

ARTICULATA: INTRODUCTION

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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).

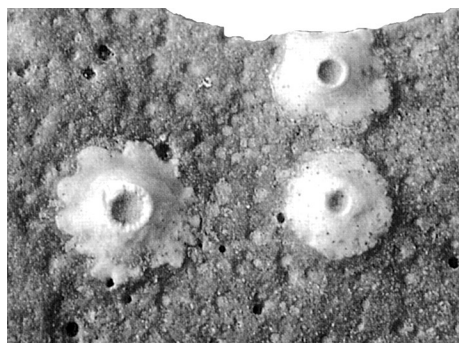
MORPHOLOGY OF ARTICULATE CRINOIDS

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.

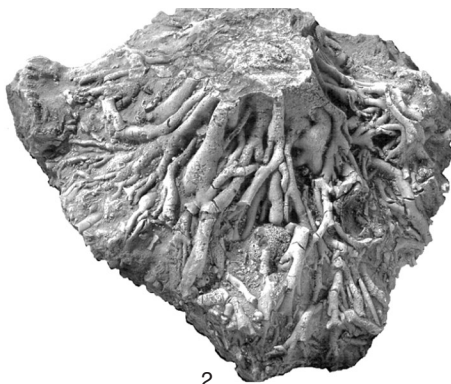
COLUMN AND ATTACHMENT

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 columnals). 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 (cirri-nodals 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 synostiosial 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



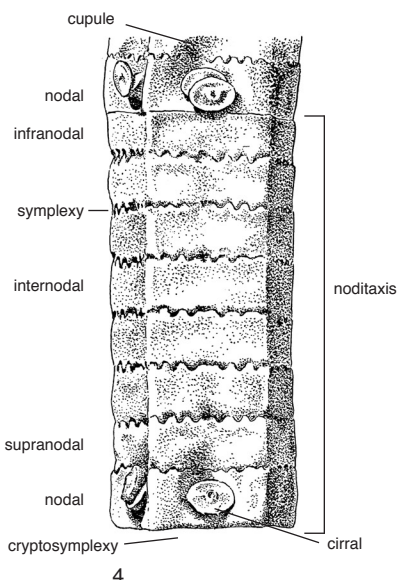
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FIG. 1. 1, *Carnallicrinus carnalli* (BEYRICH); attachment disks on hardground with *Trypanites*, Anisian, Middle Triassic, Germany, MHI 1555/1, $\times 1.3$ (Hagdorn, 1999b); 2, *Liliocrinus munsterianus* (D'ORBIGNY); root previously attached to dead microsolenid coral, Oxfordian, Upper Jurassic, Switzerland, NMB M10615, $\times 0.3$ (Hess, new); 3, *Angulocrinus* sp.; root from marlstone, Oxfordian, Upper Jurassic, Switzerland, NMB M9887, $\times 0.75$ (Hess, 1975); 4, *Chariocrinus wuerttembergicus* (OPPEL); lateral view of column, Bajocian, Middle Jurassic, Switzerland, NMB M9275, $\times 10$ (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. 17g-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. 47b). The mouth, with its radiating ambulacra, is typically central on the disk, and the anal opening is displaced toward the

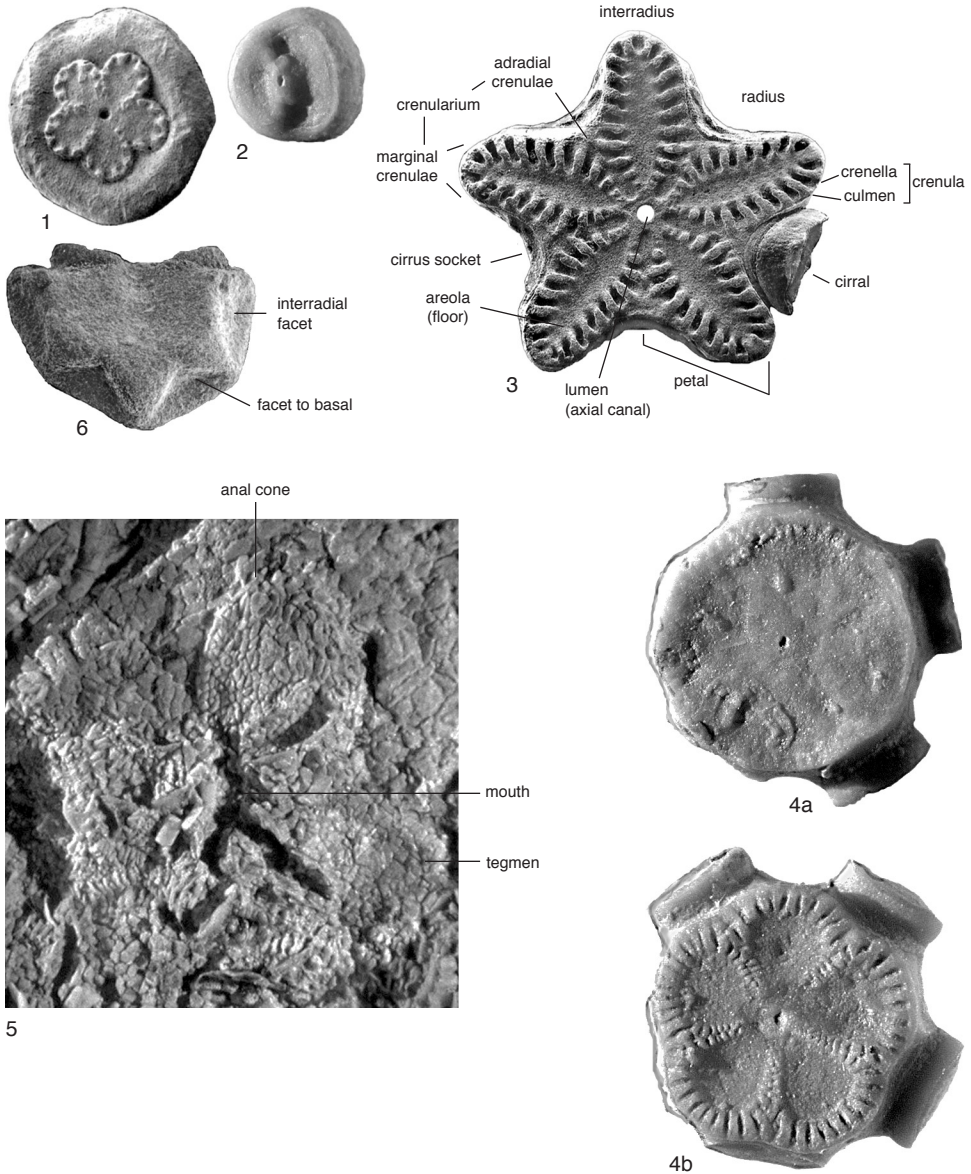


FIG. 2. 1, *Enocrinus liliiformis* (LAMARCK), nudinodal with pentalobate internodal from proximal column, Ladinian, Middle Triassic, SMNS 26628, $\times 4.5$ (Hagdorn, 1983); 2, *Solanocrinites gresslyi* (ÉTALLON); facet of proximal cirral, Oxfordian, Upper Jurassic, France, NMB M10621, $\times 5$ (Hess, new); 3, *Isocrinus desori* (THURMANN); proximal facet of nodal with cirral, Oxfordian, Upper Jurassic, France, NMB M10597, $\times 10$ (Hess, 1975); 4a–b, *Balanocrinus subteres* (GOLDFUSS); nodal with cirrals, a, cryptosymplectial distal facet, b, proximal symplectial facet, Oxfordian, Upper Jurassic, Switzerland, NMB M10613, $\times 5$ (Hess, new); 5, *Pentacrinites dargniewi* (TERQUEM & JOURDY), tegmen with anal cone, Bajocian, Middle Jurassic, Switzerland, NMB M10620, $\times 4$ (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, $\times 25$ (Hagdorn, 1996b).

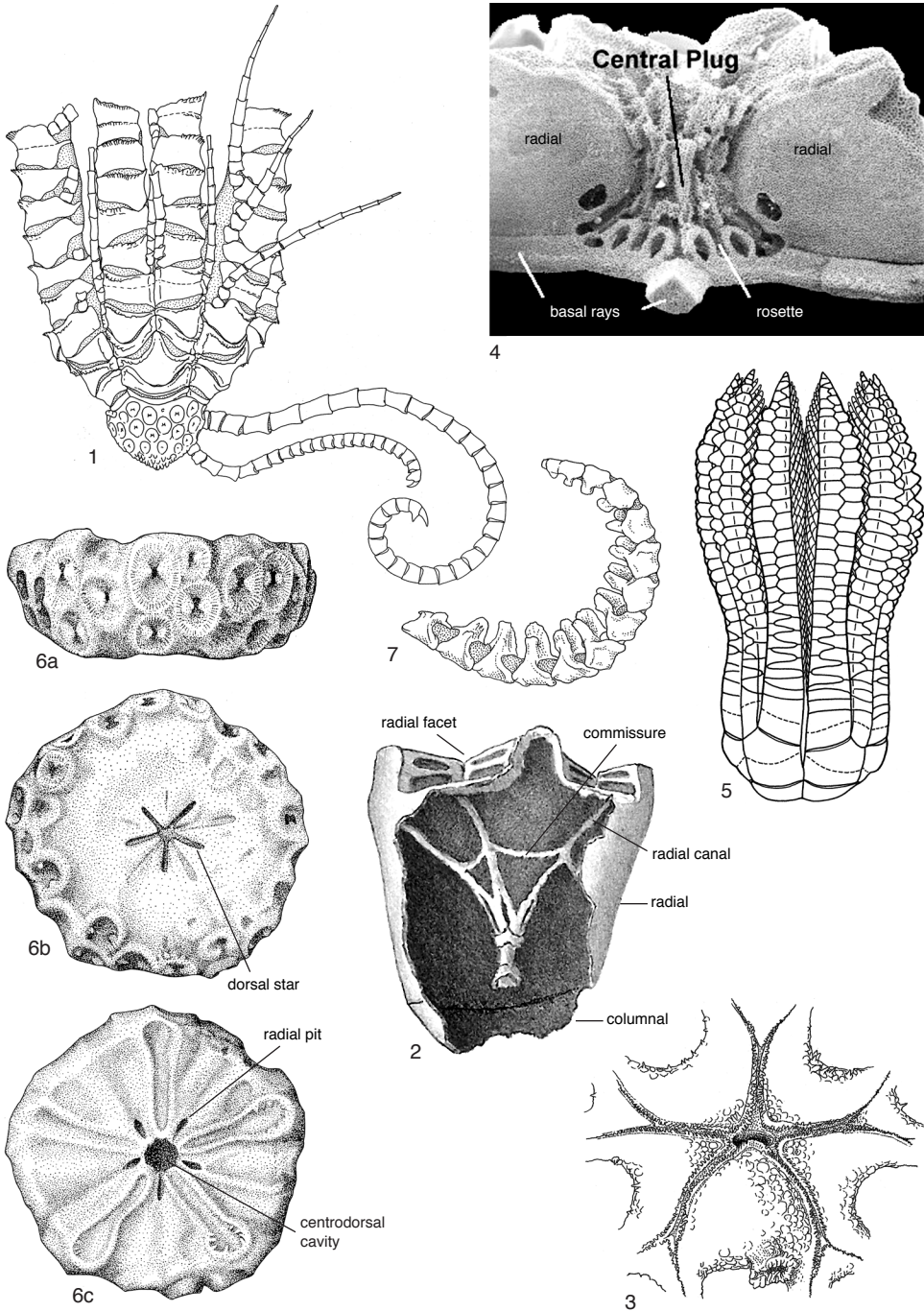


FIG. 3. 1, *Trichometra cubensis* (POURTALES); centrodorsal, small apical and large peripheral cirrus (note opposing spine on penultimate cirral) and bases of three rays with the first three pinnules, syzygy between secundibrachials 3 and 4 and 9–10 indicated by *broken line*, Holocene, USNM, $\times 5$ (Messing & Dearborn, 1990); 2, *Eugeniocrinites cariphilites* (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 interradiar. 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. 40,1*a*), or they may be hidden entirely (see Fig. 41,1*d*). 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, interradiar rods (basal rays) may radiate from the rosette (Fig. 3,4); they are sometimes visible as tubercles at the proximal corners of the radials (interradiar 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 articulata, 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 articulata.

ARM BRANCHING

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

Fig. 3. Continued from facing page.

Germany, $\times 4$ (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 circler (cut away) and basals of a comatulid, showing rosette with basal rays and central plug, enlarged (<http://nova.edu/ocean/messing/crinoids>); 5, *Encrinurus liliiformis* (LAMARCK); crown with biserial brachials, Ladinian, Middle Triassic, $\times 0.8$ (Ausich & others, 1999); 6*a*–*c*, *Remesimetra discoidalalis* (GISLÉN); centrodorsal, *a*, lateral, *b*, aboral, *c*, adoral, Cenomanian, Upper Cretaceous, Czech Republic, BMNH E14897, $\times 4$ (Rasmussen, 1961); 7, oral pinnule comb of *Davidaster rubiginosus* POURTALES, oral pinnule comb with paired teeth, Holocene, NSU, enlarged (Messing, 2001, courtesy of the *Bulletin of the Biological Society of Washington*).

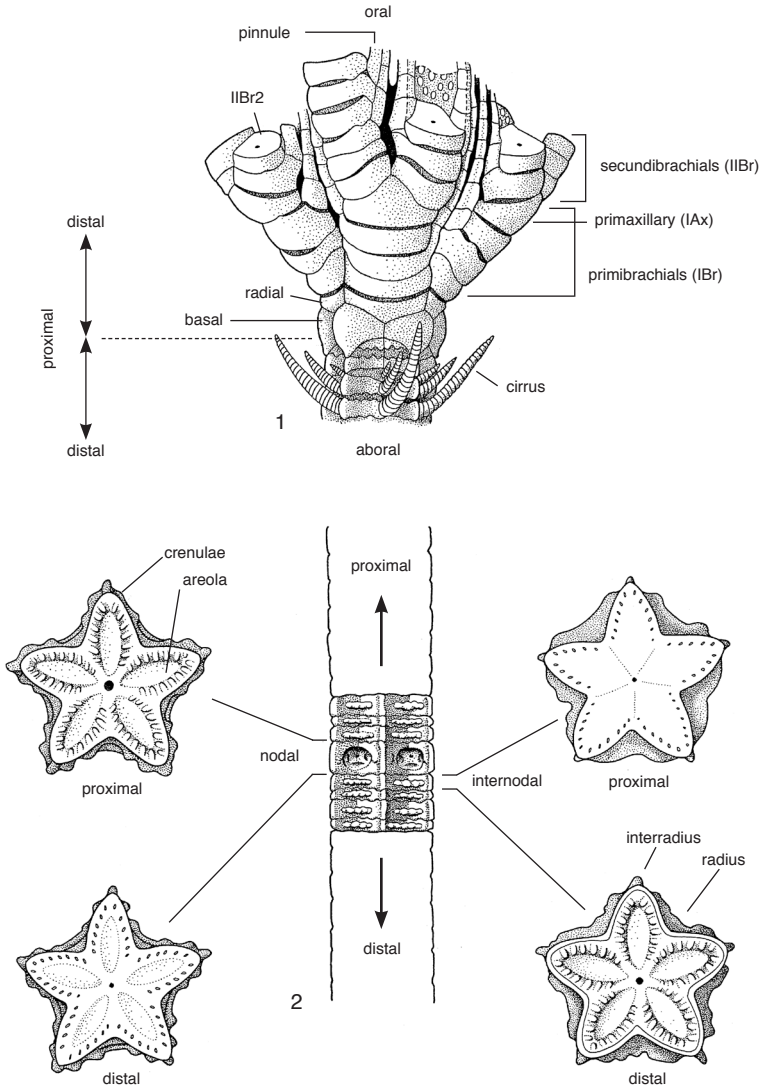


FIG. 4. 1, *Metacrinus angulatus* CARPENTER; proximal column, cup, and base of crown, Holocene, $\times 2$ (Ausich & others, 1999); 2, column with facets of nodal and internodal, Holocene, $\times 2.1$ (Ausich & others, 1999).

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

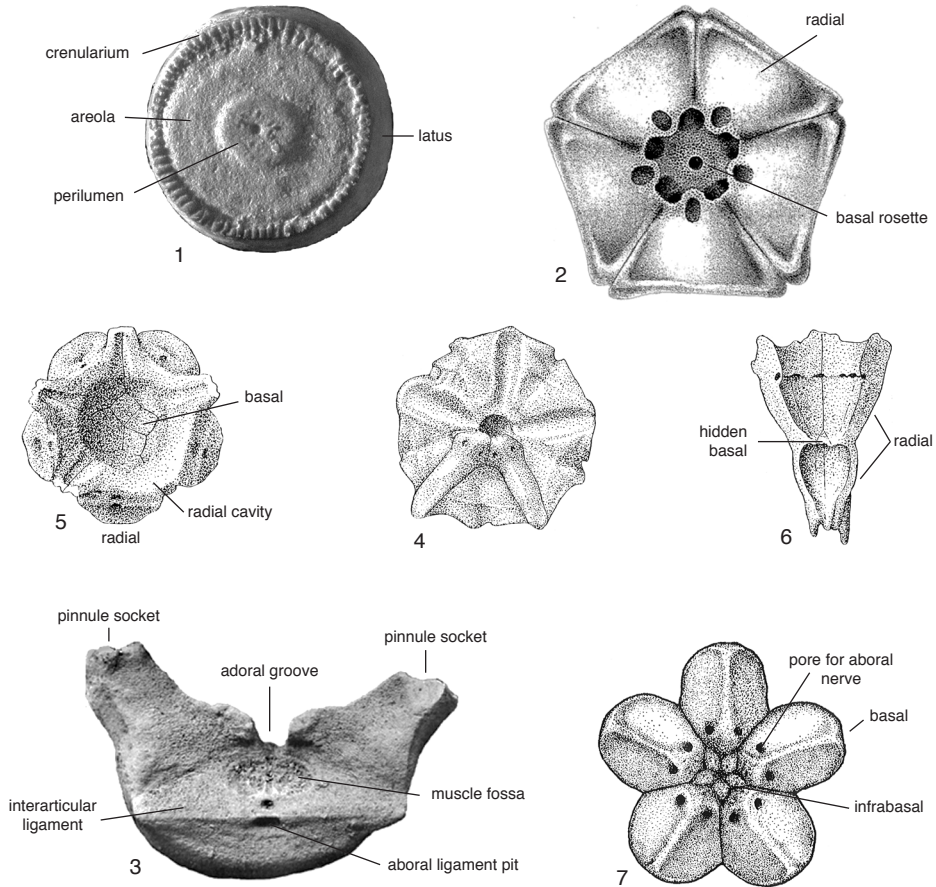


FIG. 5. 1, *Cyclocrinus rugosus* (D'ORBIGNY); columnal facet, Oxfordian, Upper Jurassic, Switzerland, NMB M10484, $\times 4$ (Hess, 2008); 2, *Antedon bifida* (PENNANT); lower (proximal) side of radial cirlet with basal rosette, Holocene, $\times 15$ (Carpenter, 1866); 3, *Cyrtocrinus nutans* (GOLDFUSS); muscular facet of brachial with two pinnule sockets (bipinnulate condition), Oxfordian, Upper Jurassic, Switzerland, NMB M9292, $\times 5$ (Hess, 1975); 4, *Bruennichometra parvicava* (GISLÉN); centrodorsal with basals, Danian, Lower Tertiary, Denmark, holotype, MGUH 1215, $\times 10$ (Rasmussen, 1961); 5–6, *Roveacrinus communis* DOUGLAS, Coniacian, Upper Cretaceous, England; 5, adoral view of cup, BMNH E25712, $\times 15$; 6, broken cup, BMNH E15484, $\times 15$ (Rasmussen, 1961); 7, *Cainocrinus tintinnabulum* (FORBES); distal view of basal cirlet with infrabasals, Danian, Lower Tertiary, England, MGUH 12763, $\times 10$ (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 interrachial 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. 37,2*d*), 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. 37,1*f*; Fig. 78,1*e*). 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 epizygial. Cryptosyzygies resemble syzygies, but the ridges are finer and are typically along the aboral edge (Fig. 6,8*a-c*; and see Fig. 36,2*b*); 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 zygossynostoses by MOORE (1978, p. 242). Zygossynostoses may be difficult to distinguish from cryptosyzygies (Fig. 6,8*a-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, I).
- 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, I).
- adoral groove**. Furrow along adoral surface of free brachials and pinnules (syn., ventral groove, ambulacral groove) (Fig. 5, 3; Fig. 6, I).
- 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, I). 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 articulate, 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 apiocrinoids (*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, I–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).

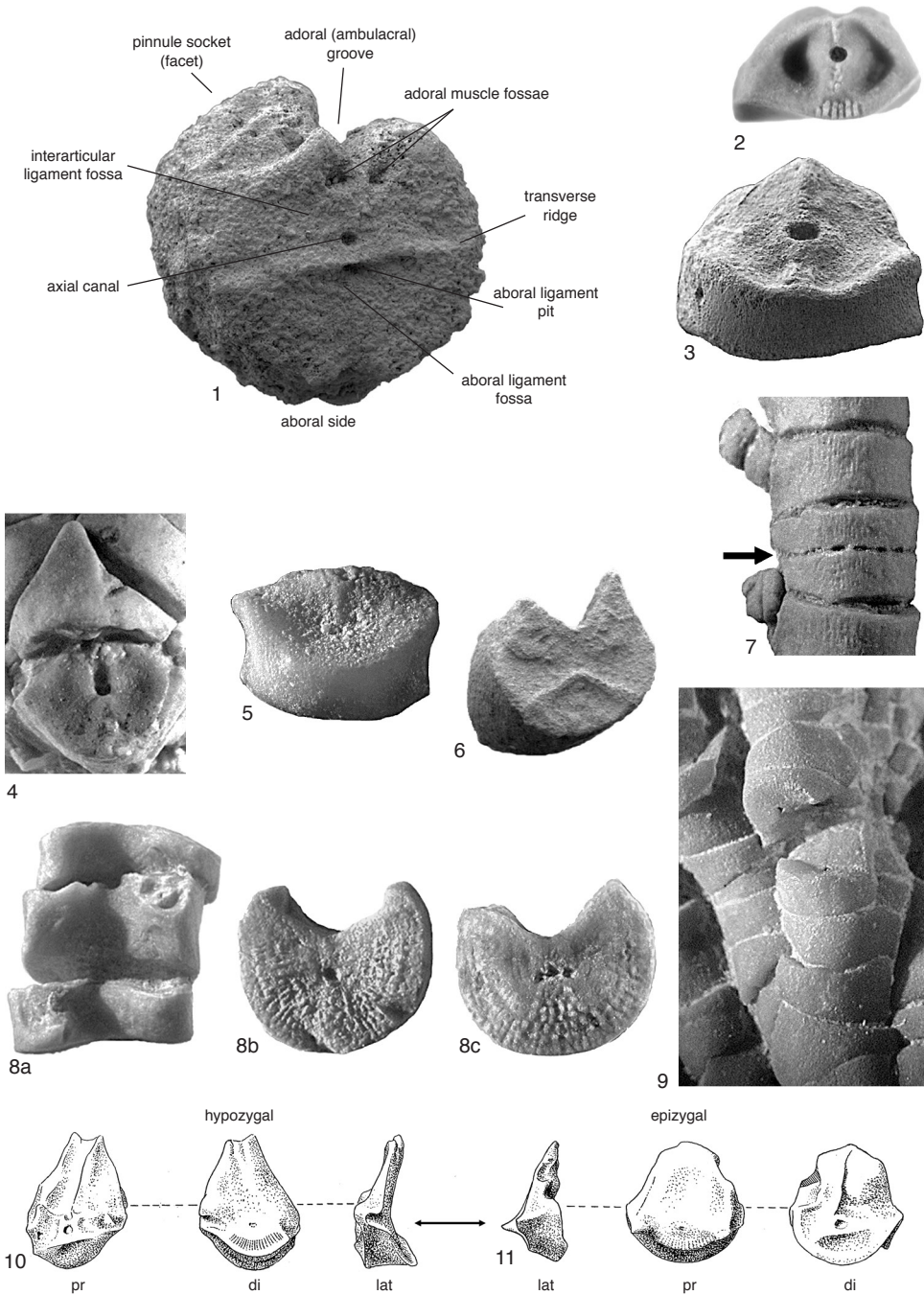


FIG. 6. 1, *Bileicrinus arenosus* HESS; oblique distal view of secundibrachial, Pliensbachian, Lower Jurassic, Switzerland, syntype, NMB M 10109, $\times 30$ (Hess, 2006); 2, *Apiocrinites roissyanus* D'ORBIGNY; synarthrial proximal facet of secundibrachial 2, Oxfordian, Upper Jurassic, France, NMB M10611,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

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

ARMS AND THEIR ARTICULATIONS

cryptosynarthry. Weakly sculptured ligamentary articulation of synarthral 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).

symmophy (Fig. 6,9–11, and see Fig. 24d; Fig. 31i–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. 21g 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 adjacent 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 synarthral articulation (see Fig. 47d) (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 synarthral 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); symmophy 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 symmophy, 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 *Eugeniocrinites*, now included in the Articulata, comprised the small division Coadunata, with "joints of the pelvis ankylosed 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, Eugeniocrinidae, 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 [Ichthyocrinidae], 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 (Plicocrinidae, Hyocrinidae, Saccocomidae)
- Subclass Dicyclica BATHER, 1899
 - Order Dicyclica Inadunata BATHER, 1899
 - Suborder Dendrocrinoidea BATHER, 1899 (Pentacrinidae, Uintacrinidae, Marsupitidae, Bathy-crinidae)
 - Order Flexibilia ZITTEL, 1895
 - Grade Pinnata WACHSMUTH & SPRINGER, 1897 (Apiocrinidae, Bourgueticrinidae, Antedonidae, Atelecrinidae, Actinometridae, Thaumacrinidae, Eugeniocrinidae, 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 Pentacrinoida (=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 Pentacrinoida 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, Eugeniocrinidae, 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 LORIOI, 1882 in 1882–1889 (including Rhizocrinidae, Bathyocrinidae)
 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 Eugeniocrinidae 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, Apiocrinidae, 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, Eugeniocrinidae, Phyllocrinidae)
 Suborder Holopodina ARENDT, 1974 (Eudescrinidae, Hemibrachiocrinidae, Holopodidae)
 Order Bourgueticrinida SIEVERTS-DORECK in UBAGHS, 1953 (Bourgueticrinidae, Bathyocrinidae, Phrynocrinidae, Porphyrocrinidae)
 Order Isocrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952 (Holocrinidae, Isocrinidae, Pentacrinidae, Proisocrinidae)

- Order Comatulida A. H. CLARK, 1908h
 Superfamily Paracomatulacea HESS, 1951 (Paracomatulidae, Atelecrinidae)
 Superfamily Solanocrinitacea JAEKEL, 1918 (Solanocrinitidae, Decameridae, Thiolliericrinidae)
 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, Apometridae)
 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 (ARENDR, 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 Eugeniocrinitacea ZITTEL, 1879, in 1876–1880
 Family Eugeniocrinitidae ZITTEL, 1879, in 1876–1880
 Family Sclerocrinidae JAEKEL, 1918
 Family Phyllocrinidae JAEKEL, 1907
 Family Hemiacrinidae 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 & HUPE, 1862
 Order Isocrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952
 Plesion (Family) Holocrinidae JAEKEL, 1918
 Plesion (Family) Pentacrinidae 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 Comatulida 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 Millericrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952 (*nom. transl.*) (=Millericrinina SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952)
 Infraorder Hyocrinida 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 Cyrtocrinida SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952 (*nom. transl.*) (=Cyrtocrinina SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952)
 Infraorder Holopodinina 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 Thiolliericrinidae A. H. CLARK, 1908b
- Family Bourgueticrinidae DE LORJOL, 1882 in 1882–1889 (including Bathyrcrinidae, 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 Roveacrinita SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952
 - Family Somphocrinidae RASMUSSEN, 1978
 - Family Saccocomidae D'ORBIGNY, 1852 in 1850–1852
 - Family Roveacrinitidae 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 Eugeniocrinitidae 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 Pentacrinitid 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 an 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 Eugeniocrinitoidea [with families Eugeniocrinitidae, 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 bathyrcrinids, 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 pentacrinidids and isocrinids, is maintained, because pentacrinidids are a derived group with characteristics for a specific lifestyle. One could use Pentacrinidida, 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 THIOILLIERICRINIDAE 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 Patručius, 1956
 Order ROVEACRINIDA Sieverts-Doreck, 1953
 Family ROVEACRINIDAE Peck, 1943
 Family AXICRINIDAE Hess, new family
 Family SACCOMIDAE 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

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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. Articulata 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 tegmental 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. Articulata 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, GLUCHOWSKI, & BO CZAROWSKI, 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. Synstosis 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 uniseriate, highly flexible, with muscular and ligamentary (cryptosyzygial or synostosal) articulations, synostosal 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, 1*p*), 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, 1*a*. **H. beyrichi* (PICARD); crown, Anisian, Germany, lectotype, MNHB MB.E 508, ×3 (Neumann, new).—FIG. 7, 1*b–n*. *H. meyeri* HAGDORN & GLUCHOWSKI, 1993, Anisian, Poland; *b–d*, nodal from mesistele, lateral, distal, proximal facets, GIUS-7-59/8*f*, ×5; *e*, facet of distal cylindrical internodal, MHI 1166/1/2, ×8; *f*, facet of distal internodal with long crenulae, GIUS-7-59/6*i*, ×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, Gluchowski, & Boczarowski, 1996).—FIG. 7, 1*o–p*. *Holocrinus* sp.; *o*, schematic view of proximal column and cup with attached arms, lateral view and section; *B*,

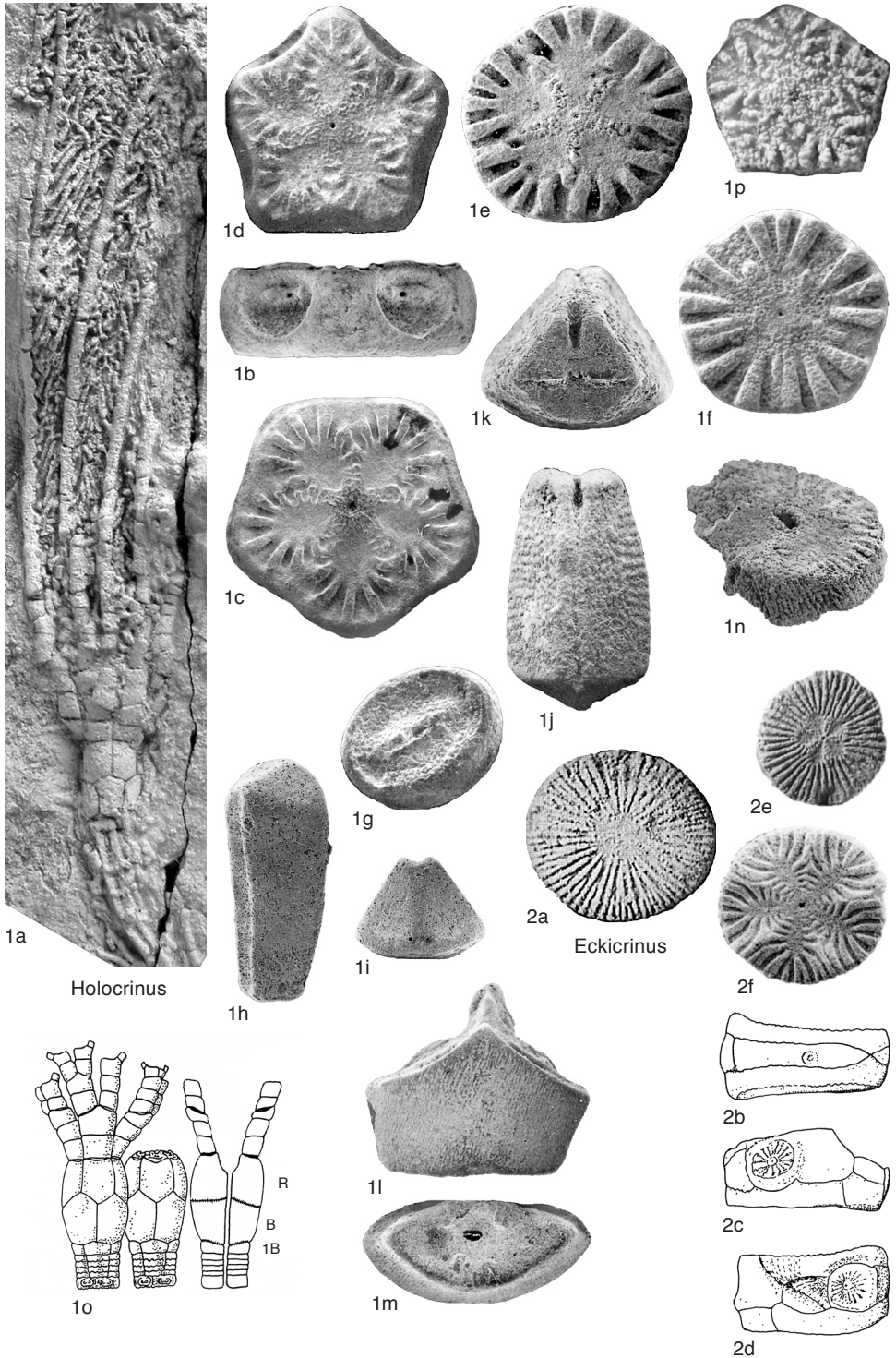


FIG. 7. Holocrinidae (p. 24–26).

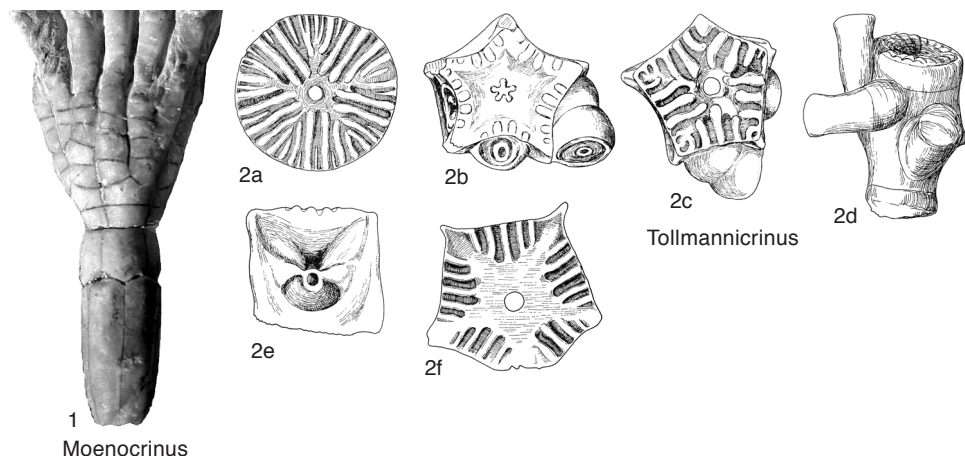


FIG. 8. Holocrinidae (p. 26–27).

basal; *R*, radial; *IB*, primibrachial; approximately $\times 3$ (Hagdorn & Baumiller, 1998); *p*, facet of internodal, Scythian (Smithian), Japan, $\times 10$ (Oji, new). **Eckicrinus** HAGDORN & GLUCHOWSKI, 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 synostosomal 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 *Laevi-*

gatocrinus. 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, $\times 5$ (Hagdorn, Głuchowski, & Boczarowski, 1996); *b–d*, pluricolumnal with 2 cirrus sockets, lateral views, Anisian, Italy, $\times 3.5$ (Hagdorn, Głuchowski, & Boczarowski, 1996; original in Quenstedt, 1876, pl. 107,87); *e*, facet of internodal, Anisian, Italy, $\times 3.5$ (Hagdorn, Głuchowski, & Boczarowski, 1996; original in Quenstedt, 1876, pl. 107,83); *f*, facet of proximal columnal, Anisian, Hungary, MHI 1563/7, $\times 7$ (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, $\times 3$ (Hagdorn, new).

Tollmannicrinus KLIKUSHIN, 1992, p. 73 [**Entrochus saklibelensis* KRISTAN-TOLLMANN, 1975, p. 292; OD]. Crown unknown. Proximal columnal 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. Distal-most 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 crypto-

symplectial 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, 2*a–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

HANS HESS

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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 synostosomal). 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* Encrininiens DUJARDIN & HUPE, 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 synostosomal, 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 interradians. 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.*; =*Jenacrinus* 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. 9a–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. 10a. **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 *Coenothyris 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. 10b–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;

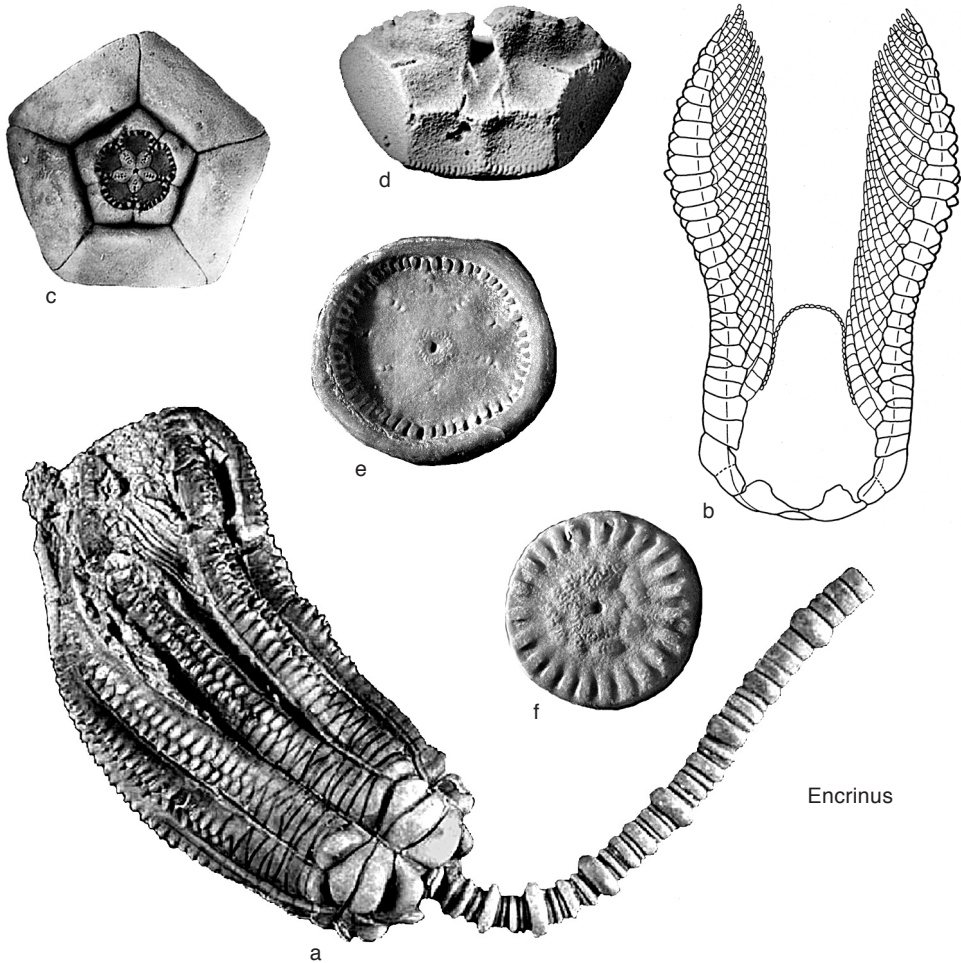


FIG. 9. Encrinidae (p. 28).

M; =*Encrinurus 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 gran-

ules around perilumen. *Middle Triassic (upper Ladinian)–Upper Triassic (lower Carnian)*: Italy, Austria, Germany, Romania.—FIG. 11, 1a–b. **C. varians* (MÜNSTER), type of *E. (C.) tetarakontadactylus* LAUBE, Italy; a, juvenile crown, NHMW 1865/IX/130, $\times 3.6$ (Hagdorn, 2004a); b–d, cup, b, lateral, c, proximal, d, distal, lectotype, BSP 1877 X 1013, $\times 2$ (Hagdorn, 2004a); e, part of biserial crown, NHMW 1865/0050/0259, $\times 3$; f, nodal, NHMW 2006z0264/0008, $\times 3$; g, columnal facet, NHMW 2006z0264/0007, $\times 3$; h, aboral view of cup, NHMW 2006z0261/0002, $\times 2$ (Hagdorn, new).

Chelocrinus VON MEYER, 1837, p. 260, *emend.*, HAGDORN 2004a, p. 247 [*Encrinites schlottheimii* QUENSTEDT, 1835, p. 223; M] [= *Chelocrinities* GEINITZ, 1846, p. 540, *nom. van.*]. Cup low, bowl shaped, pentagonal, flat base; basal pit

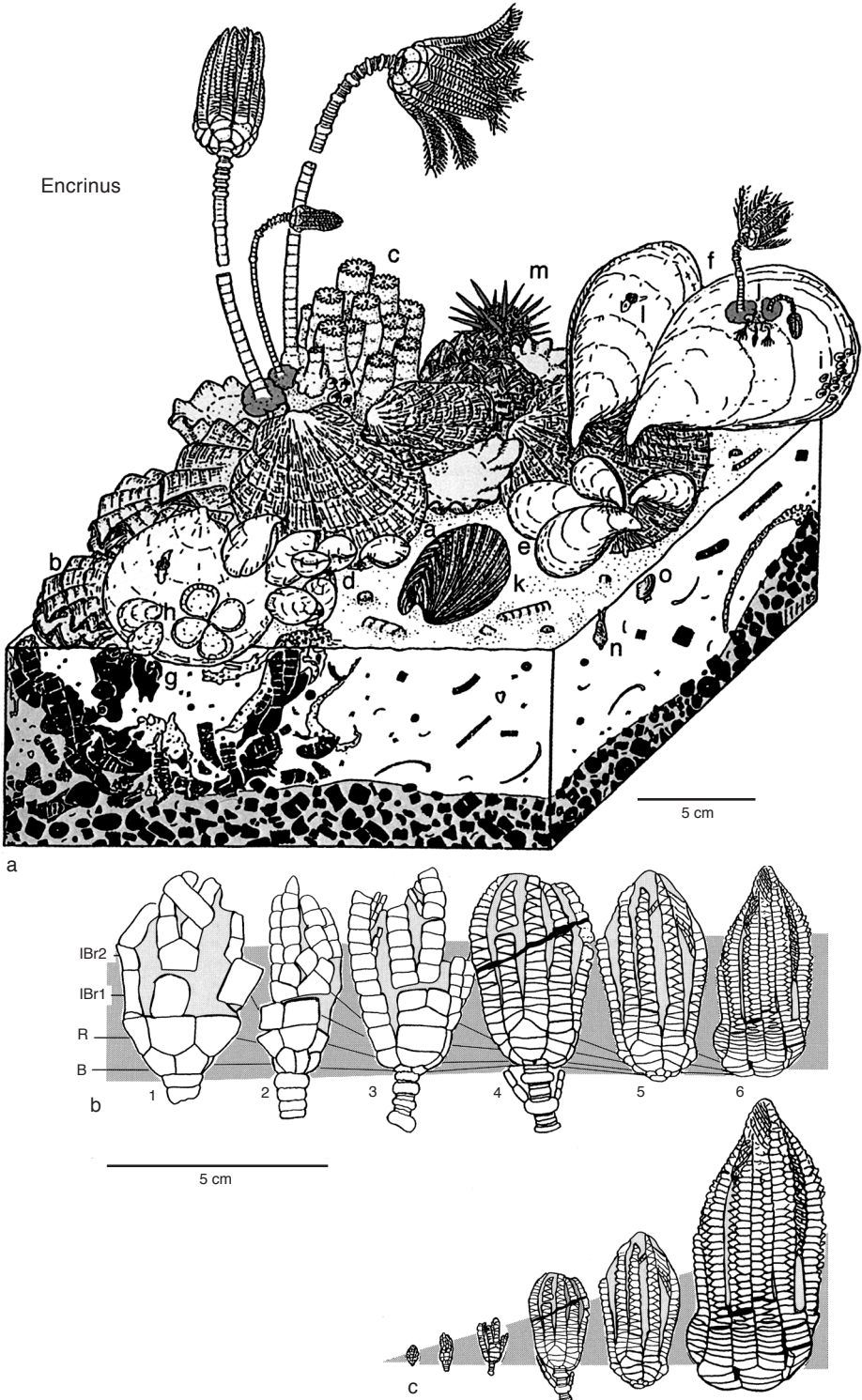
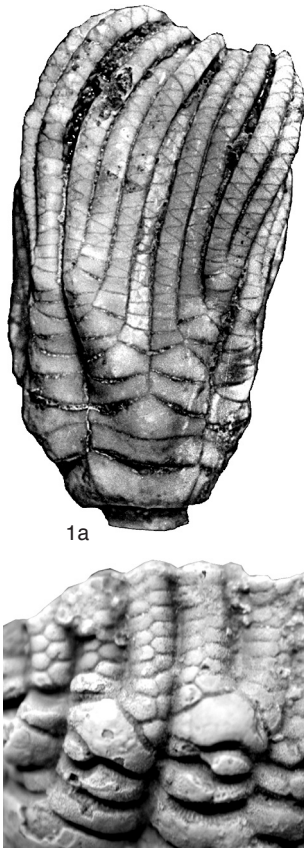
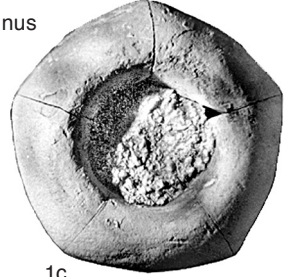
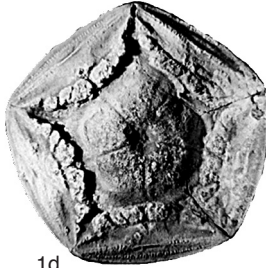


FIG. 10. Encrinidae (p. 28).



Cassianocrinus



Zardinicrinus

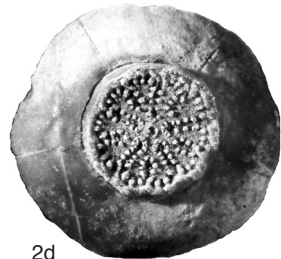
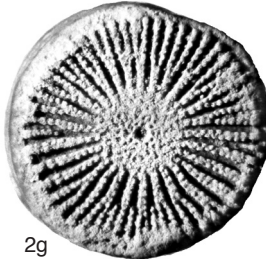
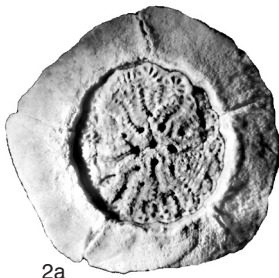
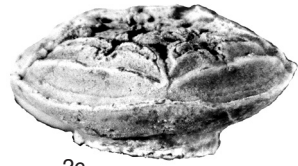
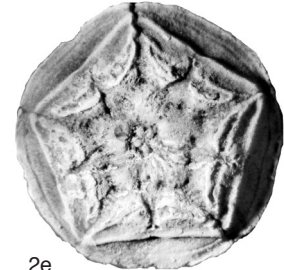


FIG. 11. Encrinidae (p. 28–33).

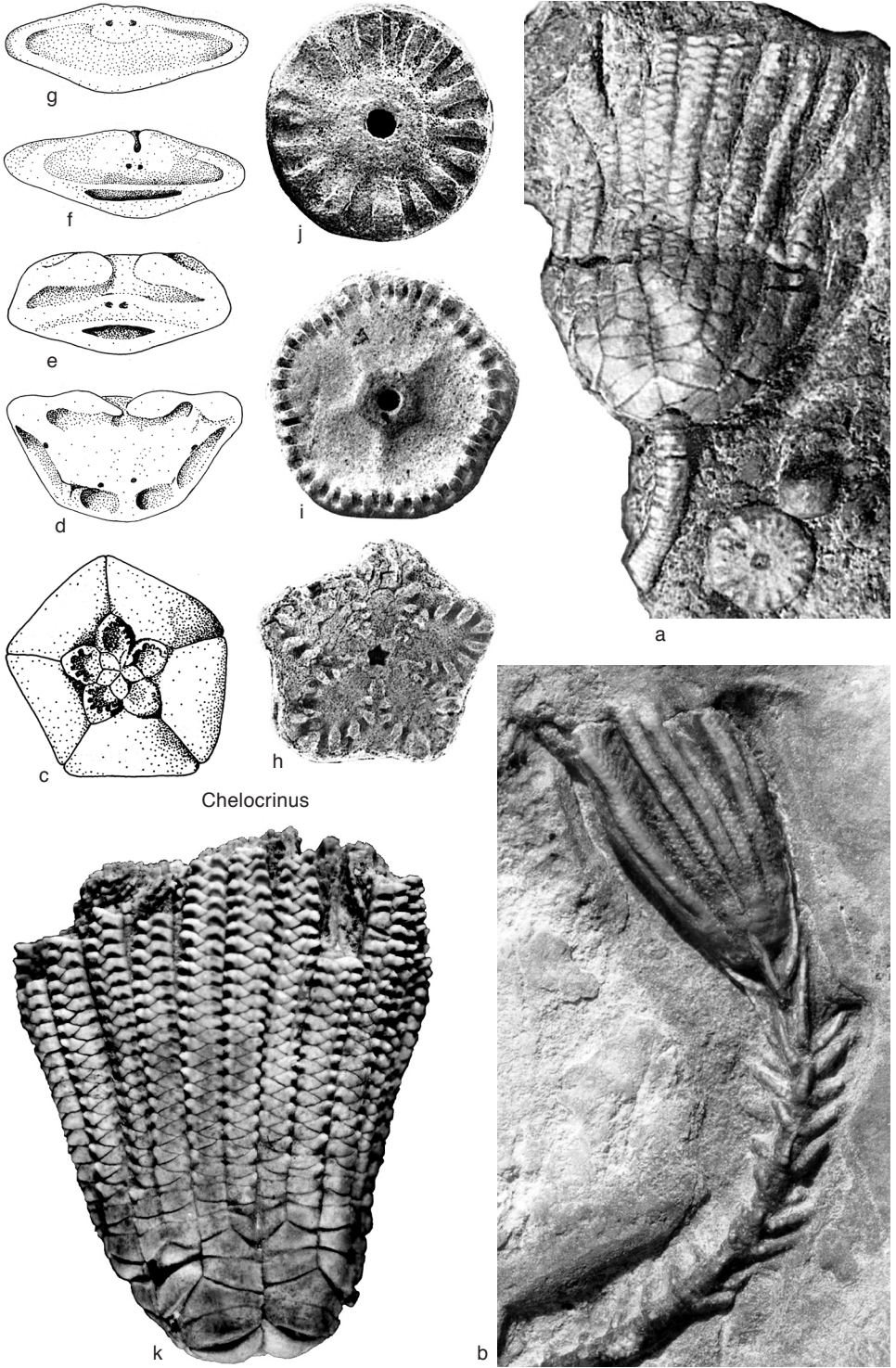


FIG. 12. Encrinidae (p. 29–33).

moderately deep to shallow, subpentagonal to subcircular; basals partly hidden in columnar pit. Primibrachial 2 and secundibrachial 2 axillary. Arms 20, biserial after secundibrachial 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 Schlottheimii* (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 schlottheimi*.] *Middle Triassic (upper Anisian)–Upper Triassic (lower Carnian)*: Germany, Italy, USA (?Nevada).—FIG. 12a–k. **C. schlottheimii* (QUENSTEDT), upper Muschelkalk, Germany; *a*, crown with tertibrachials, holotype, MNHB Quenstedt Kat. P. 1340, E 85, $\times 2$ (Hagdorn, 1982); *b*, crown of subadult specimen with strong cirri on proximal column, Coll. Weissmüller, Kassel, $\times 1$ (Weissmüller, new); *c*, proximal view of cup with infrabasals and basals, NMBi ES/mo1-2/3, $\times 3$ (Hagdorn, 1982); *d–e*, radial, *d*, adoral, interradial facets and facets to basals synostosomal with deep ligamentary pits, *e*, distal, MHI 1124/3, $\times 5$ (Hagdorn, 1982); *f–g*, primibrachial 1, *f*, proximal, *g*, distal, MHI 1124/7, $\times 5$ (Hagdorn, 1982); *h*, facet of isocrinid-like proximal internodal, MHI 1093/11, $\times 10$ (Hagdorn, 1982); *i*, facet of proximal internodal, MHI 1124/20, $\times 10$ (Hagdorn, 1982); *j*, facet of columnal from mesistele, MHI 1124/22, $\times 10$ (Hagdorn, 1982); *k*, crown, MHI 1093/14, $\times 3$ (Hagdorn, 2004b).

Zardinicrinus HAGDORN, 2004a, p. 247 [**Apiocrinites? granulatus* 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 cirlet 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. granulatus* (MÜNSTER); *a*, proximal view of cup, lectotype, BSP 1877 X 1015, $\times 3$ (Hagdorn, new; also figured by Münster, 1841); *b*, facet of proximal columnal, syntype, BSP 1877 X 1023, $\times 5$ (Hagdorn, new); *c–e*, cup with proximal column, *c*, lateral, *d*, proximal, *e*, distal, syntype, BSP 1877 X 1014, $\times 2$ (Hagdorn, new; also figured by Münster, 1841); *f–g*, column, *f*, lateral, $\times 2.5$, *g*, distal facet, syntype, BSP 1877 X 1022, $\times 5$ (Hagdorn, new; also figured by Münster, 1841).

Family AINIGMACRINIDAE Hagdorn, 1988

[Ainigmacriniidae 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, $\times 5$; *b*, reconstruction of juvenile individual protected by closed cirrus cover, $\times 5$; *c*, proximal (upper) side of calyconodal, holotype, BSP AS VII 563, $\times 20$; *d*, proximal side of calyconodal with infrabasal and basal cirlets, SMNS 24846, $\times 20$; *e*, lateral view of calyconodal with cup and proximal columnal, BMNH E5299/1, $\times 13$; *f*, oblique distal view of calyconodal with cup, MCA 1001, $\times 10$ (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

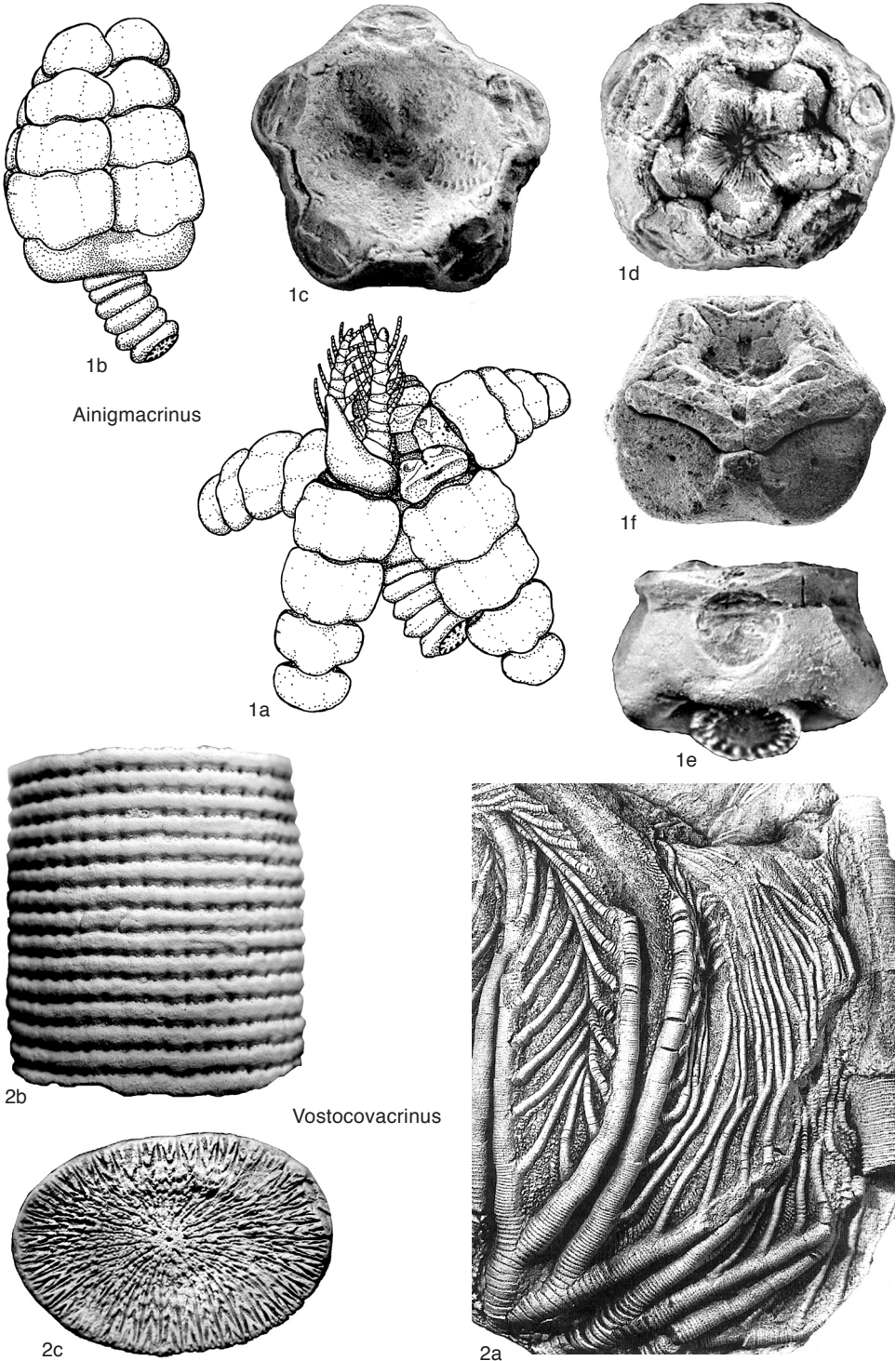


FIG. 13. Ainigmacrinidae and Traumatocrinidae (p. 33–41).

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 synostosomal with deep ligamentary pits, MHI 1283/13, $\times 25$ (Hagdorn, 1996b); *b*, adoral view of basal, interbasal facets, and facets to radials synostosomal with deep ligamentary pits, MHI 1283/15, $\times 25$ (Hagdorn, 1996b); *c*, facet of proximal columnal, MHI 1283/22, $\times 17$ (Hagdorn, 1996b).—FIG. 14*d–g*. *D. kunischi* WACHSMUTH & SPRINGER, Anisian; *d*, slab with 2 crowns, Germany, MHI 1284/1, $\times 1.6$ (Hagdorn, 1999a); *e*, attachment disk with distal column, Poland, MHI 1290, $\times 1.5$ (Hagdorn, 1996b); *f*, facet of columnal from proxistele, Poland, NMB M10604, $\times 5$; *g*, columnal facet, Poland, NMB M10605, $\times 5$ (Hess, new).—FIG. 14*h–i*. *D. grundeyi* LANGENHAN, Anisian, Poland; *h*, cup with proximal column, MHI 1287/1, $\times 6$; *i*, base of crown, MHI 1287/10, $\times 4$ (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, $\times 0.5$ (Hellmund & others, 2006); *b*, oblique proximal view of primibrachial 1, Poland, GIUS-7-59/47, $\times 7$; *c*, proximal view of primibrachial 2, Poland, GIUS-7-59/51, $\times 6$ (Hagdorn, Głuchowski, & Boczarowski, 1996); *d–e*, cup, *d*, aboral with columnal, *e*, lateral, Germany, HGD 1, $\times 3$ (Hagdorn, 1982).—FIG. 16. **C. carnalli* (BEYRICH); aboral view of splayed crown, Germany, HGD, $\times 1.2$ (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 interradians 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,



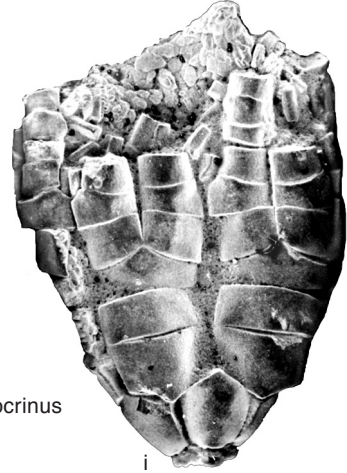
d



e

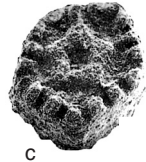


h



i

Dadocrinus



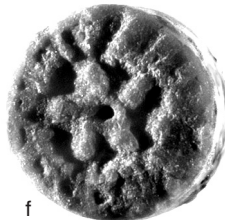
c



a



b

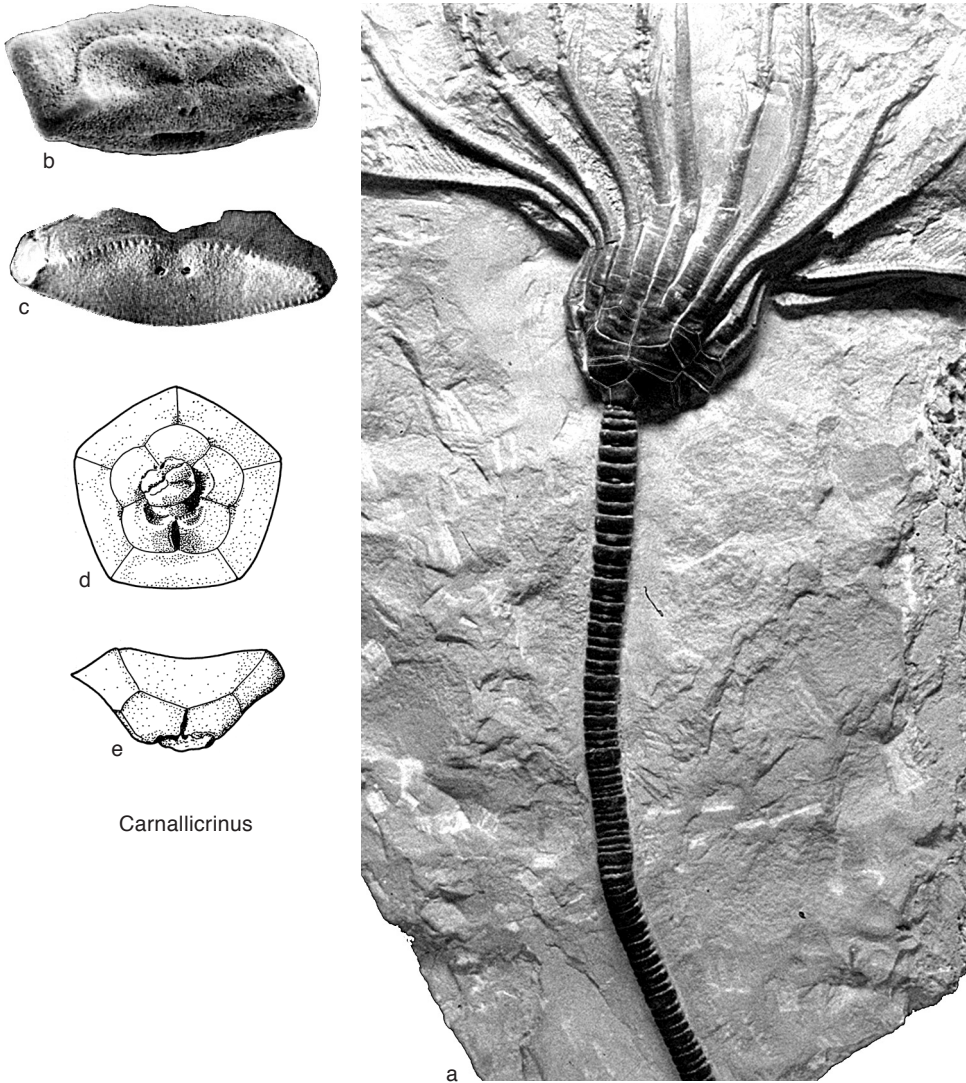


f



g

FIG. 14. Dadocrinidae (p. 35).



Carnallicrinus

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 multiradial 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 multiradial 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



Carnallicrinus

FIG. 16. Dadocrinidae (p. 35).

single species. *T. caudex*, a large distal pluricolossal, 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 *Zardincrinus* 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, $\times 2$ (Hagdorn, new); *b–c*, column, *b*, lateral, *c*, proximal facet, Austria, holotype, MNHB MB.E 2286, $\times 0.7$ (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, $\times 3$ (Kristan-Tollmann, 1991).—FIG. 18*a–b*. *T. hsui* MU, lower Carnian, China; *a*, crown and proximal column, YIGMR XT3xH-10, $\times 0.35$; *b*, adoral view of semiadult crown with tegmen, anal cone, and distal arms, MHI 1882/3, $\times 1.5$ (Hagdorn, new).—FIG. 17*e–h*. *T. hsui* MU, lower Carnian, China; *e*, terminal column with radicular cirri, MHI 1882/1, $\times 1.75$; *f*, cirrus sockets with multiradiate facets on side of column, MHI 1882/2, $\times 6$; *g–h*, proximal column, *g*, lateral with nodal-internodal sequence, $\times 3$, *h*, interior

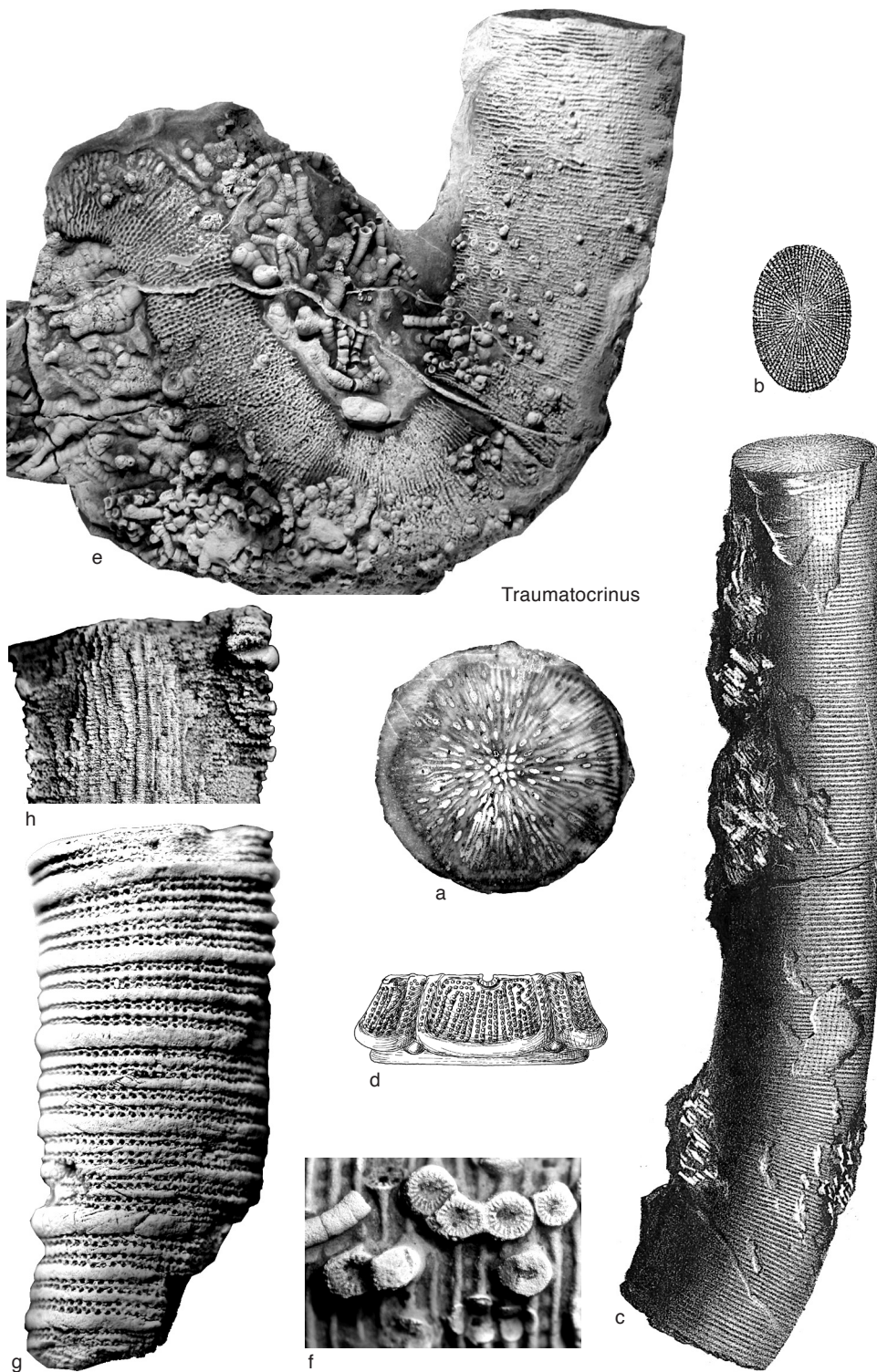


FIG. 17. Traumatocrinidae (p. 35-41).



a

Traumatocrinus



b

FIG. 18. Traumatocrinidae (p. 35–41).

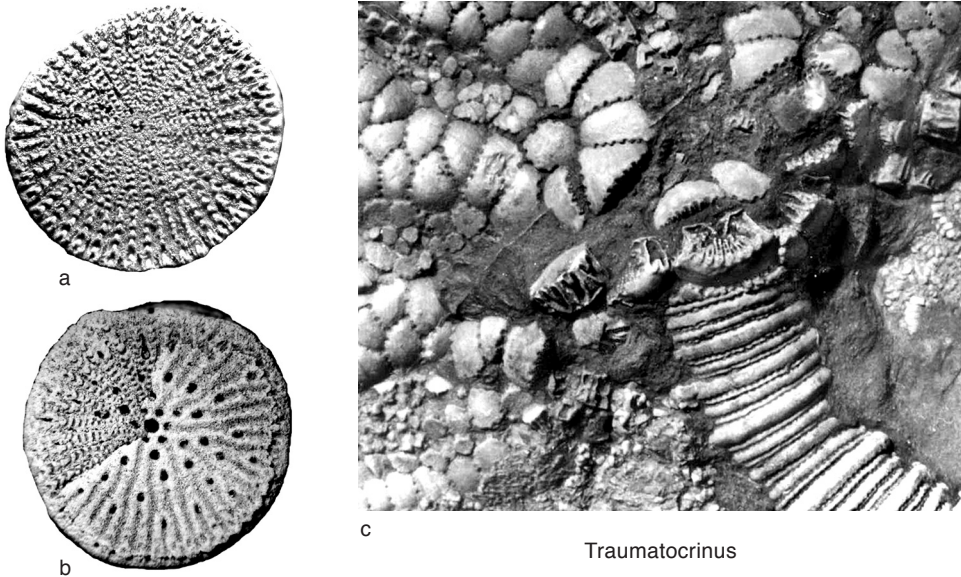


FIG. 19. Traumatocrinidae (p. 35–41).

view of weathered side with tubuli, MHI 1880/2, $\times 5$ (Hagdorn, new).—FIG. 19*a–c*. *T. bsui* MU; *a*, facet of proximal columnal, lower Carnian, China, MHI 1880/5, $\times 5$; *b*, facet of immature internodal with fossulae overlying mature nodal with crenulate loops, lower Carnian, China, MHI 1880/4, $\times 5$ (Hagdorn, new); *c*, proximal column and proximal part of crown with radial articular facet exposed, MHI 1850, $\times 1$ (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. 13,2*a–c*. **V. boreus*; *a*, crown, Russia, $\times 0.6$ (Ausich & others, 1999); *b–c*, pluricolumnal from mesistele, *b*, lateral, *c*, facet, Spitsbergen, MHI 1684/5, $\times 3$ (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 Pentacrinitidae D'ORBIGNY. They rejected the notion of 2 families, the uniquely fossil Pentacrinitidae (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]

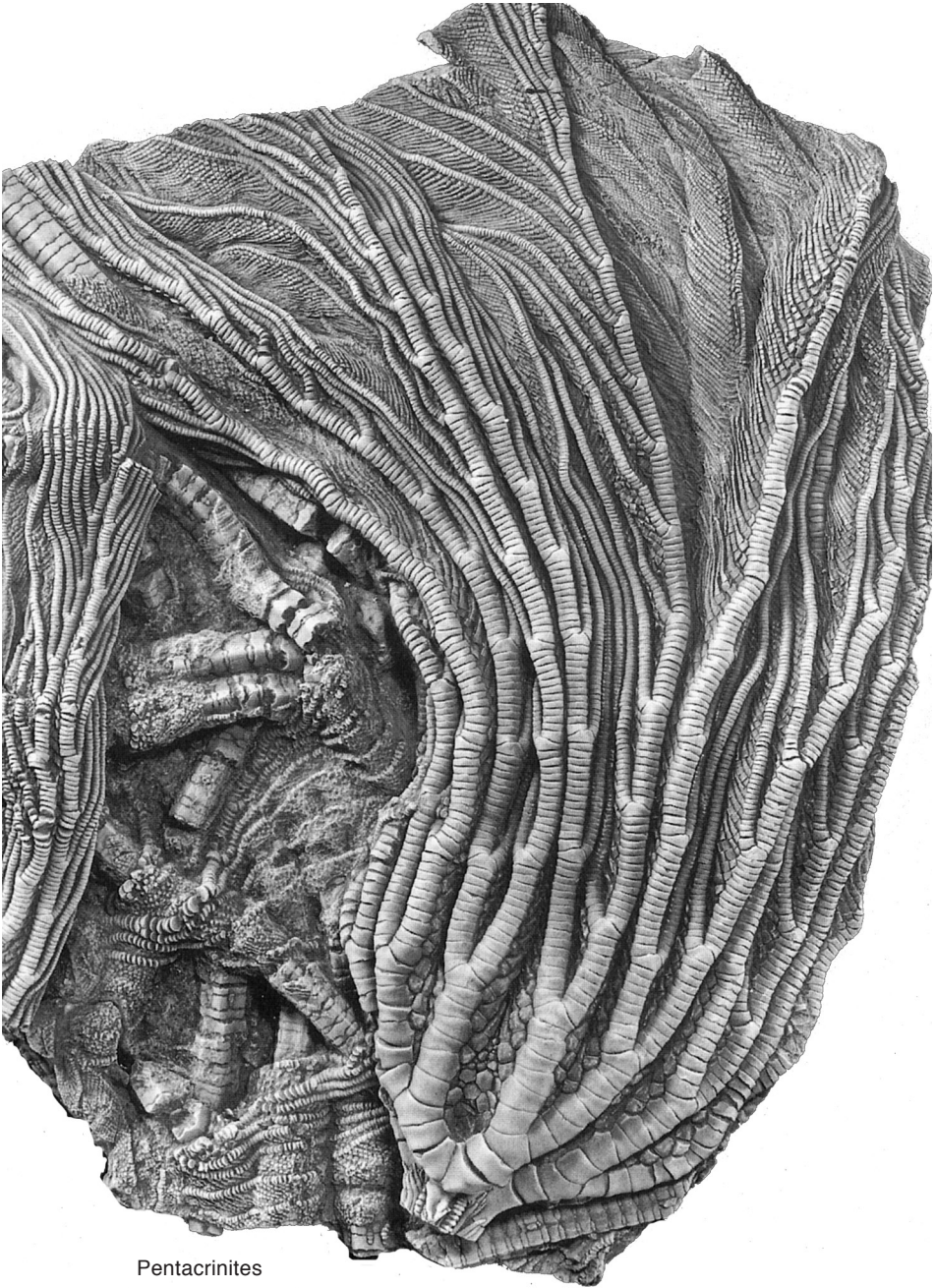
Radials large and projected outward or downward, lower edge of basals more or less curved downward, overhanging the top of the column. Arms divided at primibrachial

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] [=Pentacrinitidae 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-



Pentacrinites

FIG. 20. Pentacrinitidae (p. 43–46).

ments of France, England, and Switzerland (DE LORIO, 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 Pentacrinitis 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,

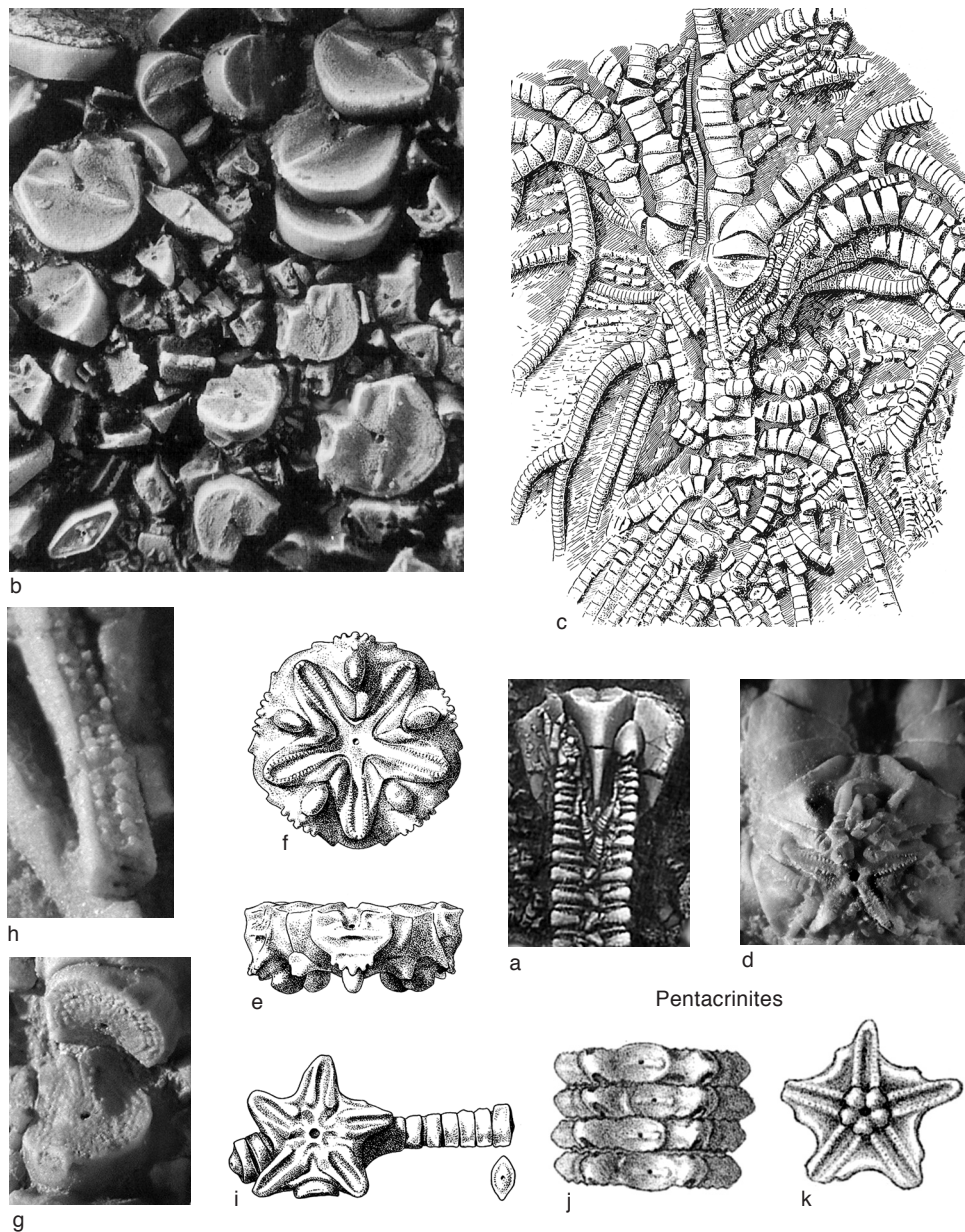


FIG. 21. Pentacrinitidae (p. 43–46).

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); =*Pentacrinus* 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. Synarthy 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. Pentacrinidae (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, $\times 1$ (Simms, 1999).—FIG. 21a–b. **P. fossilis*, Sinemurian, England; a, cup and

proximal column, BMNH E70315, $\times 3$; *b*, brachial facets, BMNH E69872, $\times 3$ (Simms, 1989a).—FIG. 22. *P. dichotomus* (M'COY); intact columns and base of crowns, Toarcian, Germany, SMNS 7389, $\times 0.45$ (Hess, 1999a).—FIG. 21*c–k*. *P. dargniesi* TERQUEM & JOURDY, Bajocian; *c*, proximal column and base of crown, Switzerland, NMB M9661, $\times 2$ (Hess, 1975); *d*, base of cup with topmost columnals, Switzerland, NMB M10568, $\times 3.5$ (Hess, new); *e–f*, cup, *e*, lateral, *f*, proximal, Switzerland, NMB M9324, $\times 2.5$ (Hess, 1975); *g*, secundibrachials 6 and 7 with cryptosyzygy or synostosis, Switzerland, NMB M10569, $\times 6$ (Hess, new); *h*, adoral view of pinnules with cover plates, Switzerland, NMB M10570, $\times 15$ (Hess, new); *i*, nodal with cirrus and cirral facet, Switzerland, NMB M9315, $\times 2.3$ (Hess, 1975); *j–k*, column, *j*, lateral, *k*, facet of nodal with small internodal, France, $\times 4$ (de Loriol, 1889 in 1882–1889).

Seiurocrinus 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. 11*b* 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, 1*a–f*. **S. subangularis* (MILLER); *a*, radial articular facet, Pliensbachian, England, BGS 91097, $\times 3.3$; *b*, facet of proximal secundibrachial, Pliensbachian, England, BGS 91097, $\times 4$ (Simms, 1989a); *c*, columns with facet, Toarcian, Germany, Werkforum Dotternhausen, $\times 0.9$ (Hess, 1999a); *d*, proximal column and cup, radials black, Toarcian, Germany, Hauff, $\times 1.5$

(Seilacher & Hauff, 2004); *e–f*, top of column, *e*, lateral, *f*, proximal, Toarcian, Germany, $\times 1.5$ (Quenstedt, 1876).—FIG. 23, 1*g*. *S. klikushini* SIMMS, 1989a; proxistele (left) and mesistele, Rhaetian, Kotelny Island, $\times 1$ (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

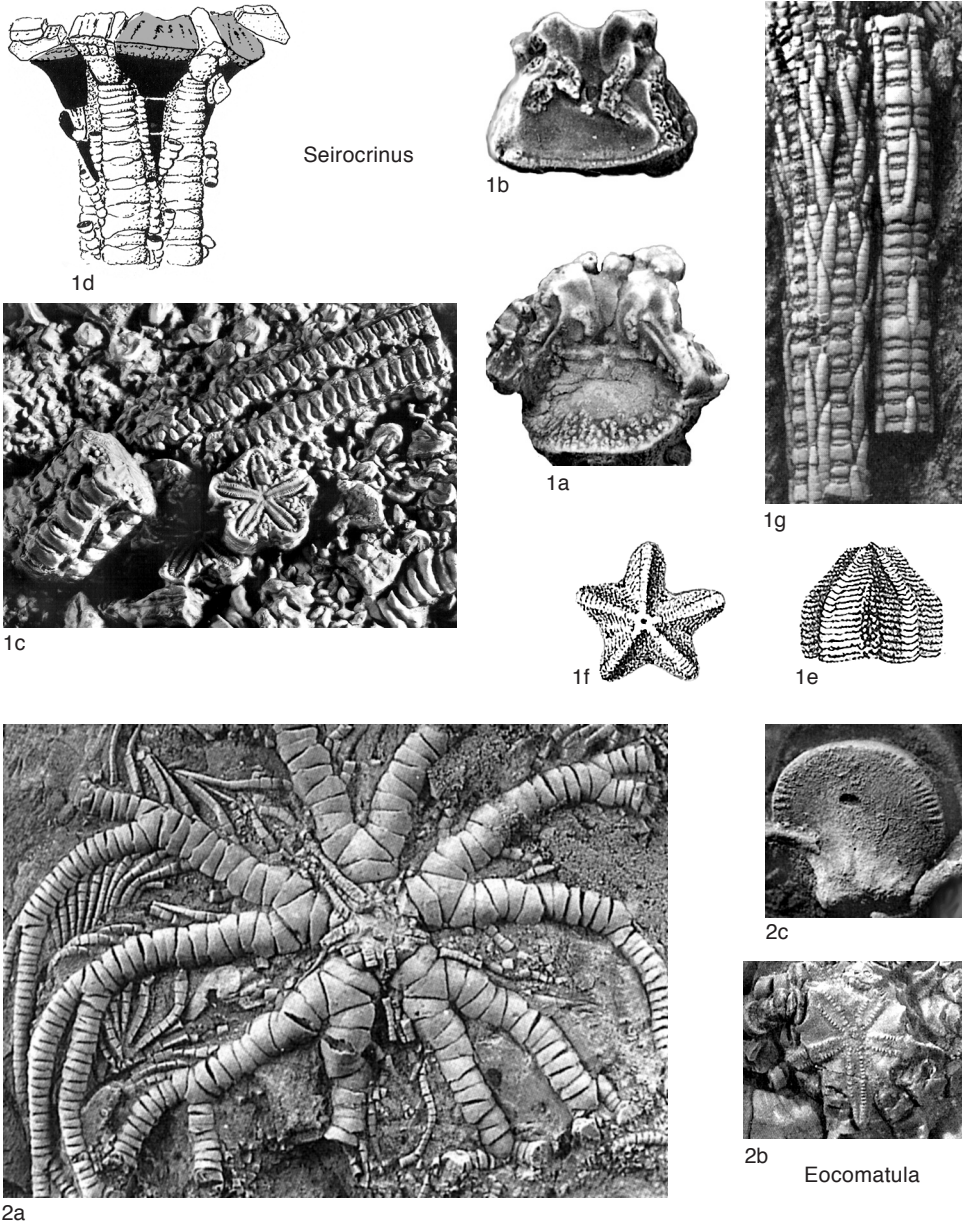


FIG. 23. Pentacrinitidae and Eocomatulidae (p. 46–48).

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 synostosal 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 synostosal 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 Isselocrininae KLIKUSHIN, 1977, and Isselocrinidae 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 Isselocrininae 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 Isselocrinidae) 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. [Subdivision 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 *Seiocrinus*. 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 Isselocrininae 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 Isselocrinidae.] *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

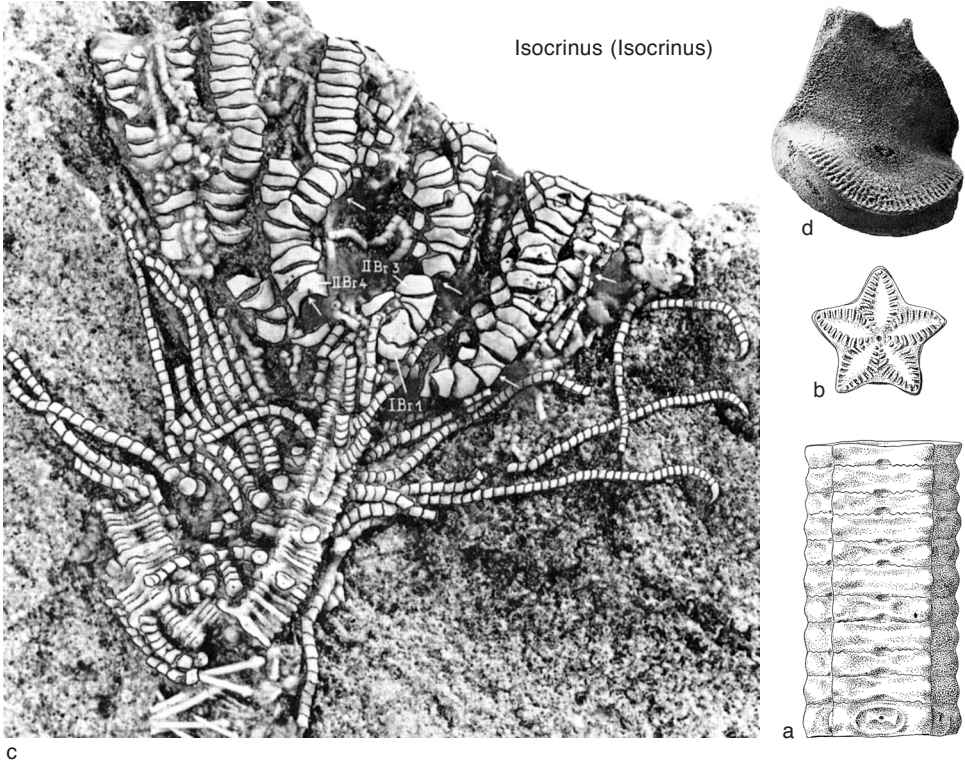


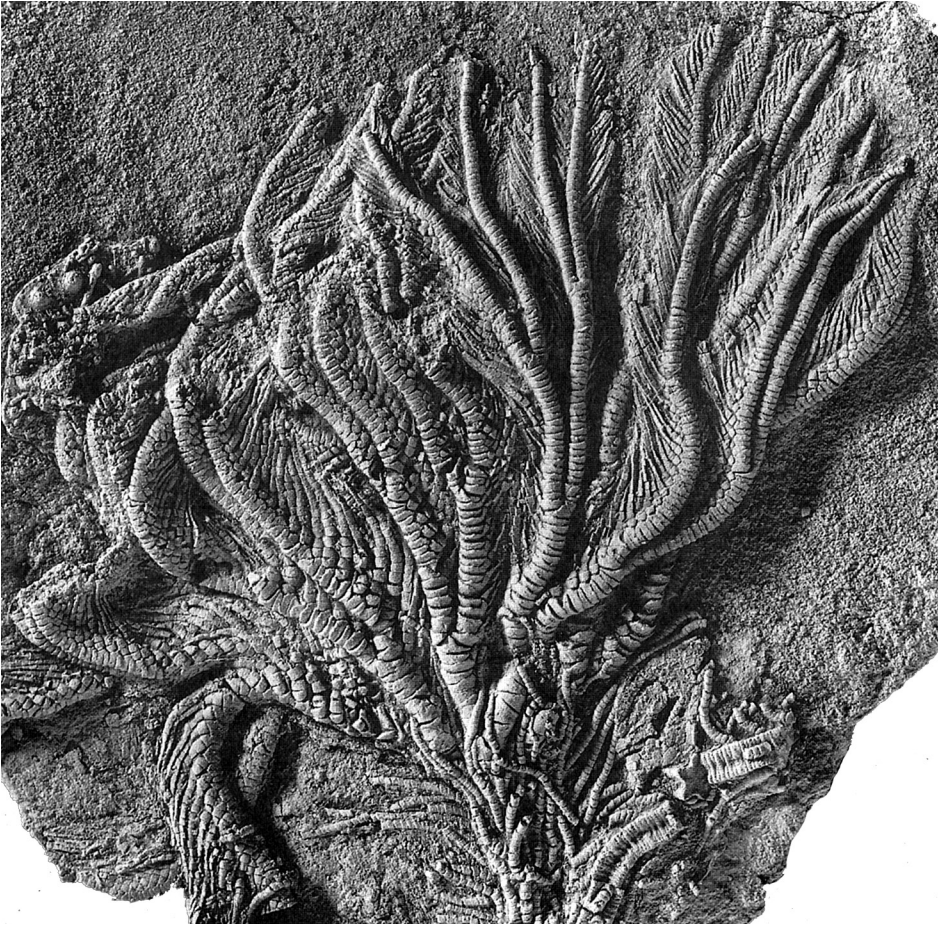
FIG. 24. Isocrinidae (p. 50–51).

this subfamily. Herein, *Cenocrinus* is assigned to Isselocrinidae, 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 circler. 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 LORIO, 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 LORIO, 1887 in 1882–1889, p. 247; HESS, 1972a, p. 198).] *Upper Triassic* (?Carnian), *Lower Jurassic–Lower Cretaceous*: Europe, Russia, Crimea, Caucasus, Japan.

I. (Isocrinus). Symmophy 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* (REPÉLIN) 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 symmophy 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. 24a–b. **I. (I.) pendulus* (VON MEYER), Oxfordian, Switzerland; a, column, NMB M9594, $\times 3$; b, facet of internodal,



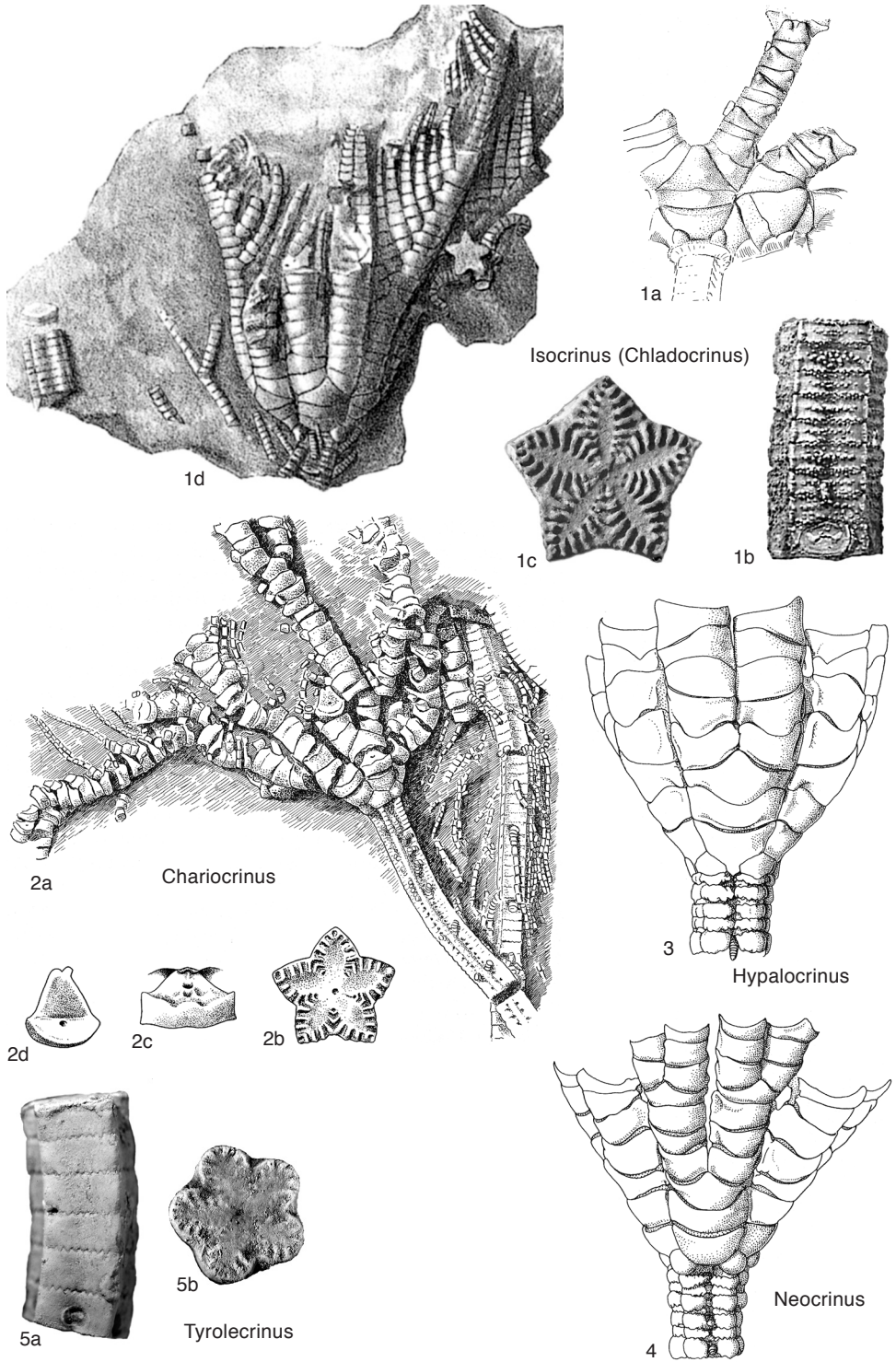
Isocrinus (Isocrinus)

FIG. 25. Isocrinidae (p. 50–51).

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



Isocrinus (Chladocrinus)

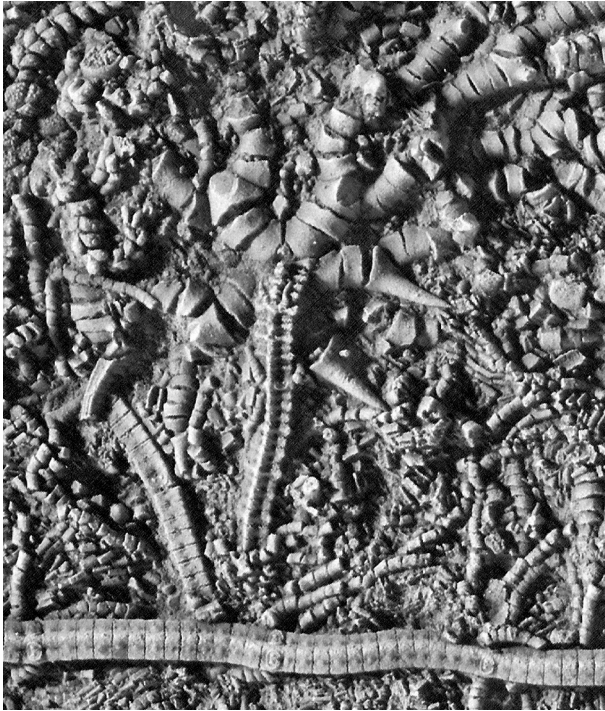
Chariocrinus

Hypalocrinus

Neocrinus

Tyrolecrinus

FIG. 26. Isocrinidae (p. 51-56).



1c



3c



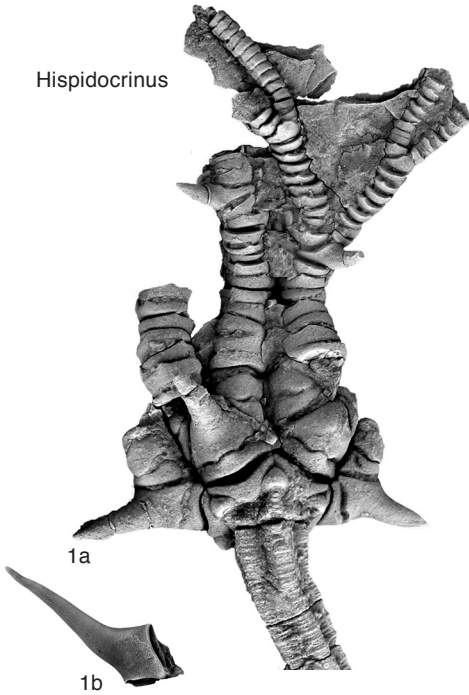
3b



3a

Percevalicrinus

Hispidocrinus

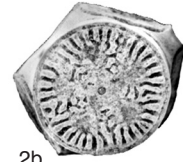


1a

1b



2a



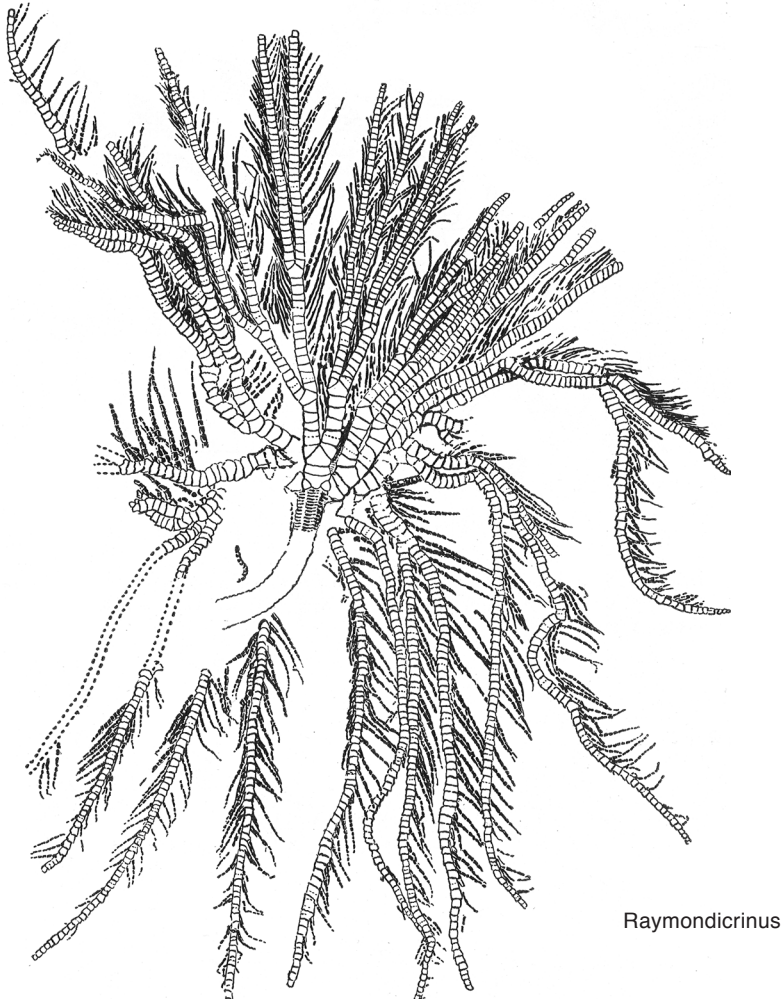
2b



2c

Laevigatocrinus

FIG. 27. Isocrinidae (p. 55-58).



Raymondicrinus

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, $\times 2$ (Sieverts-Doreck, 1971); b, column, England, BMNH E70323, $\times 2$ (Simms, 1989a); c, facet of internodal, Germany, $\times 4$ (Sieverts-Doreck, 1971).—FIG. 26, 1d. *I. (C.) tuberculatus* (MILLER); partly preserved crown with proximal

column, Lower Jurassic, France, EM 12 126, $\times 1$ (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 cirlet. Weakly embayed synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Cryptosyzygy to weak symmetry 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

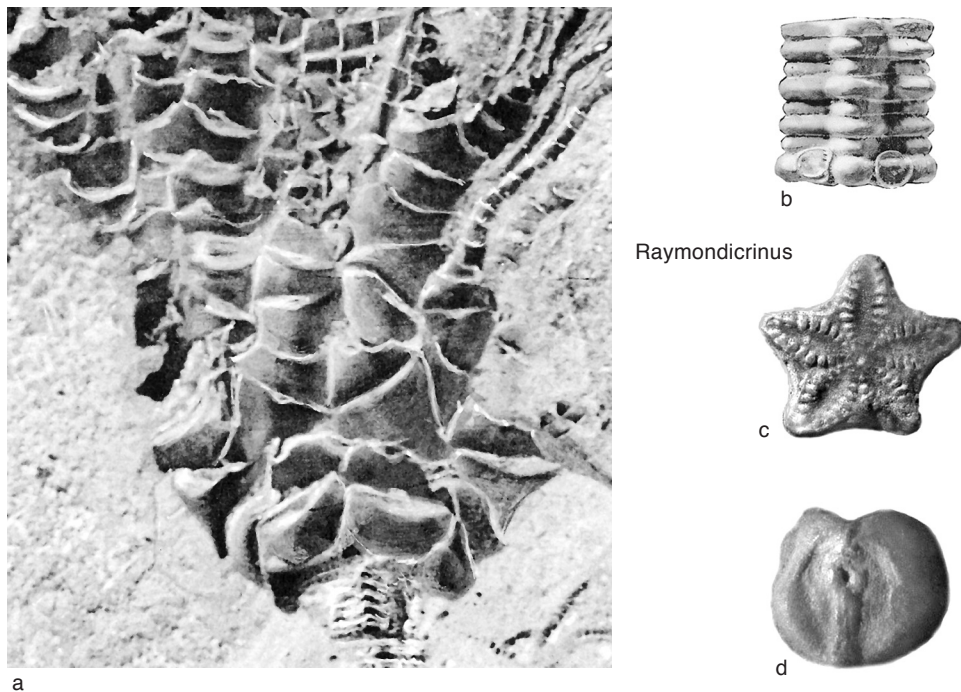


FIG. 29. Isocrinidae (p. 56).

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, $\times 2$; *b*, facet of internodal, NMB M9891, $\times 5$; *c*, distal facet of primibrachial 1, NMB M9891, $\times 5$; *d*, distal facet of secundibrachial 3, NMB M9891, $\times 5$ (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 LORIO) 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 *Chario-*

crinus 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, $\times 1.5$; *b*, axillary brachial, BMNH E69896, $\times 2$ (Simms, 1989a).—FIG. 27,1c. *H. leuthardti* (DE LORIO, 1894); proximal column and crown, mesistele, Bathonian, Switzerland, topotype, NMB M9770, $\times 2.2$ (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, $\times 3$ (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, $\times 3$ (Roux, Messing & Amézière, 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, $\times 0.7$ (Moore & Vokes, 1953).—FIG. 29a–d. **R. oregonensis* (MOORE & VOKES), Oregon; a, proximal part of crown, holotype of *Isocrinus nebailemensis* MOORE & VOKES, USNM 560792K, $\times 3$; b, column, paratype, USNM 560903A, $\times 2.5$ (Moore & Vokes, 1953); c, proximal facet of nodal, topotype, NMB M10603, $\times 5$; d, distal view of primibrachial 1, topotype, NMB M10604, $\times 5$ (Hess, new).

Tyrolocrinus 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, $\times 6$; b, facet of internodal, syntype, GBA 1865/3/83, $\times 7$ (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, cryp-

tosyzygies 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

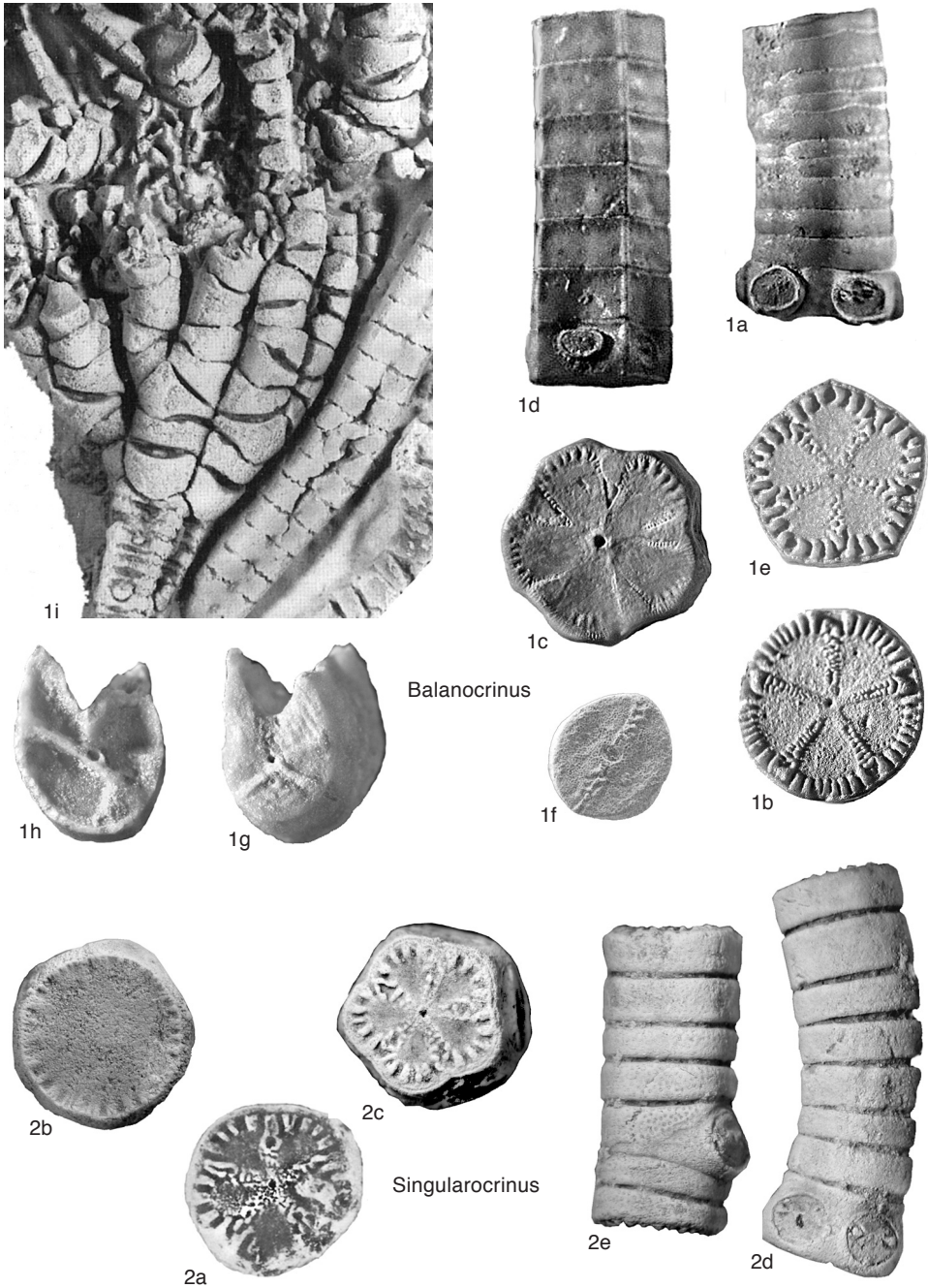


FIG. 30. Isocrinidae (p. 56–58).

in the bands of adradial crenulae, and in having fewer than 20 rather than supposedly more than 30 internodals per nodotaxis (see SIMMS, 1989a, p. 56). KLIKUSHIN (1982a) subsequently raised both to generic status and created a third genus, *Teroocrinus*, to accommodate several Lower Jurassic and one Triassic species, with *Pentacrinites subteroides* QUENSTEDT (1858) as type species. *Teroocrinus* 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 *Teroocrinus* 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, cryptosymplectical 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; epizygial 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 [**Pentacrinites 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 Isselocrinidae seems problematic because of the wide stratigraphic gap between this Late Triassic form and remaining Isselocrinidae, 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 LORIOI in DE LORIOI & PELLAT, 1875, p. 298, *non* ÉTALLON, 1857, p. 282, *nom. nud.* [**Picteticrinus beaugrandi* DE LORIOI in DE LORIOI & PELLAT, 1875, p. 298; M]. Basals large, forming contiguous circler; 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 LORIOI in DE LORIOI & PELLAT, 1875, p. 298 is junior homonym of *Picteticrinus* ÉTALLON, 1857, p. 282, *nom. nud.* The genus was rejected as a homonym by DE LORIOI (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 (Titthonian)—Lower Cretaceous (Valanginian):* France, Russia, Siberia, ?North America.—FIG. 27, 3a–c. **P. beaugrandi* (DE LORIOI), 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).

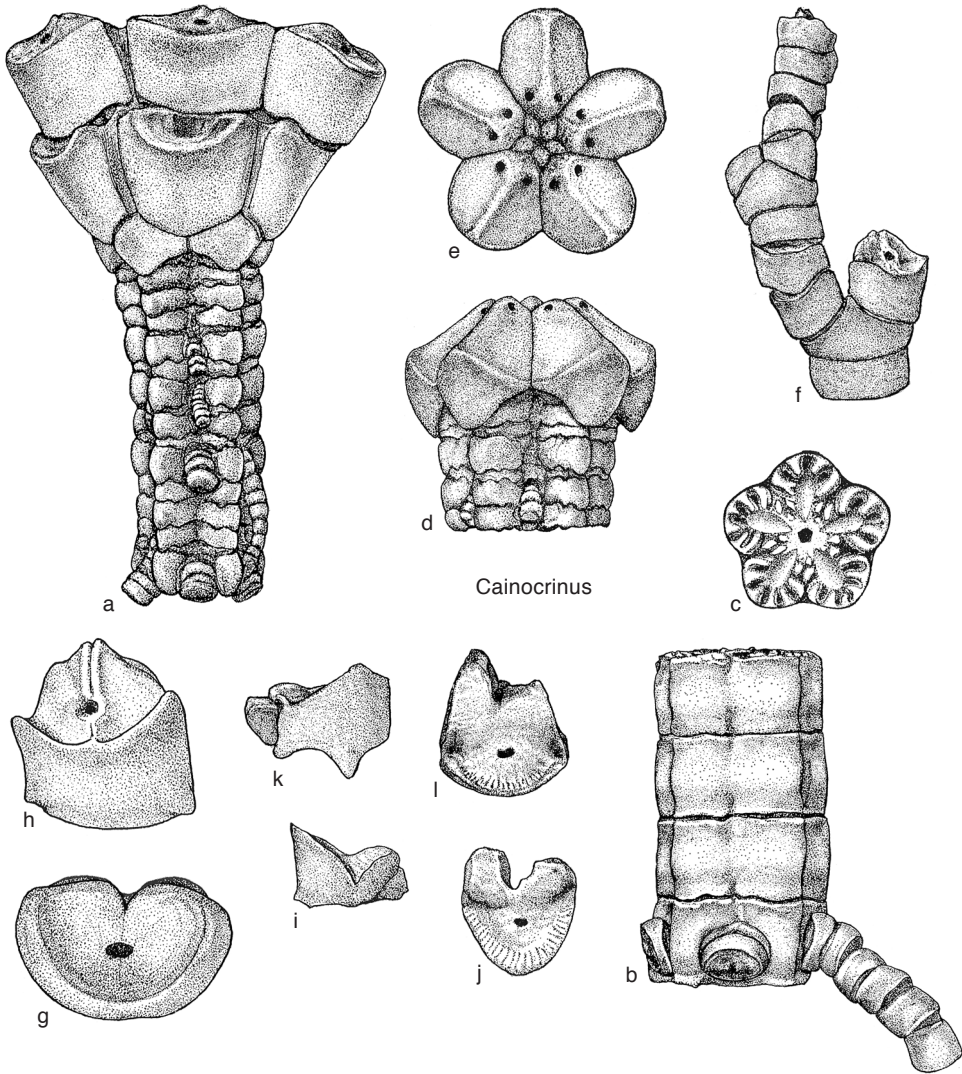


FIG. 31. Cainocrinidae (p. 59–61).

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 symmorfy between secundibrachials 3 and 4. *Lower Cretaceous (Hauterivian)–Holocene.*

Cainocrinus FORBES, 1852, p. 33 [*C. tintinnabulum*; M; *emend.*, RASMUSSEN, 1972a, p. 26]. Symmorfy between secundibrachials 3 and 4; muscular articulation between tertibrachials 1 and

2, and symmorfy between tertibrachials 2 and 3. Further symmorfies 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 LORIOI in DE LORIOI & PELLAT, 1875, p. 298, was referred to *Cainocrinus* by DE LORIOI (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. 31a–l. **C. tintinnabulum*,

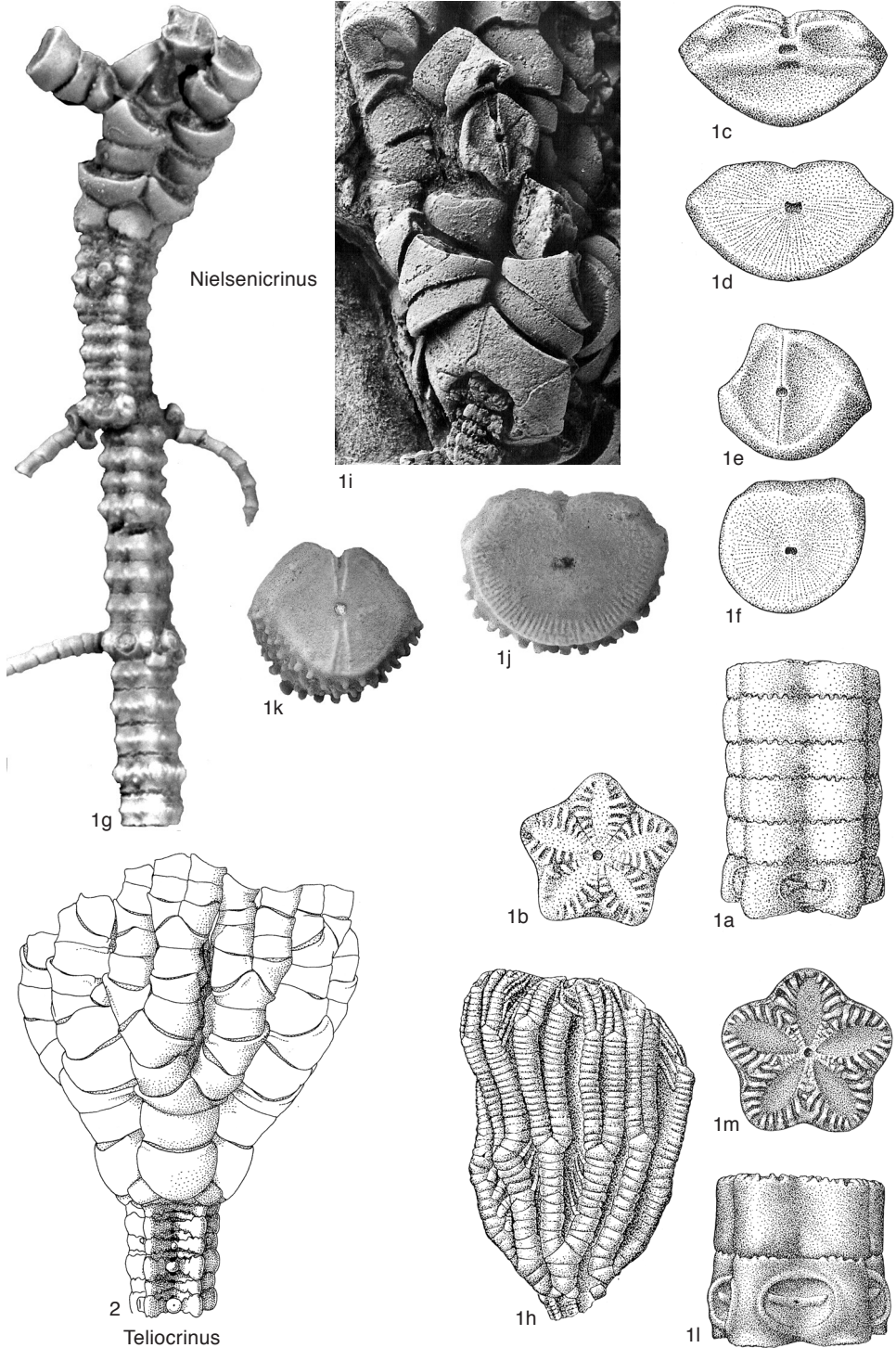


FIG. 32. Cainocrinidae (p. 61).

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

Nielsenicrinus RASMUSSEN, 1961, p. 94 [**Pentacrinus obsoletus* NIELSEN, 1913, p. 97; OD]. Cryptosyzygy between secundibrachials 3 and 4, no symmorph. [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, 1*a-f*. **N. obsoletus* (NIELSEN), Danian, Denmark; *a-b*, column, *a*, lateral, *b*, facet of internodal, MGUH 8884, $\times 5$; *c-d*, primibrachial 1, *c*, proximal, *d*, distal (cryptosyzygy), MGUH 8889, $\times 5$; *e*, distal view of secundibrachial 1, MGUH 8891, $\times 5$; *f*, distal view of secundibrachial 3 (cryptosyzygy), MGUH 8893, $\times 5$ (Rasmussen, 1961).—FIG. 32, 1*g*. *N. cretaceus* (LEYMERIE, 1842), proximal column and part of crown, Cenomanian, England, BMNH E22104, $\times 2$ (Smith & Wright, 2002).—FIG. 32, 1*b*. *N. chavannesi* (DE LORIO, 1879 in 1877–1879), crown, Hauterivian, Switzerland, lectotype, MHNG 28548, $\times 2.5$ (Rasmussen, 1961).—FIG. 32, 1*i*. *N. japonicus* OJI & others, 1996, proximal part of crown, Upper Cretaceous, Japan, holotype, UMUT ME19811, $\times 4$ (OJI & others, 1996).—FIG. 32, 1*j-k*. *N. carinatus* (ROEMER, 1840 in 1840–1841), Campanian, Netherlands; *j*, proximal view of primibrachial 2 (cryptosyzygy), NHMM MB 1044p, $\times 7$; *k*, distal view of secundibrachial 1 (weak synarthry), NHMM MB 1044r, $\times 7$ (Jagt, 1999a).—FIG. 32, 1*l-m*. *N. fionicus* (NIELSEN, 1913), Danian, Denmark; column, *l*, lateral, *m*, facet of internodal, MGUH 8896, $\times 4$ (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. oiji* 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, $\times 3$ (Roux, Messing, & Améziâne, 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 synostiosial (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 *Austino-crinus*. *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 cirlet. Basals large, lower edge with median projection

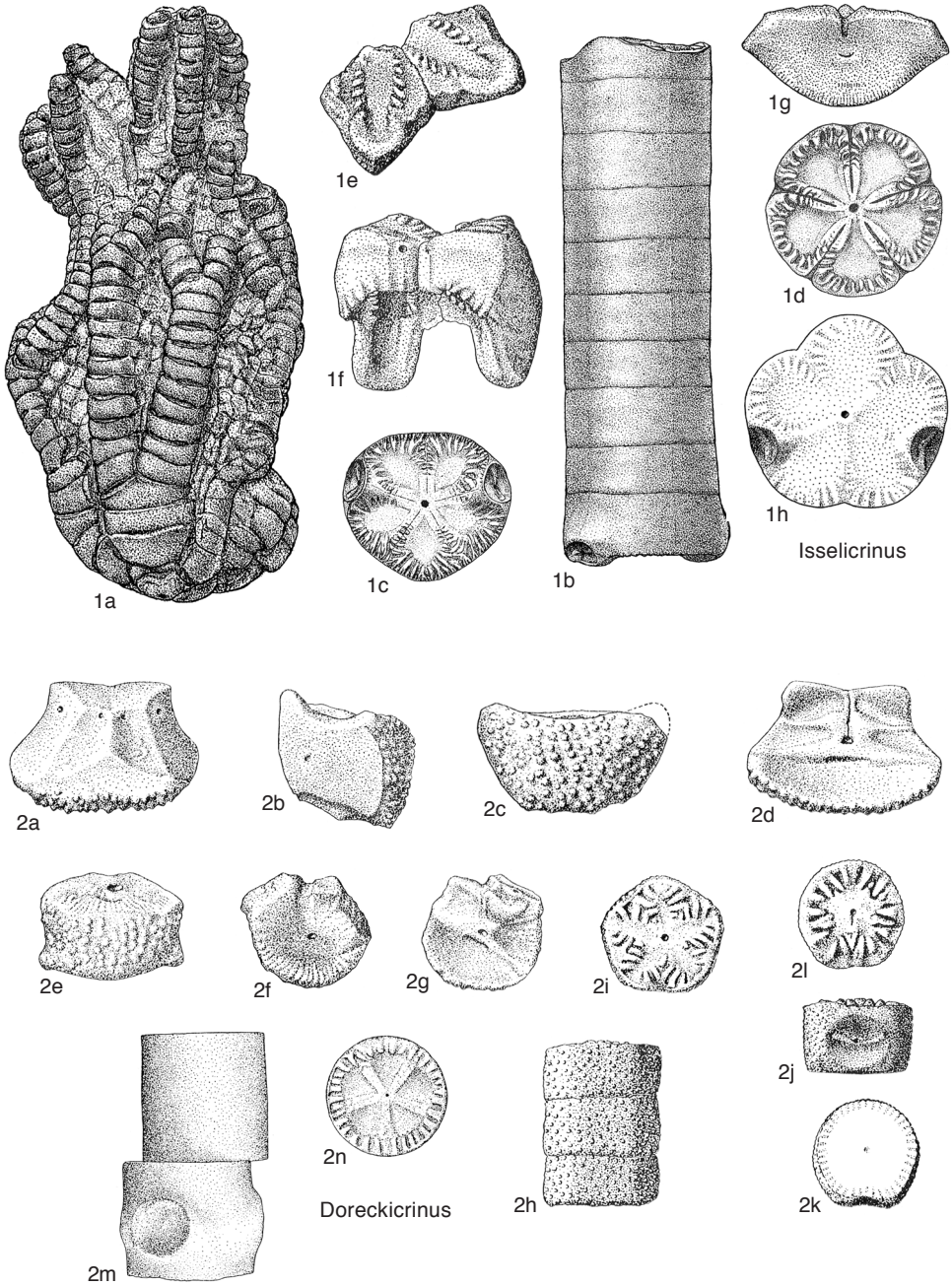


FIG. 33. Isselicrinidae (p. 61–65).

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 *Iselocrinus* 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 *Iselocrinus*. 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, $\times 1.8$; *b–c*, column, *b*, lateral, *c*, distal facet of nodal, MGUH 12753, $\times 4$; *d*, facet of internodal, MGUH 12754, $\times 4$ (Rasmussen, 1972a).—FIG. 33, 1e–h. *I. paucicirrus* (NIELSEN, 1913), Danian, Denmark; *e–f*, 2 basals, *e*, lower (proximal) side, *f*, lateral, MGUH 1198, $\times 5$; *g*, proximal view of primibrachial 2, Coll. Geol. Survey Denmark, $\times 2.5$; *h*, distal facet of nodal, MGUH 1163, $\times 3$ (Rasmussen, 1961).

Austinoocrinus DE LORIO, 1889a, p. 153 [**A. komaroffi*; M; =*Pentacrinus erkerti* DAMES, 1885, p. 219; =*Pentacrinus sulcifer* EICHWALD, 1871, p. 83, sp. indet.] [=*Austinoocrinus* (*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, *Austinoocrinus* s. str., and *Penroseocrinus*. Following RASMUSSEN (1961, p. 28), this subdivision 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 (cryptosymplectical 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 *Austinoocrinus* (see for example, KLIKUSHIN 1979b, fig. 1b; HAGDORN, GLUCHOWSKI, & BOZAROWSKI, 1996, pl. 5,g).] *Upper Cretaceous (Campanian–Maastrichtian)*: Denmark, England, Germany, Netherlands, Spain, Turkey, Caucasus, Turkmenistan, Tunisia, Mexico, Cuba.—FIG. 34, 1a–b. **A. erkerti* (DAMES), Maastrichtian; *a*, facet of cirral, Spain, MHNG 28473, $\times 2.5$ (Rasmussen, 1961); *b*, proximal facet of supranodal (nodal with 5 cirri), Turkmenistan, LGI KT-48-17, $\times 2.5$ (Klikushin, 1985b).—FIG. 34, 1c–h. *A. rothpletzi* STOLLEY, 1892; *c*, base of crown, Senonian, Germany, $\times 1$ (Jaekel, 1904); *d*, facet of proximal internodal, Campanian, Germany, Hamburg coll. 218, $\times 5$ (Rasmussen, 1961); *e–g*, column (nodal with 3 cirrus sockets), *e*, lateral, *f*, distal facet, *g*, proximal facet, Campanian, Turkmenistan, NMB M10589, $\times 3$; *h*, facet of distal internodal, Campanian, Turkmenistan, NMB M10590, $\times 4$ (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

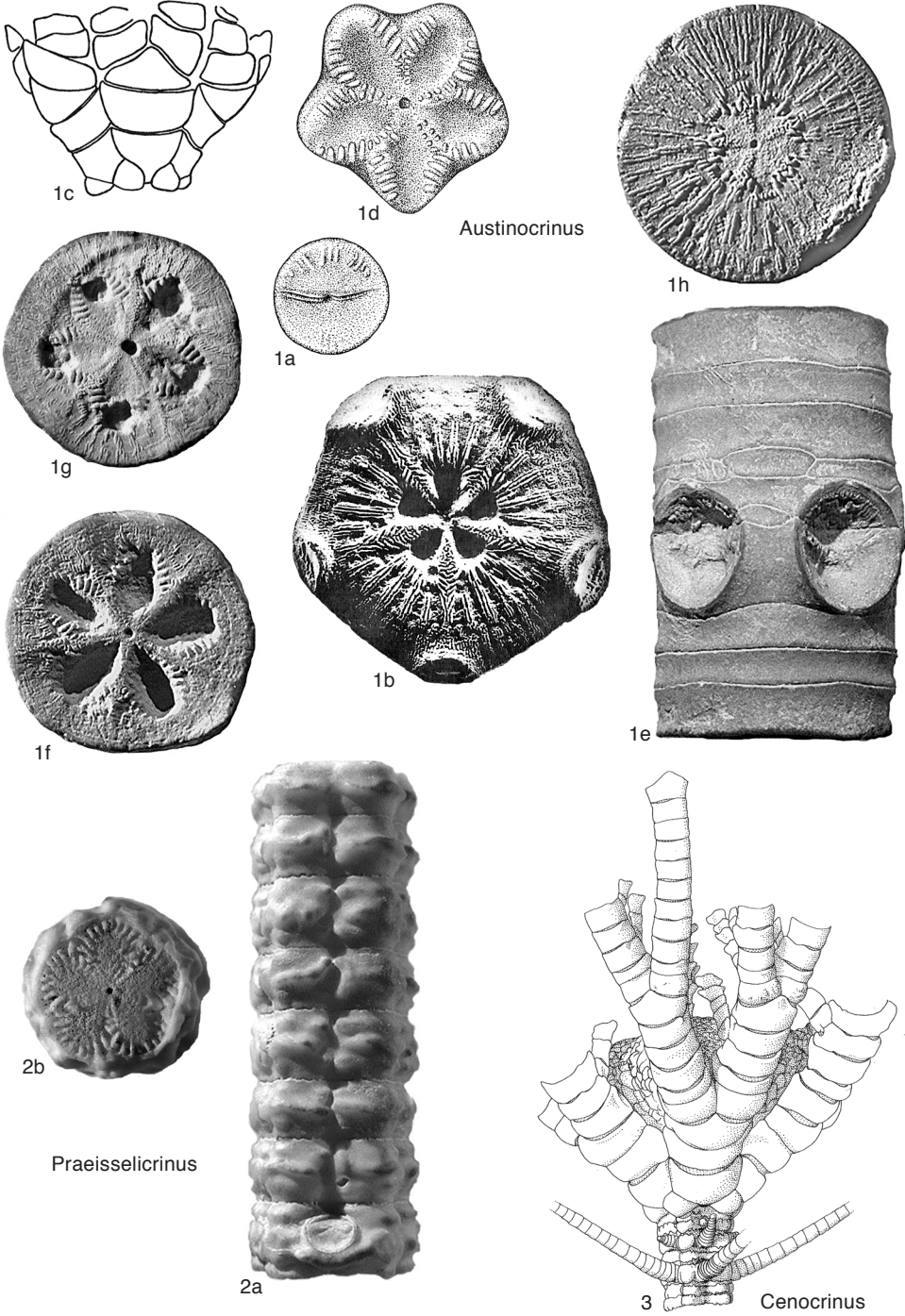


FIG. 34. Isselocrinidae (p. 63–65).

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 synostosis. 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).

Praeisselicerinus KLIKUSHIN, 1977, p. 92 [**Isselicerinus atabekjani* KLIKUSHIN, 1973, p. 43; OD] [= *Isselicerinus* (*Praeisselicerinus*) KLIKUSHIN, 1977, p. 92 (type, *Isselicerinus 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

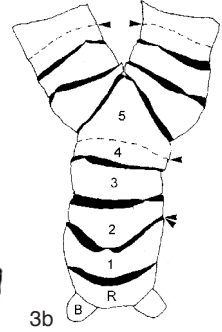
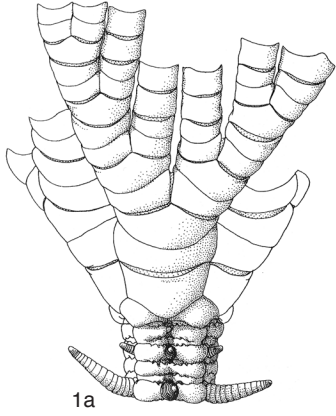
[Diplocrininae ROUX, 1981, p. 482]

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*).

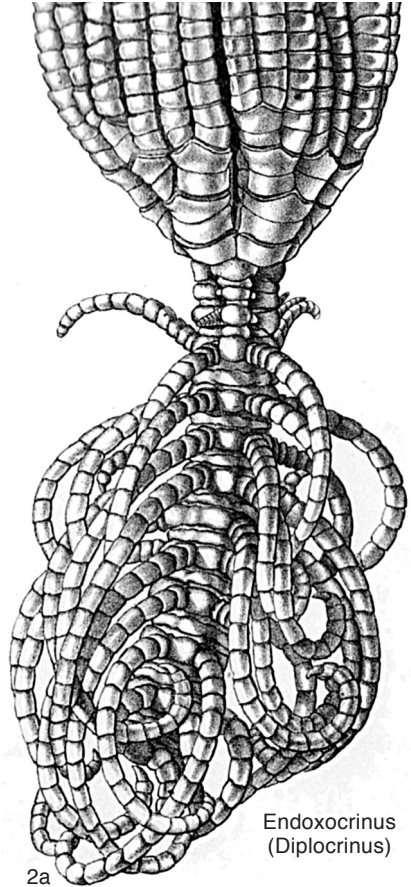
Endoxocrinus A. H. CLARK, 1908i, p. 151 [**Encrinus parrae* GERVAIS, 1835, p. 49; OD; =*Pentacrinus muelleri* ØRSTED, 1857, p. 202; DAVID and others (2006, p. 34) designated ØRSTED's specimen of *Pentacrinus mülleri* as the neotype of *E. parrae*, thus treating *muelleri* as a junior objective synonym of *parrae*.] [= *Isocrinus* (*Diplocrinus*) DÖDERLEIN, 1912, p. 21 (type, *Pentacrinus maclarceanus* 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 cirlet; 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,



Eometacrinus



1b Endoxocrinus (Endoxocrinus)



Endoxocrinus (Diplocrinus)

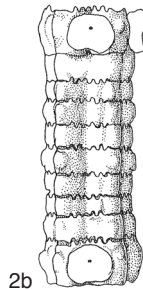


FIG. 35. Isselocrinidae (p. 67–69).

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, $\times 2.5$ (Roux, Messing, & Améziâne, 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, $\times 2$ (P. H. Carpenter, 1884a, pl. 16, I).—FIG. 35, 2b. E. (*D.*) *alternicirrus* (CARPENTER, 1882c); portion of column between 2 nodals, $\times 2$ (Roux, Messing, & Améziâne, 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 synarthral 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, $\times 1.2$ (Carpenter, 1884a, pl. 48, I).—FIG. 36, 1b. *M. fossilis* RASMUSSEN, 1979; crown, Eocene, Antarctic Peninsula, USNM 459260, loc. 500, $\times 1.5$ (Meyer & Oji, 1993).—FIG. 36, 1c. *M. levii* AMÉZIANE-COMINARDI in AMÉZIANE & others, 1990; cryptosyzygy on proximal facet of primibrachial 2, Holocene, MNHN EcPh50, $\times 8$ (Améziâne, 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, $\times 2$, b, cup plates and proximal brachials (B, basal; R, radial; 1–5, IBr1–5; single arrows, syzygies; double arrow, synarthry),

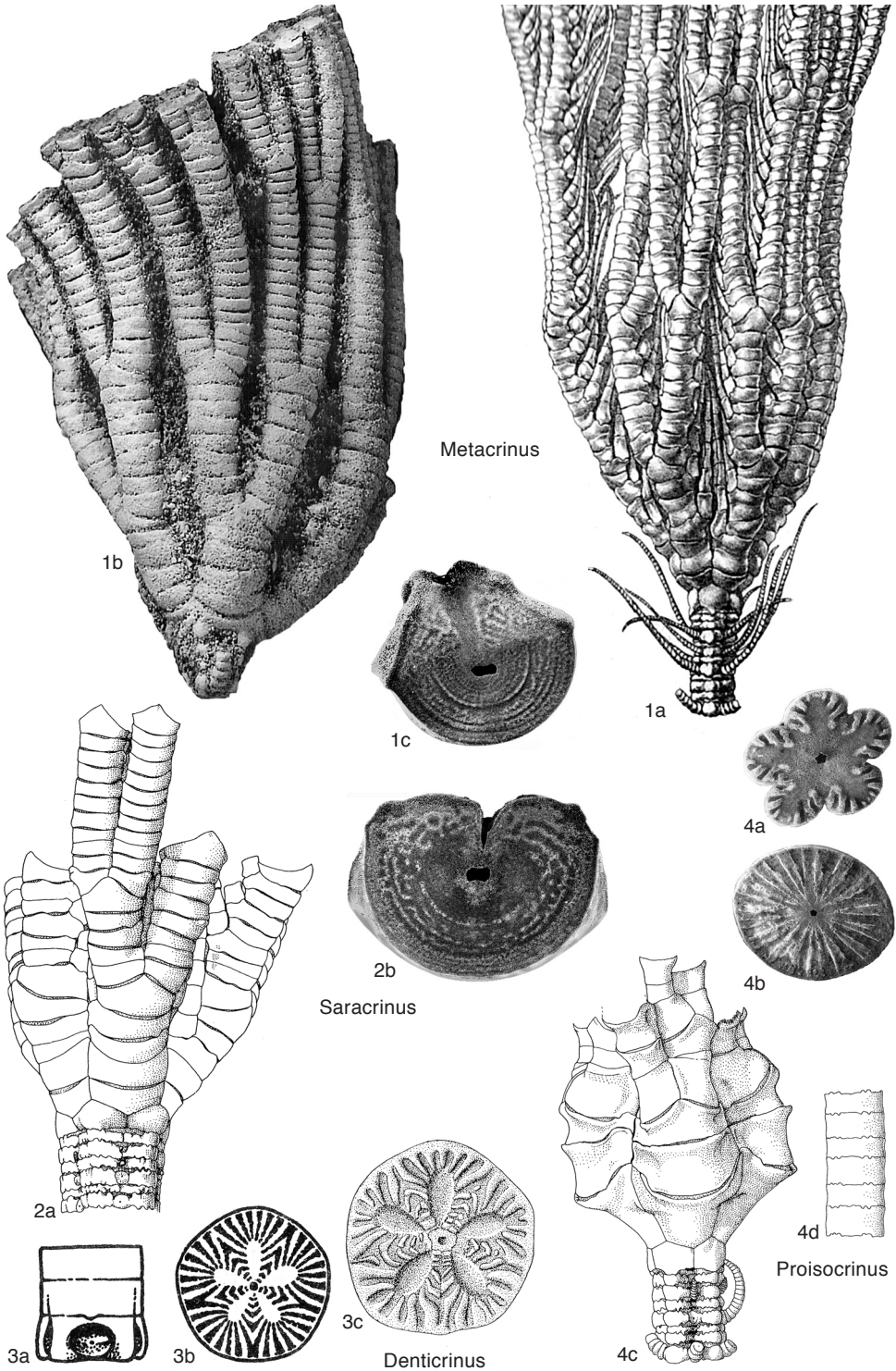


FIG. 36. Isselocrinidae and Proisocrinidae (p. 67–69).

Eocene, Antarctic Peninsula, ZPAL Ca.V/3, $\times 3$ (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, $\times 2.5$ (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, $\times 8$ (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 *Austinoecrinus*. Five cirrus sockets restricted to one columnal distinguish it from *Austinoecrinus*.] *Paleogene (Danian)*: Russia, Bulgaria.—FIG. 36,3a–b. **D. dentifer*, Russia; a, pluricolumnal, $\times 2$; b, facet of internodal, $\times 2$ (Klikushin, 1992).—FIG. 36,3c. *D. gocevi* (SIEVERTS-DORECK, 1951a); facet of internodal, Bulgaria, holotype, $\times 4$ (Rasmussen, 1961).

Family PROISOCCRINIDAE

Rasmussen, 1978

[Proisocrinidae RASMUSSEN, 1978, p. 866]

Cup with a rather low, cylindrical circler of 5 basals and a larger, broadly conical circler 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 (synostosomal) 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. Synostosomal articulation between the primibrachials suggests that *Proisocrinus* is probably derived from Isocrinina with cryptosyzygial or synostosomal, 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, GLUCHOWSKI, & 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, $\times 4$; b, facet of distal columnal, holotype, USNM 24308, $\times 4$ (Bourseau & others, 1991); c, proximal column and base of crown, Bishop Museum 1992.340, $\times 1.5$; d, portion of mesistele, MNHN EcPs 10247, $\times 1.5$ (Roux, Messing, & Améziane, 2002; photos courtesy of the *Bulletin of Marine Science*).