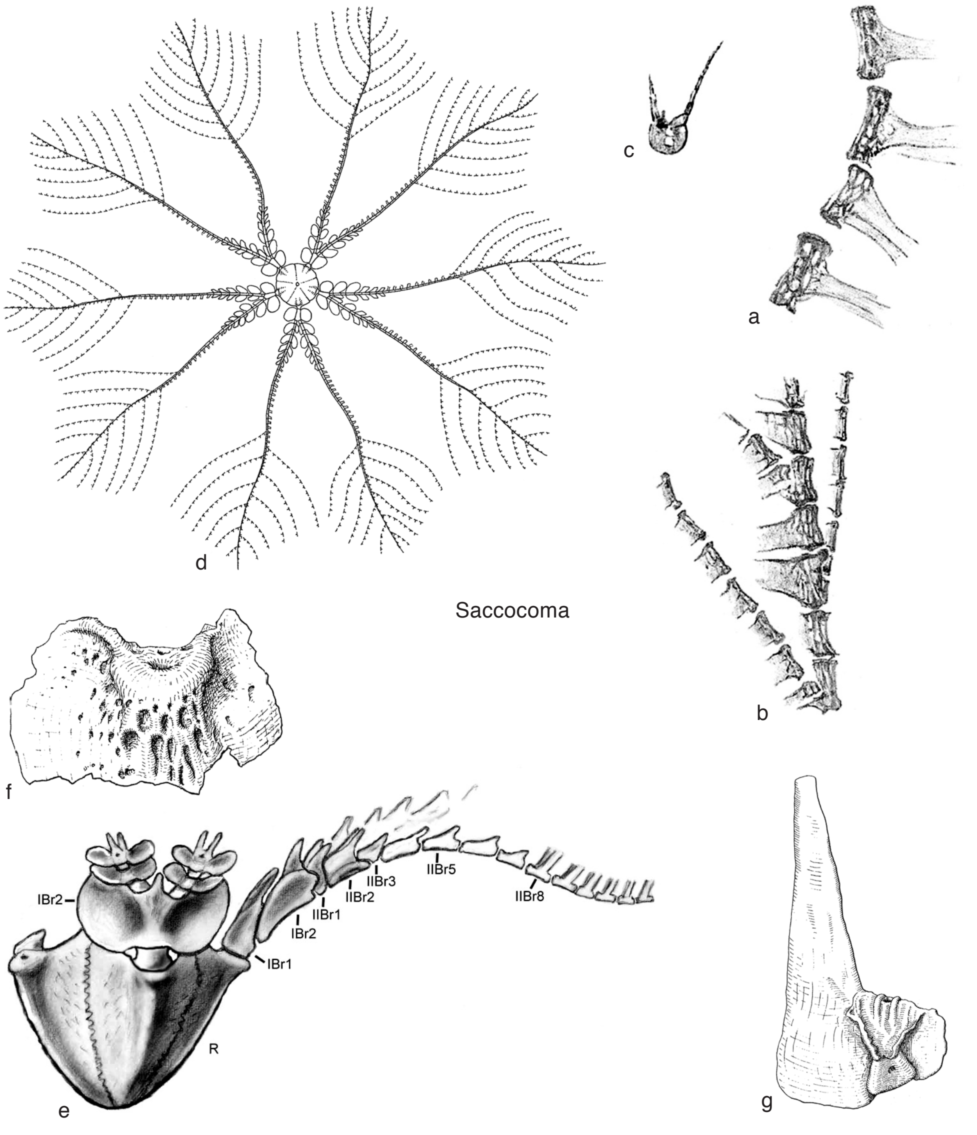


Fig. 107. Saccocomidae (p. 211–213).

branches, Tithonian, Germany, ×15 (Jaekel, 1892); *c*, facet of brachial with adoral processes, Tithonian, Germany, ×20 (Jaekel, 1892); *d*, aboral projection, ×1.6 (Hess, 1999c, adapted from Jaekel, 1918); *e*, reconstruction in life position, sculpturing omitted; *R*, radial, *IBr*, primibrachial, *IIBr*, secundibrachial, ×10 (Hess & Etter, 2011, adapted from Brodacki, 2006).——Fig. 107*f–g*. *S. longipinna* Hess, 2002, Kimmeridgian–Tithonian, France; *f*, aboral view of upper part of radial with articular socket, MHNG 73691; *g*, adoral view of proximal brachial, holotype, MHNG 73690, ×20 (Hess, 2002).

Crassicoma Sieverts Doreck & Hess in Hess, 2002, p. 11 [**C. schattenbergi*; OD]. Cup low, composed of thick-walled to thinner radials with interradial processes and basals that may be fused with a centrale. Radial cavity shallow. Aboral apex sunken or with protruding knob. Radials articulated to each other by flat synostoses; aboral surface of radials coarsely reticulate or pitted to finely rugose, without median ribs; lower edge truncated. Muscle fossae of radials strongly developed, attached to daggerlike interradial processes, in some forms encroaching from base of processes on inner wall of the radial. Primibrachial 1 high and flat with narrow profile, winglike lateral processes apparently forming a protective wall around adoral side of cup, proximal facet with ligamentary part forming an angle of 60 to 80 degrees with the commonly scalloped muscle fossae situated on inner side, distal facet a flat cryptosynarthry visible on approximately half the outer surface and nearly parallel (angle approximately 20 degrees) to the inner side. Brachials mostly dumbbell shaped. Pinnules or ramules present but few. *Upper Jurassic (Oxfordian–Kimmeridgian):* Germany, western Atlantic Ocean sediments.——FIG. 108,*1a–f.* **C. schattenbergi,* Kimmeridgian, Germany; *a,* proximal view of cup, holotype, SMNS 64734, ×8; *b,* aboral-distal view of radial, paratype, SMNS 64726, ×11; *c,* aboral view of primibrachial 1, SMNS 64728, ×15; *d,* adoral view of primibrachial 1, SMNS 64715, ×15; *e–f,* radial, primibrachial 1, and primibrachial 2 combined, *R,* radial, *IBr1,* first primibrachial, *IBr2,* second (axillary) primibrachial, *e,* aboral, *f,* lateral, paratypes, SMNS 64697–64699, ×2.3 (Hess, 2002).

Subfamily APPLINOCRININAE Hess, new subfamily

[Applinocrininae HESS, herein] [type genus, *Applinocrinus* PECK, 1973, p. 95]

Cup highly variable in profile and sculpturing. Basals small, may be elongated aborally. Radials lacking articular facet for attachment of arms. Radial cavity covered by oral plates nearly radial in position and meeting at center of adoral side with clockwise twist. [PECK (1973) found no articular facets for the attachment of arms on cups of *Applinocrinus cretaceus* but detected 2 small openings to the oral cavity on the aboral surface of the covering plates (PECK 1973, pl. 1,*1–2*). DONOVAN, MILSOM, and VELTKAMP (1996) thought it unlikely that *Applinocrinus* was armless, although they could not identify a distinct articular facet on the cups. A second species, *Applinocrinus texanus* PECK, 1973, with a high-domed oral cover and an elongate basal circlet open at the proximal end, was considered by JAGT (1999a) to represent an extreme morphology, with material from the lower Maastrichtian of Rügen linking the 2 species. Among several hundreds of cups in JAGT's (1999a) material, only a few had the oral covering plates preserved, suggesting that these plates were only weakly articulated to the margin of the radials. FERRÉ (written communication, 2005) collected brachial plates similar to those of *Saccocoma* in strata with cups of *Applinocrinus cretaceus*.] *Upper Cretaceous (Campanian–Maastrichtian).*

Applinocrinus PECK, 1973, p. 95 [**Saccocoma cretacea* BATHER, 1924, p. 113; OD]. Characters as for subfamily. *Upper Cretaceous (Campanian–Maastrichtian):* USA, Mexico, Jamaica, England, Belgium, Germany, Netherlands, Sweden, India.——FIG. 108,*2a–e.* **A. cretaceus* (BATHER), Campanian; *a–b,* cup with cover plates, *a,* lateral, *b,* distal, England, holotype, BMNH E24767, ×10 (Rasmussen, 1961); *c,* oblique distal view of cup, USNM 179144, ×30 (Peck, 1973); *d,* distal view of cup without cover plates, USNM 179141, ×40; *e,* lateral view of cup with aboral and distal projections, USNM 179140, ×40 (Peck, 1973, as *A. texanus* PECK).

Family SOMPHOCRINIDAE Peck in Rasmussen, 1978

[*nom. transl.* HESS, herein, *ex* Somphocrininae PECK in RASMUSSEN, 1978, p. 923]

Cup composed of 5 radials resting aborally on a hollow central piece, probably representing fused basals, commonly prolonged into a spinelike projection (so-called dorsal spine; has also been called the centrodorsal); only one radial cavity. [SIMMS (1990a) considered the status of many of the somphocrinid taxa described from Upper Triassic strata as uncertain; specimens were commonly isolated by treatment of limestones with acid, leading to corrosion.] *Middle Triassic (Ladinian)–Upper Triassic (Carnian).*

Somphocrinus PECK, 1948, p. 82 [**S. mexicanus*; OD] [=*Vasculicrinus* DONOFRIO & MOSTLER, 1975, p. 18 (type, *V. inflatus*, OD)]. Upper part of aboral projection embayed, articulated to radial circlet along central rim. Radials thin, in contact with each other. Primibrachials wide, adoral processes of axillary primibrachial 2 high and serrated. First secundibrachials low. [*Vasculicrinus* differs from *Somphocrinus* by its inflated aboral projection, and it was considered by SIMMS (1990a) to be probably congeneric with *Somphocrinus*.] *Upper Triassic (Carnian):* Mexico, Austria, Italy, Timor.——FIG. 109,*1a–i.* **S. mexicanus*; *a,* aboral projection, centrodorsal, Mexico, holotype, USNM 104235 (Peck, 1948, pl. 20-15); *b,* aboral view of radial, Mexico, paratype, USNM 104237e (Peck, 1948, pl. 20-34); *c,* adoral view of radial, Mexico, paratype, USNM 104237f (Peck, 1948, pl. 20-35); *d,* aboral view of primibrachial 1, Mexico, paratype, USNM 104237c (Peck, 1948, pl. 20-32); *e,* adoral view of primibrachial 1, Mexico, paratype, USNM 104237b, ×10 (Peck, 1948, pl. 20-31); *f,* facet of

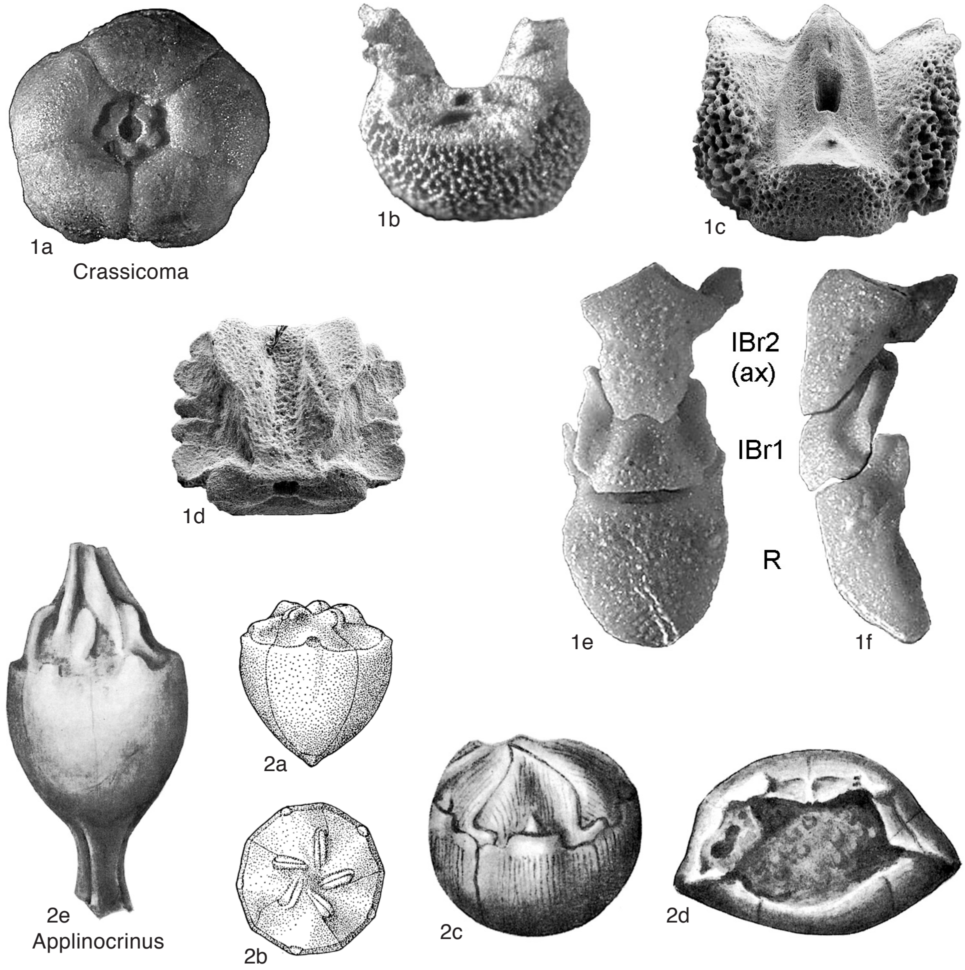


FIG. 108. Saccocomidae (p. 213–214).

centrodorsal to radial circlet, Austria, Kr-To collection, ×35 (Kristan-Tollmann, 1977); *g*, aboral view of radial, Austria, Kr-To collection, ×20 (Kristan-Tollmann & Tollmann, 1983); *h*, aboral view of primibrachial 2, Austria, Kr-To collection, ×35; *i*, lateral view of secundibrachial, Austria, Kr-To collection, ×35 (Kristan-Tollmann, 1977).

Ossicrinus KRISTAN-TOLLMANN, 1970, p. 788 [**O. reticulatus*; OD]. Radials joined to aboral projection along notched ring. Radial articular facet lacking adoral ridge and groove; muscle fossae small and on distal end of radials. Brachials unknown. *Middle Triassic (Ladinian):* Italy, southern Alps.——FIG. 109,*2a–b*. **O. reticulatus*; cup with aboral projection, tip broken, *a,* lateral, *b,* distal, Italy, holotype, Kr-To collection, ×40 (Kristan-Tollmann, 1970).

Osteocrinus KRISTAN-TOLLMANN, 1970, p. 784 [**Rhabdotites rectus* FRIZZELL & EXLINE, 1956, p. 66; OD] [=*Poculicrinus* MOSTLER, 1972, p. 720 (type, *P. glaber,* OD)]. Aboral projection of variable length, articulated to radial circlet along broad ring. Radials compact; articular facets strongly bent at transverse ridge, with large aboral ligament fossa directed outward and muscle fossae encroaching adorally (on inner side). Interarticular ligament fossae and muscle fossae divided centrally by narrow ridge sloping toward interior of cup and carrying a fairly deep furrow. Brachials elongate and thin, with swollen ends; terminal brachials (so-called palmalia) palmate. [According to KRISTAN-TOLLMANN (1977), *Poculicrinus* may be a junior synonym of either *Osteocrinus* or *Ossicrinus*.] *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* Austria, Italy, Romania, Turkey, Afghanistan, China, Nepal, Timor.——FIG. 109,*3a–f*. **O. rectus* (FRIZZELL & EXLINE); *a,* reconstruction of cup with aboral projection, Ladinian, ×20 (Kristan-Tollmann, 1977); *b*, adoral view of primibrachial

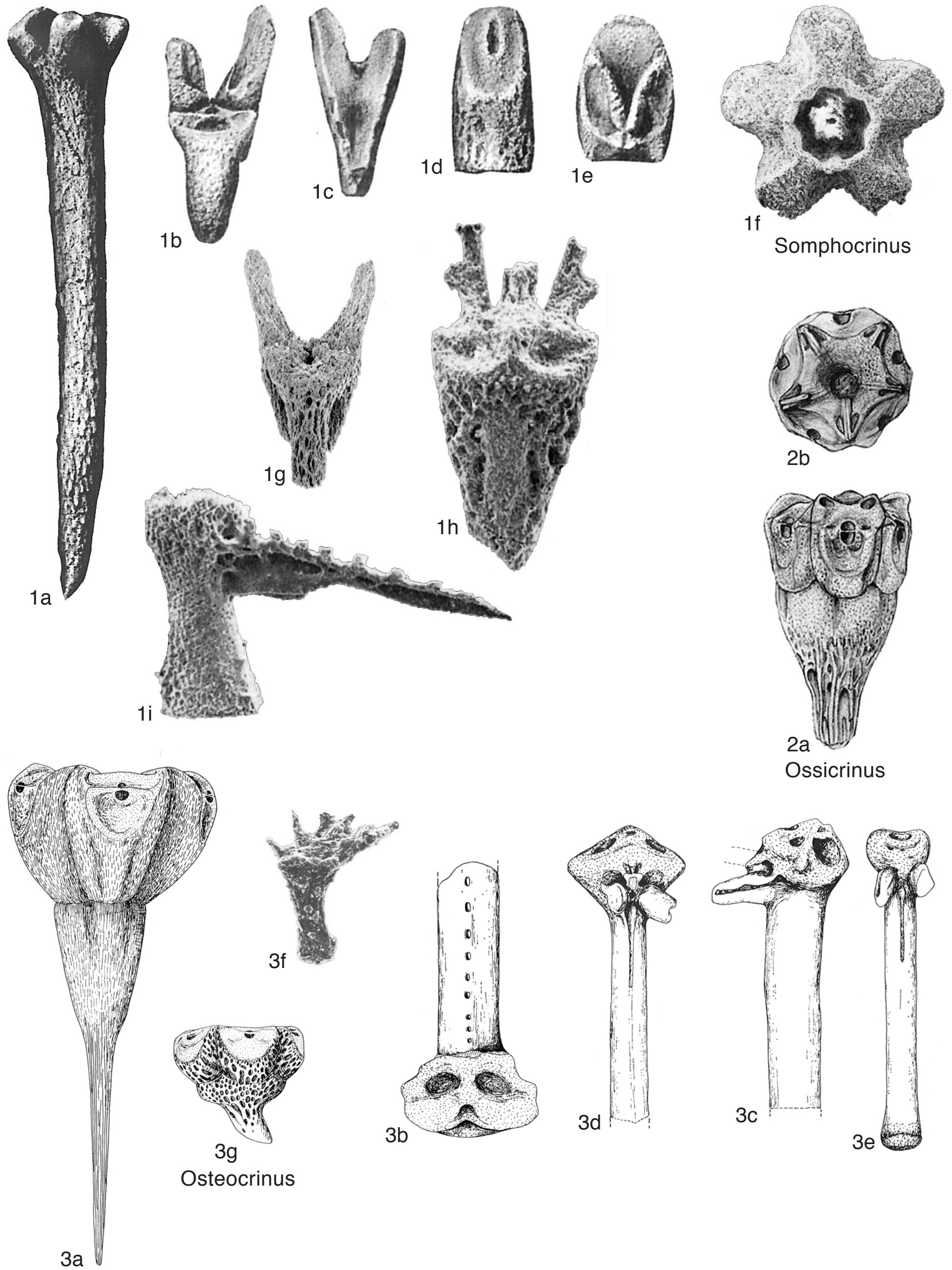


FIG. 109. Somphocrinidae (p. 214–216).

1, partly broken, Ladinian, Italy, Kr-To collection, ×40; *c–d*, primibrachial 2, broken proximally, *c,* lateral, *d,* adoral, Ladinian, Italy, Kr-To collection, ×50; *e*, adoral view of secundibrachial, Ladinian, Italy, Kr-To collection, ×50 (Kristan-Tollmann, 1970); *f*, terminal brachial (so-called palmal), Anisian, China, ×60 (Kristan-Tollmann & Tollmann, 1983).——FIG. 109,*3g. O. rimosus* KRISTAN-TOLLMANN; reconstruction of cup with centrodorsal, ×20 (Kristan-Tollmann, 1977).

UNCERTAIN

HANS HESS

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Order UNCERTAIN

Family CYCLOCRINIDAE Sieverts-Doreck, 1953

[Cyclocrinidae SIEVERTS-DORECK in UBAGHS, 1953, p. 764]

Crown unknown. Pluricolumnals exceptional. Columnals cylindrical, mostly large and low, latera may be weakly convex; presence of axillary columnals or columnals with additional facets indicate branching, lateral sockets for small side branch also occur. Lumen very narrow. Facets with numerous tubercles that may be uniformly distributed or arranged in groups, rarely ringlets, vermiculi, or a smooth surface. There may be a fine marginal crenulation. Small columnals may have a few, mostly paired, radial crenulae. Loose stereom near articular facets and around lumen. Attachment by disk with one to multiple concave column facets. [*Cyclocrinus* has been classified in the Millericrinida, family Apiocrinidae by BIESE (1935–1937), or as a separate family, Cyclocrinidae, in the Cyrtocrinida by SIEVERTS-DORECK (in UBAGHS, 1953) and HESS (1975). RADWAŃSKA and RADWAŃSKI (2003) interpreted the columnals as elements of radicles or radicular cirrals and, thus, placed the form in the order Bourgueticrinida. HESS (2008, p. 475) saw affinities with *Amaltheocrinus* but left assignment to the order Millericrinida open, pending discovery of cup plates.] *Middle Jurassic (Bajocian)–Lower Cretaceous (Albian).*

Cyclocrinus D'ORBIGNY, 1850 in 1850–1852, p. 291 [**Bourgueticrinus rugosus* D'ORBIGNY, 1841 in 1840–1841, p. 96; SD DE LORIOL, 1886 in 1882–1889, p. 2] [=*Acrochordocrinus* TRAUTSCHOLD, 1859, p. 112 (type, *A. insignis*, M)]. Characters as for family. *Middle Jurassic (Bajocian)–Lower Cretaceous (Albian):* France, Germany, Poland, Russia, Switzerland, *Bajocian–Oxfordian;* England, *Albian.*——FIG. 110,*1a–k*. **C. rugosus* (D'ORBIGNY); *a,* attachment disk with three column facets, Callovian, Switzerland, NMB M10482, ×3; *b–c*, small high columnal, *b,* lateral, *c,* facet, Callovian, Switzerland, NMB M10483, ×6 (Hess, 2008); *d–f*, columnal, *d,* lateral, *e,* facet, *f,* part of facet enlarged, Bajocian, France, syntype, ×1; *g–h*, columnal with lateral socket, *g,* lateral, *h,* facet, Bajocian, France, syntype, ×1; *i–k*, axillary columnal, *i, k,* lateral, *j,* 2 facets, Callovian, France, ×1 (de Loriol, 1886 in 1882–1889).

Family LANTERNOCRINIDAE Kristan-Tollmann, 1990

[Lanternocrinidae KRISTAN-TOLLMANN, 1990, p. 87]

Microcrinoids with reduced arms or armless. Cup with small basals and narrow, high, keeled radials. Radial articular facet small, deeply sunken between interradial processes. First primibrachials may be tightly joined by corrugated margins. *Upper Triassic (Norian–Rhaetian).*

Lanternocrinus KRISTAN-TOLLMANN, 1988b, p. 135 [**L. lanterna lanterna*; OD; a holotype for the species was designated only in KRISTAN-TOLLMANN, 1990, p. 56]. Microcrinoids with cup of minute basals and triangular keeled radials with short interradial processes, arms reduced to shovel-shaped, keeled primibrachials with corrugated margins, all elements tightly fitting when closed. Total height of cup 3 to 6 mm. Column unknown but probably short and thin; attachment unknown. *Upper Triassic (Norian–Rhaetian):* Tethys realm (Austria, Timor).——FIG. 110,*2a–d*. **L. lanterna*, Austria; *a–b,* juvenile crown of cup and primibrachials, *a,* lateral, *b,* proximal, Rhaetian, holotype, Kr-To sample R330, ×20; *c*, aboral view of radial, Norian, Kr-To sample R26, ×15; *d*, adoral view of primibrachial, Rhaetian, Kr-To sample R330, ×20 (Kristan-Tollmann, 1990).

Nasutocrinus KRISTAN-TOLLMANN, 1990, p. 60 [**N. dentatus*; OD]. Microcrinoids with reduced arms. Cup composed of basals and radials. Radial articular facet in deep notch, high interradial extensions with grooves and ridges for articulation of primibrachial 1; primibrachial 2 axillary, trapezoidal, laterally closely fitting; arms short, with only few secundibrachials. Secundibrachials thin, with wide ambulacral furrow, articulated by flat synostosis; no pinnules. *Upper Triassic (Norian):* Tethys realm (Turkey, Timor, Germany).——FIG. 110,*3a–h*. **N. dentatus*; *a,* reconstructed cup and base of crown, ×10; *b–d*, radial, *b,* adoral, *c,* lateral, *d,* distal, Turkey, holotype, Kr-To sample V 154, ×15; *e,* aboral view of radial, Turkey, Kr-To collection, ×20; *f,* adoral view of radial, Turkey, Kr-To collection, ×20; *g*, proximal view of primibrachial 1, Turkey, Kr-To collection, ×25; *h*, adoral view of

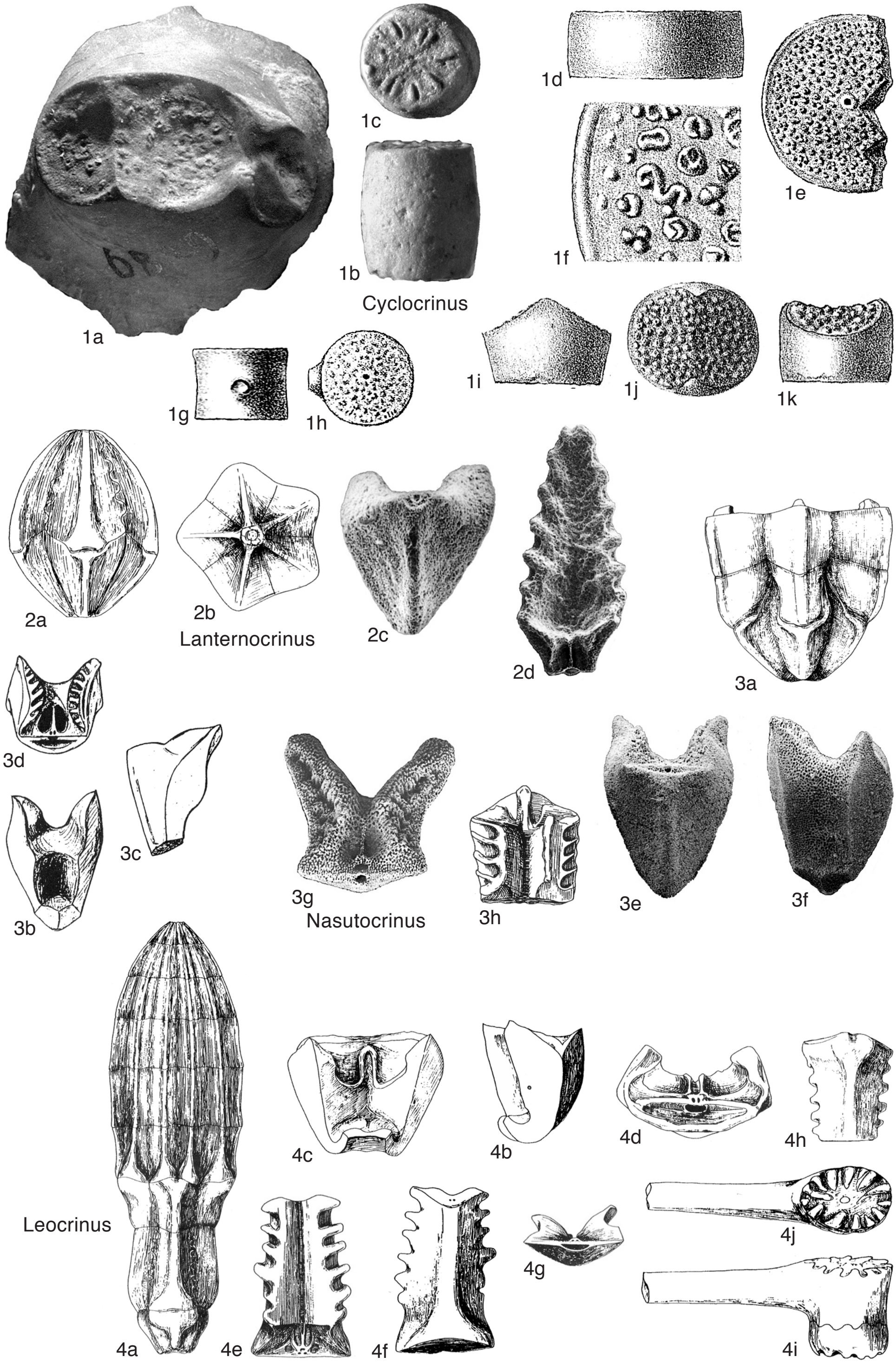

FIG. 110. Cyclocrinidae, Lanternocrinidae, and Leocrinidae (p. 217–219).

primibrachial 2, Timor, Kr-To sample A16, ×10 (Kristan-Tollmann, 1990).

Family LEOCRINIDAE
Kristan-Tollmann, 1990

[Leocrinidae KRISTAN-TOLLMANN, 1990, p. 87]

Microcrinoids with cup of 5 basals, possibly infrabasals, and radials. Radials robust, trapezoidal, aborally curved, outer side flat, broad orally, large articular facet not visible from outside. Arms short, branched at axillary primibrachial 2; primibrachials and the 4 to 6 secundibrachials high, rectangular; brachials of the different rays united laterally symplectially (by grooves and ridges); secundibrachials articulated by synostosis, no pinnules. Column probably short and compact. *Upper Triassic (Norian–Rhaetian).*

Leocrinus KRISTAN-TOLLMANN, 1990, p. 64 [**L. krystyni*; OD]. Characters as for family. *Upper Triassic (Norian–Rhaetian):* Tethys realm (Austria, Turkey, Timor).——FIG. 110,*4a–h*. **L. krystyni*, Norian; *a,* reconstruction, ×4; *b–d*, radial, *b,* lateral, *c,* adoral, *d,* distal, Timor, holotype, Kr-To V 156, ×10; *e–g*, primibrachial 1, *e,* adoral, *f,* aboral, *g,* proximal, Turkey, Kr-To Su/2b, ×8; *h*, aboral view of primibrachial 2, Turkey, Kr-To Su/2b, ×8 (Kristan-Tollmann, 1990).——FIG. 110,*4i–j*. *L. armatus* KRISTAN-TOLLMANN; 2 columnals, *i,* lateral, *j,* upper facet, Norian, Austria, Kr-To sample S359, ×8 (Kristan-Tollmann, 1990).

Family QINGYANOCRINIDAE
Stiller, 2000

[Qingyanocrinidae STILLER, 2000, p. 34]

Crown unknown. Column long, cylindrical, with numerous cirri; nodals of all parts of column with 1 to 5 circular cirrus sockets; larger cirrus sockets crenulated around lumen. Nodals very numerous, commonly several successive cirrinodals. Columnal articular facets symplectial with radial crenulae; bifurcation of culmina and insertion of additional culmina possible. Lumen circular or lobed; mostly with perilumen, sometimes with areola. Distal holdfast rootlike (radix). *Middle Triassic (Anisian).*

Qingyanocrinus STILLER, 2000, p. 34 [**Cyclocyclicus kueichounensis* DUBATOLOVA & SHAO, 1959, p. 47; M; =*Entrochus rotiformis* KOKEN, 1900, p. 188, 212–214, pl. 10,*16–19, partim* (*non* pl. 10,*20–25*, which is *Bangtoupocrinus kokeni* STILLER, 2000, p. 42)]. Characters as for family. *Middle Triassic (Anisian):* China (Qingyan, Guizhou Province).——FIG. 111,*1a–f.* **Q. kueichounensis* (DUBATOLOVA & SHAO); *a–b,* distal pluricirrinodal, *a,* lateral, *b,* facet, NIGPAS B3B-1.Cr2.F37-1; *c–d*, nodal from mesistele, *c,* lateral, *d,* facet, NIGPAS B3B-1.Cr2.F43-3; *e*, pluricirrinodal, NIGPAS B3B-1.Cr2.Fbt-6; *f,* dististele, NIGPAS B3B-1.Cr2.Fbt-21, ×3 (Stiller, 2000).

Family TULIPACRINIDAE
Kristan-Tollmann, 1980

[Tulipacrinidae KRISTAN-TOLLMANN, 1980, p. 224]

Microcrinoids with compact, biconical cup composed of 5 fused radials and thin ring of fused basals; distally narrowing to blunt cone with narrowing axial canal, no radial cavity. Radial articular facet concave, divided by strong fulcral ridge into somewhat larger proximal part with broad and deep ligament fossa and distal part with single elliptical to triangular muscle fossa. Facet to column synostosial and deeply concave with relatively wide axial canal. Arms reduced to 5 single, high, triangular brachials with adorally encroaching muscle fossa; lateral synostoses indicate formation of a pyramid-like roof over the cup. [Cup shape of this form is unique among articulate crinoids, with its distally narrowing part leaving no room for a radial cavity proper. KRISTAN-TOLLMANN (1980, 1990) assigned low internodals and high nodals with large cirrus sockets to this form; if paired, they are barrel shaped. Such a column with alternating nodals and noncirriferous internodals would support assignment to the Isocrinida (SIMMS, 1990a, p. 73), a classification that is considered doubtful. No articulate order is known where the cup narrows distally with a narrow axial canal in place of a radial cavity, and a single triangular muscle fossa is also quite unique among articulates. The family Tulipacrinidae was proposed for this form by KRISTAN-TOLLMANN (1980, p. 224), who in 1990 established a second species, *Tulipacrinus latus*, from the same lower Carnian Cassian Beds. However, *T. latus* may be conspecific with *T. tulipa*. KLIKUSHIN (1992, p. 64) proposed an order for *Tulipacrinus*,

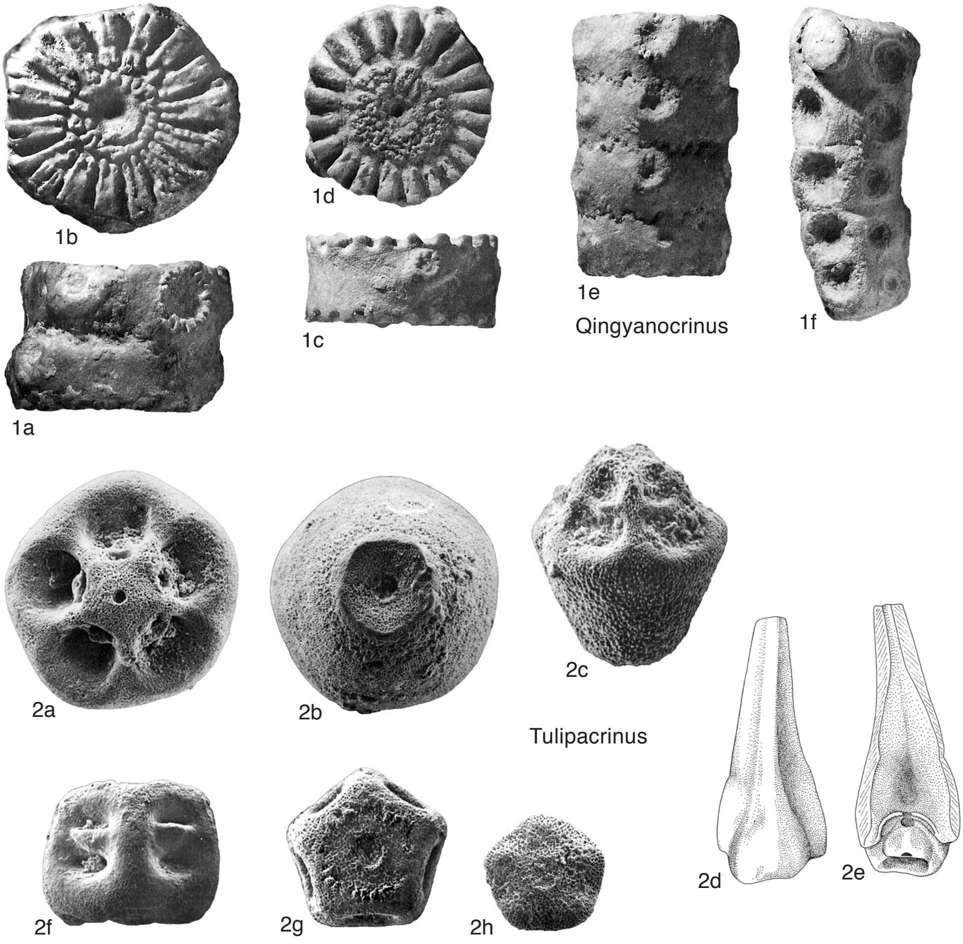

FIG. 111. Qingyanocrinidae and Tulipacrinidae (p. 219–220).

Tulipacrinida, with the following diagnosis (*fide* MIRONOV, personal communication, 2002): "Dwarfish forms with short column composed of cirri-bearing nodals alternating with internodals; cup composed of fused radials and basals; brachial series transformed into long plates with muscular articulations." The small size is suggestive of a paedomorphic form, and establishment of a separate order does not seem justified without further knowledge.] *Upper Triassic (Carnian–Norian).*

Tulipacrinus KRISTAN-TOLLMANN, 1980, p. 225 [**T. tulipa*; M]. Characters as for family. *Upper Triassic (Carnian–Norian):* Italy, Austria.——FIG. 111,*2a–h*. **T. tulipa*, Carnian, Italy, holotype, Kr-To x 21; *a,* distal view of cup; *b*, proximal view of cup, ×20; *c*, lateral view of juvenile cup, ×40; *d–e*, brachial, *d,* aboral, *e,* adoral, ×15; *f,* lateral view of nodal; *g*, proximal facet of nodal; *h*, facet of internodal, ×20 (Kristan-Tollmann, 1980).

Order and Family UNCERTAIN

Bihaticrinus KRISTAN-TOLLMANN, 1990, p. 85 [**B. manipulus*; M]. Microcrinoids with column composed of very long, thin columnals. Columnals round, dumbbell shaped, articular facets elliptical to circular-elongate with strong radial crenulae. Nodals with 5 very small, circular cirrus sockets. [The circular cirrus sockets and multiradiate articular facets exclude assignment to the holocrinids or isocrinids, and assignment to any taxonomic group is not possible without additional material.] *Upper Triassic (Norian):* Austria, Timor.——FIG. 112,*1a–b*. **B. manipulus*; nodal, *a,* lateral, *b,*

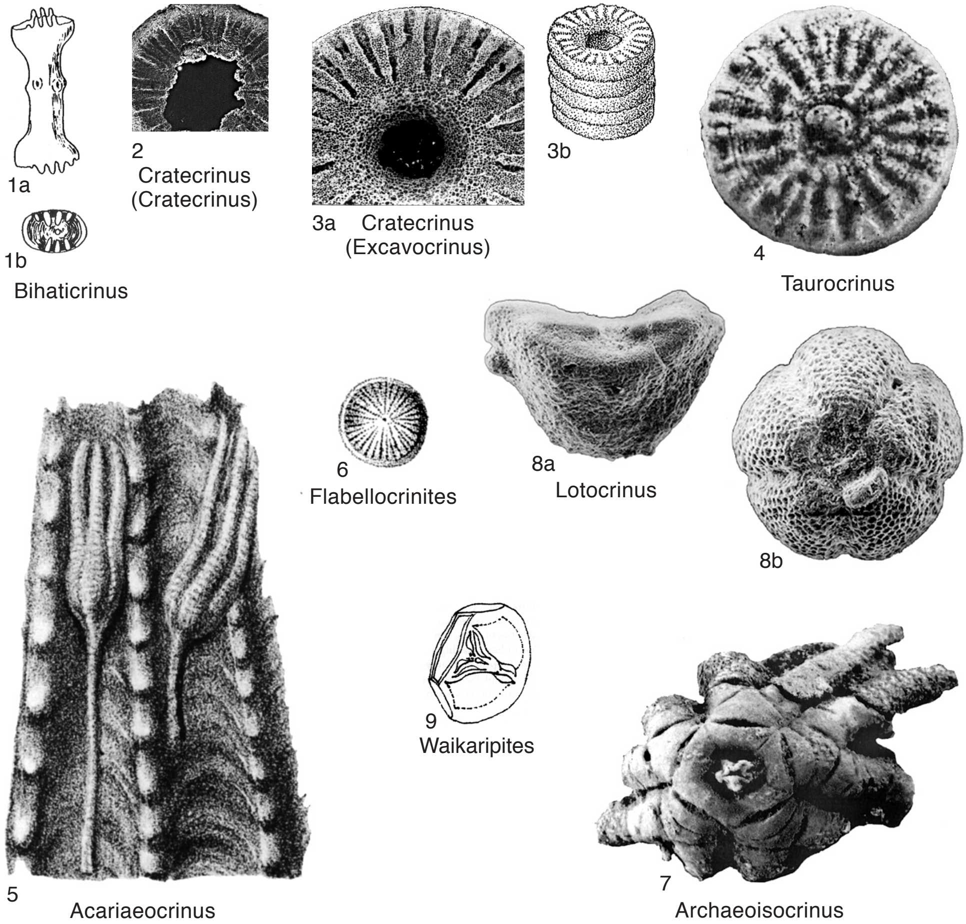

Fig. 112. Uncertain and nomina dubia (p. 220–223).

facet, Timor, holotype, Kr-To sample V 161, ×25 (Kristan-Tollmann, 1980).

Cratecrinus Mironov, herein, p. 225, *nom. nov. pro Craterocrinus* Mironov & Sorokina, 1998b, p. 63, *non* Goldring, 1923, p. 185 (type, *C. ruedemanni* Goldring, 1923, p. 186) [**Craterocrinus geminatus* Mironov & Sorokina, 1998b, p. 63; OD]. Columnals circular, nontuberculate with concave articular facet or with concave areola and flat crenularium. Crenulae 24 to 36, not grouped or with tendency to grouping into crenular units; crenulae long, straight, simple or bifurcated. [The genus was proposed for columnals collected from bottom sediments of seamounts of unknown age and for 2 Lower Cretaceous forms. Its assignment to Hyocrinida is doubtful.] *Lower Cretaceous–Paleogene (Danian), ?Holocene.*

C. (**Cratecrinus**). Characters as for genus, with concave articular facet. Areola absent. Crenulae 24 to 26, reaching lumen, simple or bifurcated. Fossil component of sediment from seamount in the northern Atlantic. Subgenus also contains *Cratecrinus (C.) crimicus* (Mironov & Sorokina), 1998b, p. 64, *Lower Cretaceous:* Crimea.——Fig. 112,*2*. **C. (C.) geminatus* (Mironov & Sorokina); part of columnal facet, subfossil, northern Atlantic, holotype, ZMM C-22, ×5 (Mironov & Sorokina, 1998b).

C. (**Excavocrinus**) Mironov & Sorokina, 1998b, p. 65 [**E. actinodromus*; M]. Characters as for genus, with concave areola and flat crenularium. Crenulae 28 to 36, undivided. *C. (Excavocrinus) actinodromus,* fossil component of sediment from seamount, northern Atlantic. Subgenus also contains *C. (E.) ilimanangei* (Rasmussen), 1972a, p. 28 (as *Calamocrinus*). *Paleogene (Danian):* Greenland.——Fig. 112,*3a.*

**C. (E.) actinodromus*; part of columnal facet, subfossil, northern Atlantic, holotype, ZMM C-23, ×10 (Mironov & Sorokina, 1998b).——Fig. 112,*3b. C. (E.) ilimanangei* (Rasmussen); pluricolumnal, Danian, Greenland, MGUH 12757, ×8 (Rasmussen, 1972a).

Taurocrinus Klikushin, 1984, p. 81 [**T. tauricus*; M]. A genus possibly related to Hyocrinida with flat columnal articular facets. Basal circlet low, fused, with gradual transition to upper part of column. Columnals as much as 5.7 mm in diameter, elliptical or subcircular; sides nontuberculate or 5 or 6 tubercles in small columnals. Lumen circular, proximally wide, distally narrow. Numerous (17 to 22) crenulae with tendency for grouping into crenular units. Crenulae thick, curved or straight, simple or bifurcated, extending from margin almost to lumen. Some crenulae with narrow, longitudinal fissure. Column with attachment disk. *Lower Cretaceous (Albian):* Crimea.——Fig. 112,*4.* **T. tauricus*; facet of columnal, syntype, LGI KK-42-4, ×10 (Klikushin, 1984).

NOMINA DUBIA

Acariaeocrinus Biese, 1935 in 1935–1937, p. 109, *nom. nov. pro Microcrinus* Terquem & Piette, 1865, p. 122, 158, *non* Emmons, 1858, p. 311 [**Microcrinus liasinus* Terquem & Piette, 1865, p. 122, 158; M]. Genus and only species based on 2 specimens of an extremely small crinoid attached to shell of a *Pecten* with a 3 mm high, cylindrical column consisting of 40 to 50 columnals unequal in height. Crown 2 mm high, with 5 atomous arms. *Lower Jurassic (Sinemurian):* France.——Fig. 112,*5.* **A. liasinus* (Terquem & Piette); 2 specimens on shell of *Pecten*, ×9 (Terquem & Piette, 1865).

Carpenterocrinus A. H. Clark, 1908c, p. 319 [**Pentacrinus mollis* Carpenter, 1884a, p. 338; M]. Dubious genus, based on a very irregular and small single crown with a few columnals attached, probably a strongly regenerated specimen of *Endoxocrinus alternicirrus*. The specimen was collected by the Challenger off southern Japan, where many specimens of *Endoxocrinus alternicirrus* are known (Oji, 1989, p. 32).

Flabellocrinites Klipstein, 1845 in 1843–1845, p. 277 [**F. cassianus;* M]. [Based on a badly preserved pluricolumnal of an encrinid, *nomen dubium* according to Hagdorn, 2004a, p. 247.] *Middle Triassic (Ladinian):* Italy.——Fig. 112,*6.* **F. cassianus*; columnal facet, ×1 (Klipstein, 1845 in 1843–1845).

Polycerus Fischer von Waldheim, 1811, p. 28. Proposed to replace name *Pentacrinites* for Isocrinida, including *Polycerus stoloniferus* Fischer (a synonym of *Pentacrinus basaltiformis*, according to Bronn, 1848 in 1848–1849) and the living so-called palmier marin (=*Isis asteria*, type of *Cenocrinus*).

Tauriniocrinus Rovereto, 1939, p. 616 [**Pentacrinus gastaldi* Michelotti, 1847, p. 59; OD]. Genus of Isocrinidae, insufficiently characterized. Crown unknown. Column pentalobate or rounded subpentagonal, rarely circular in section. Columnals commonly alternating in height, proximal columnals with radial pores in the suture. Length of internodes unknown, but as many as 14 internodals or more. Articular facet of columnals similar to *Isocrinus*, crenulae not very long, generally leaving a smooth, radial, marginal area. Nodals higher than internodals, with 5 rather large, elliptical cirrus sockets occupying entire height of nodal and facing outward. Very rarely less than 5 sockets. *Paleogene (Oligocene)–Neogene (Miocene):* Austria, Czech Republic, France, Italy.

Subclass UNCERTAIN

Archaeoisocrinus Webster & Jell, 1999, p. 334 [**A. occiduaustralis*; M]. Cup cryptodicyclic; supposed infrabasals and basals in deep basal cavity, covered by proximal columnals. Radials forming base and cup wall; no anal or anal notch in cup. Radial articular facet wide, gap between radial and primibrachial 1 indicates well-developed aboral ligament fossa. Arms 10, primibrachial 2 axillary. Brachials cuneate uniserial, with small, dual, internal, entoneural canals. Brachial articulations alternating between oblique muscular and cryptosyzygial. First pinnule on secundibrachial 1. Proximal column pentalobate with thin columnals. More distal parts of column and articulation facets unknown. [This form is known only from one small, insufficiently preserved specimen. It was assigned by Webster and Jell (1999) to the Isocrinidae, thus extending the range of the isocrinids back approximately 30 myr. According to these authors, *Archaeoisocrinus* differs from all other isocrinids in that the basals lie within the basal cavity and are not visible in aboral or lateral views. However, basals and infrabasals are not readily visible in the type specimen, the column is unknown, and brachials facets are not displayed, so the presence of cryptosyzygial and syzygial articulations cannot be ascertained. The first Articulata after the end-Permian extinction event were the holocrinids, and these have distinct infrabasals, very high basals, and a column of cirrinodals and internodals. In the isocrinids, which evolved from holocrinids, basals are distinct, although they are much lower than the radials. Thus, *Archaeoisocrinus* cannot be assigned to either holocrinids or isocrinids. Some characters invite comparison with encrinids. Very flat cups with low radials and hidden basals and infrabasals are characteristic of adult encrinids or subadult specimens that were partly compressed (Hagdorn & Schulz, 1996). Pentalobate, isocrinid-like proximal columns are known from encrinids such as *Chelocrinus* (Hagdorn, 1982), a form with uniserial arms in early ontogeny. Paired or unpaired axial canals occur in the same taxa of small Triassic crinoids (HAGDORN, personal communication, 2004). Pending further discoveries, the systematic position of *Archaeoisocrinus* remains doubtful.] *Lower Permian (Artinskian):* western Australia.——FIG. 112,7. **A. occiduaustralis*, aboral view of crown, holotype, QMF 38879, ×3 (Webster & Jell, 1999).

NOMINA NUDA

Lotocrinus KRISTAN-TOLLMANN in TOLLMANN, 1976, p. 280, fig. 165 [**L. reticulatus*; M]. Cup perhaps belonging to cyrtocrinids. [This genus was figured without description and designation of type.] *Upper Triassic (upper Norian–Rhaetian):* Austria.——FIG. 112,*8a–b*. **L. reticulatus*, Rhaetian; *a,* aboral view of radial; *b*, proximal view of basal circlet with infrabasal, ×40 (Tollmann, 1976).

Picteticrinus ÉTALLON, 1857, p. 282 [**P. parasiticus*; M]. A *nomen nudum*, *non Picteticrinus* DE LORIOL in DE LORIOL & PELLAT, 1875, p. 298, which is a junior homonym.

Waikaripites EAGLE, 2005, p. 35 [**W. tekumi*; M]. Two articular facets for arms on each radial. [Genus and species based on single radials, holotype not designated in the only figured radial. Figures and description are insufficient for proper recognition.] *Paleogene (Paleocene)*: New Zealand.——FIG. 112,*9*. **W. tekumi*; oblique view of radial, enlarged (Eagle, 2005).

REJECTED NAMES

Alecto LEACH, 1815, p. 61 [**A. horrida*; SD A. H. CLARK, 1908d, p. 449]. According to CLARK (1908d), genus name, previously used for several extant and fossil comatulids, was based on *A. horrida*, which he considered unidentifiable. This view was accepted by RASMUSSEN (1978, p. 927). Name was subsequently introduced as a junior homonym by LAMOUROUX, 1821, for a bryozoan.

Asteriatites VON SCHLOTHEIM, 1813, p. 68, 99, 109. Name unavailable (*Code*, 1999, Art. 20), introduced by VON SCHLOTHEIM in the combination *A. pennatus* (=*Pterocoma pennata*), *A. filiformis* (=*Saccocoma filiformis*), *A. rosaceus* (=*Saccocoma filiformis*), *A. eremita* (*nom. nud*., =*Asteriacites ophiurus* VON SCHLOTHEIM, 1820, p. 325, an indeterminable ophiuroid), *A. spinosus* (*nom. nud.*), *A. pentagonatus* (*nom. nud*.), and probably as a misprint *Osteratites siderolites* (*pro* MONTFORT, 1808, p. 150, =*Siderolites calcitrapoides*). LOEBLICH and TAPPAN (1964, in *Treatise*, Part C, p. 796) incorrectly claimed *Asteriacites ophiurus* VON SCHLOTHEIM, 1820, to be the type species by subsequent monotypy. SPENCER and WRIGHT (1966 in *Treatise*, Part U, p. 103) considered *Asteriatites* (=*Asteriacites*) to be a dubious synonym of *Saccocoma*.

Astropodium LHWYD, 1699, p. 19 [=*Astropoda* DE BLAINVILLE, 1830, p. 239, *nom. null.*]. Pre-Linnean name used by LHWYD for various crinoid columnals, also recorded in BERTRAND, 1763 (publication rejected by ICZN, 1999, for nomenclatorial purposes), in WALCH, 1769 in 1768–1773, and in URE, 1793, but not as a proper genus name. DEFRANCE (1819, p. 467–468), adopted this name from German authors (presumably WALCH, 1769 in 1768–1773, p. 72) and used it in the combination "*astropode elegante*" or "*astropodium elegans*" for a species of *Apiocrinites*. He was considered by RASMUSSEN (1978, p. 927) to have established a new species, *A. elegans,* in combination with a genus name not available (ICZN, 1999, Art. 17).

Leiocrinus D'ORBIGNY, 1850 in 1850–1852, p. 180, *non* SPRINGER, 1902, p. 95 [**Eugeniacrinites essensis* F. A. ROEMER, 1840 in 1840–1841, p. 26; M]. Based on strongly corroded, cylindrical columnals, commonly with radiating marginal crenulae or a marginal furrow. According to RASMUSSEN (1961, p. 155), genus indeterminable, although probably belongs to the Millericrinida or Cyrtocrinida. Found in Cenomanian conglomerate, but may well be of Jurassic origin from Germany.

Symphytocrinus. Name unavailable, attached by KOENIG to 4 figured but undescribed species in his unpublished second part of *Icones Fossilium Sectiles* (KOENIG, 1825, p. 195). Quoted by AGASSIZ, 1836, as a synonym of *Apiocrinus* and of *Eugeniacrinus*. DE LORIOL (1878 in 1877–1879, p. 62) identified *S. caryophyllum* as a copy of VON SCHLOTHEIM's (1820) figure of *Eugeniacrinites cariophilites*, and BATHER (1900) recorded the name as a synonym of *Eugeniacrinus*.

NAMES NOT BASED ON CRINOIDS

Gasterometra GISLÉN, 1925a, p. 1, 30 [**G. polycirra*; M]. Originally referred to Palaeantedonidae but demonstrated by NIELSEN (1943, p. 61) to be dorsal plate of asteroid *Stauranderaster*.

Nodolanx KRISTAN-TOLLMANN in TOLLMANN, 1976, p. 145, fig. 65 [**N. multinodosa*; M] [*Nomen nudum*, figured without description and designation of type]. According to BIZZARINI (1993, p. 160), a central and a radial shield from the dorsal side of an asteroid. In a later paper, BIZZARINI (2001, p. 189) assigned the remains to the Ophiuroidea and established a second species, *N. gambillarai*. *Upper Triassic (Carnian):* Austria, Italy.

Pogocrinus GAGNEBIN, 1930, p. 219 [**P. raafensis*; M]. Unidentified fossil from Middle Triassic of Switzerland, interpreted as arms of a crinoid. Rejected by RASMUSSEN (1978, p. 927) from echinoderms.

Rhabdocrinus. Misprint by ETHERIDGE, 1882, p. 179, for the echinoid *Rhabdocidaris*.

Trigonocrinus BATHER, 1889a, p. 161 [**T. liratus*; M]. A fossil described as the cup of a crinoid referred to Eugeniacrinitidae from the Upper Jurassic (Oxfordian) of Germany. Interpreted by RASMUSSEN (1978, p. 927) as the tube of a serpulid.

NOMENCLATORIAL NOTE

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ANTHOMETRINA, NEW NAME FOR THE GENUS *ANTHOMETRA* A. H. CLARK, 1915 (CRINOIDEA, COMATULIDINA), PREOCCUPIED BY *ANTHOMETRA* BOISDUVAL, 1840 (ARTHROPODA, LEPIDOPTERA)

During preparation of the manuscript for volume 3 of the revised crinoid *Treatise on Invertebrate Paleontology.* it was realized that the comatulid crinoid genus *Anthometra* A. H. Clark, 1915, p. 135, is preoccupied by a lepidopteran genus published by Boisduval, 1840, p. 231 (see p. 135 herein). According to Article 60 of ICZN rules (1999), we here propose the name *Anthometrina* as replacement name for *Anthometra* A. H. Clark, 1915. The type species for *Anthometrina* is *Antedon adriani* Bell, 1908, p. 4.

ACKNOWLEDGMENTS

We would like to thank Jill Hardesty for her advice on this matter.

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NOMENCLATORIAL NOTE

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CRATECRINUS, NEW NAME FOR THE GENUS *CRATEROCRINUS* MIRONOV & SOROKINA, 1998 (CRINOIDEA, ORDER UNCERTAIN), PREOCCUPIED BY *CRATEROCRINUS* GOLDRING, 1923 (CRINOIDEA, MONOBATHRIDA)

During preparation of the manuscript for volume 3 of the revised crinoid *Treatise on Invertebrate Paleontology,* it was realized that the articulate crinoid genus *Craterocrinus* MIRONOV & SOROKINA (1998, p. 63) is preoccupied by a crinoid genus published by GOLDRING, 1923, p. 185 (see p. 221 herein). According to Article 60 of ICZN rules (1999), the name *Cratecrinus* as replacement name for *Craterocrinus* GOLDRING, 1923, is here proposed (A. MIRONOV, personal communication, 2002). The type species for *Cratecrinus* is *Craterocrinus geminatus* MIRONOV & SOROKINA, 1998, p. 63.

ACKNOWLEDGMENTS

I would like to thank Jill Hardesty for her advice on this matter.

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