COMATULIDA

Hans Hess and Charles G. Messing

[Natural History Museum Basel, Switzerland, e-mail: hans.hess@bluewin.ch; Nova Southeastern University Oceanographic Center, Dania Beach, Florida, USA, e-mail: messingc@nova.edu]

Order COMATULIDA A. H. Clark, 1908

[Comatulida A. H. Clark, 1908h, p. 135] [=Comatuladae Fleming, 1828, p. 494; =Comatulidae d'Orbigny, 1852 in 1850–1852, p. 138, including Uintacrinida and excluding Thiollericrinidae A. H. Clark, 1908b, p. 209]

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

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

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

truncated or discoidal centrodorsal with apical cirri and sockets reduced (obsolete) or obliterated and commonly with a cirrus-free, flattened-to-concave aboral apex. Crowded marginal sockets are generally described as lying in irregular horizontal rows, circles, or verticils.

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

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

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

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

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

Basals are well developed in the larval and postlarval stages of all comatulids. In the paracomatulids and the oldest true comatulids (such as *Palaeocomaster*), the basals form a stellate circlet of 5 rather stout plates, exposed interradially, joined centrally, and articulated to the centrodorsal with a petaloid pattern of crenulae, similar to that in *Pentacrinites*. In living *Atelecrinus* and *Sibogacrinus* and in the fossil *Jaekelometra*, the basals maintain their postlarval character as a circlet of large plates, although they may gradually shrink during

growth. In the Cretaceous Decameridae, the inner ends of the basals grow into large plates, forming a stout basal circlet surrounded by the radial circlet. In all other comatulids, the basals are more or less reduced to 5 interradial rods or tongues lodged in the shallow interradial furrows in the centrodorsal plus a central perforated plate called the rosette that roofs the centrodorsal cavity. In many Mesozoic species, the rodlike basals may have faint crenulae. Their tips may be exposed interradially between centrodorsal and radials, or they may be concealed. In Mariametroidea and most Antedonoidea, the rodlike portions are reduced, and only the rosette remains (Fig. 3,*4;* Fig. 5,*2*).

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

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

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

1895; Leuthardt, 1911; Manni, Nicosia, & Riou, 1985; Simms, 1988b; Hagdorn & Campbell, 1993; Baumiller & Gaździcki, 1996; Hess, 1999c), although some preserve details of centrodorsal structure (de Loriol, 1879 in 1877–1879, 1889 in 1882–1889; Bigot, 1938).

Suborder COMATULIDINA A. H. Clark, 1908

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

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

Superfamily PARACOMATULOIDEA Hess, 1951

[*nom. correct.* Hess & Messing, herein, *pro* Paracomatulacea Rasmussen, 1978, p. 869, *nom. transl. ex* Paracomatulidae Hess, 1951, p. 208]

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

Family PARACOMATULIDAE Hess, 1951

[Paracomatulidae Hess, 1951, p. 208]

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

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

Superfamily ATELECRINOIDEA Bather, 1899

[*nom. transl.* Hess & Messing, herein, *ex* Atelecrinidae Bather, 1899, p. 923; *emend*., Messing, 2003a, p. 280]

Centrodorsal conical; adoral rim with 5 interradial depressions or deep pits; centrodorsal cavity broad and deep. Cirrus sockets in 10 or 15 columns, bearing weak to strong,

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

Family ATELECRINIDAE Bather, 1899

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

Characters as for superfamily. *Holocene.*

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

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

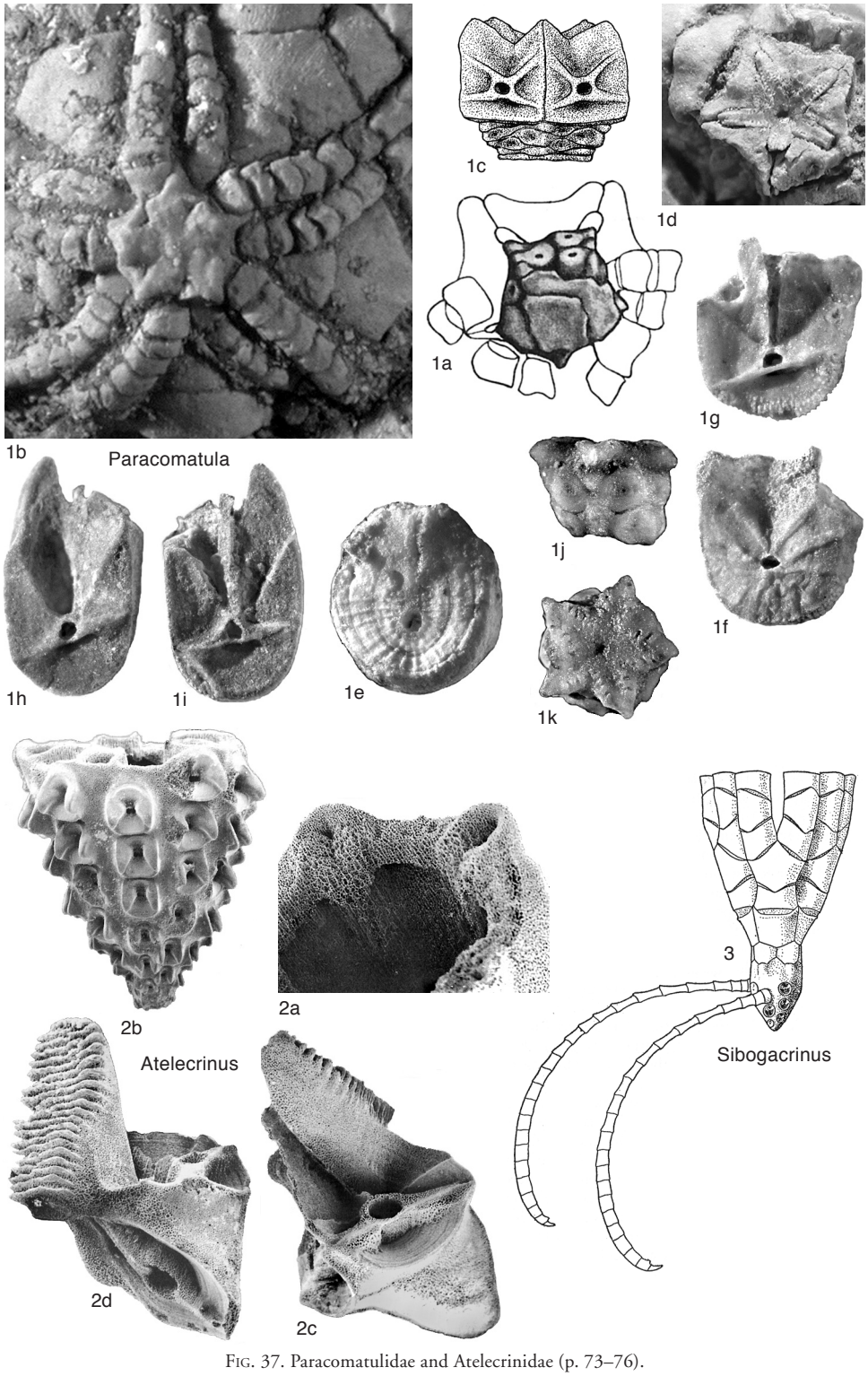


FIG. 37. Paracomatulidae and Atelecrinidae (p. 73–76).

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

Superfamily SOLANOCRINITOIDEA Jaekel, 1918

[*nom. correct.* Hess & Messing, herein, *pro* Solanocrinitacea Rasmussen, 1978, p. 873, *nom. transl. ex* subfamily Solanocrininae Jaekel, 1918, p. 73]

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

Family SOLANOCRINITIDAE Jaekel, 1918

[*nom. correct.* Rasmussen, 1978, p. 873, *pro* Solanocrinidae Gislén, 1924, p. 145, *nom. transl. ex* subfamily Solanocrininae Jaekel, 1918, p. 73]

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

Solanocrinites Goldfuss, 1829 in 1826–1844, p. 166 [**S. costatus*; SD de Loriol, 1884–1889 in 1882–1889, p. 526; *emend.*, Carpenter, 1881a, p. 192, designating Goldfuss, 1831 in 1826–1844, pl. 50,*7a–b,* as lectotype of *S. costatus*] [=*Milleria* Goldfuss in Hartmann, 1830, p. 45 (type, *Solanocrinites costatus* Goldfuss, 1829 in 1826–1844, p. 166); =*Solacrinus* Agassiz, 1836, p. 196, *nom. van.;* =*Solanocrinus* Münster, 1839, p. 89, *nom. van.*]. Centrodorsal moderately high discoidal or truncated conical, more or less 5-sided, with 10 columns of 1 to 3 large cirrus sockets separated by distinct ridges. Aboral apex flattened or concave, commonly rugose or with radiating irregular furrows. Rod-shaped basals generally exposed interradially. Vestigial infrabasals occur in *S. gresslyi*. Exposed surface of radials commonly moderately large and may be slightly overhanging. Interarticular ligament area rather low. Adoral muscle fossae low, forming narrow bands along adoral edge or low triangular areas separated by a median notch. First and second primibrachials fused or joined by synostosis; rays divided at primibrachial 1 in fused primibrachials or at primibrachial 2. Secundibrachials commonly wedge shaped and tumid to spinose. Arms may be biserial. Syzygies in *S. depressus* (d'Orbigny, 1852 in 1850–1852) but absent in *S. gresslyi* (Étallon, 1862). [The holotype of the Tithonian *S. costatus* has a comparatively narrow radial cavity. Except for this character, the cups and centrodorsals of the upper Oxfordian *Solanocrinites gresslyi* (Étallon) are quite similar. A series of well-preserved remains of this characteristic *Solanocrinites*, collected at a single locality in the neighborhood of Basel, are figured herein. Specimens include a basal circlet with vestigial infrabasals and separated and fused primibrachials. There are no syzygies present

among 1500 brachials examined of this species. *S. lambertsi* Sieverts-Doreck (1958a), figured by Rasmussen (1978, fig. 585,*2b–d*), is considered to be a synonym of *S. gresslyi*.] *Middle Jurassic–Upper Jurassic (Tithonian):* Germany, France, Poland, Switzerland.——Fig. 38*a–b*. **S. costatus;* cup with centrodorsal, *a*, lateral, *b*, distal, Kimmeridgian, Germany, lectotype, IPB Goldfuss 378a, ×2.5 (Goldfuss, 1829 in 1826–1844).——Fig. 38*c–d*. *S. depressus* (d'Orbigny), Oxfordian, France; *c,* crown, centrodorsal missing, MNHN B11492, ×1; *d*, brachial syzygy, ×3 (de Loriol, 1889 in 1882–1889).——Fig. 38*e–s*. *S. gresslyi* (Étallon, 1862), Oxfordian, France; *e–g,* cup with centrodorsal, *e*, lateral, *f*, aboral, *g*, distal, NMB M10599, ×3.5; *h–i*, cup with conical centrodorsal and granular exposed surface of radials, *h*, lateral, *i*, aboral, NMB M10600, ×3.5; *j*, proximal view of cup with basal circlet and vestigial infrabasals, NMB M10601, ×3.5; *k–l*, fused primibrachials 1 and 2 with suture still visible, *k*, adoral, *l*, proximal, NMB M10623, ×5; *m–n*, completely fused primibrachials 1 and 2, *m*, adoral, *n*, proximal, NMB M10624, ×6; *o*, proximal view of primibrachial 2 (synostosis), NMB M10605, ×5; *p–q*, distal secundibrachial, *p*, proximal view, *q*, distal view, NMB M10606, ×5; *r–s*, proximal secundibrachial, *r,* adoral view, *s*, distal view, NMB M10607, ×5 (Hess, new).——Fig. 39. *S. thiollierei* (de Loriol, 1889 in 1882–1889); aboral view of intact specimen, Tithonian, France, holotype, MHNL 20015976, ×1 (P. Ageneau, new).

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

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

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

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

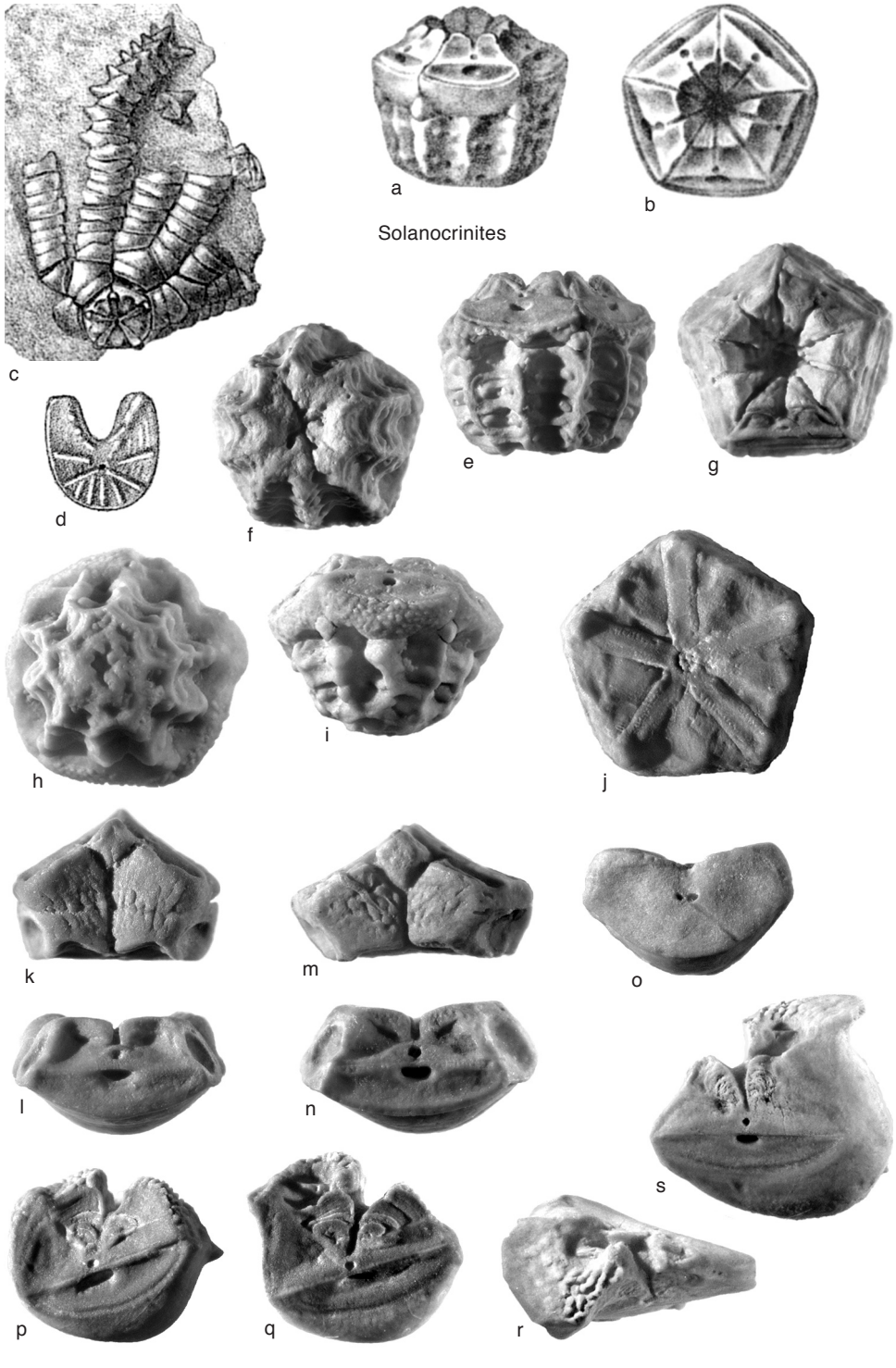
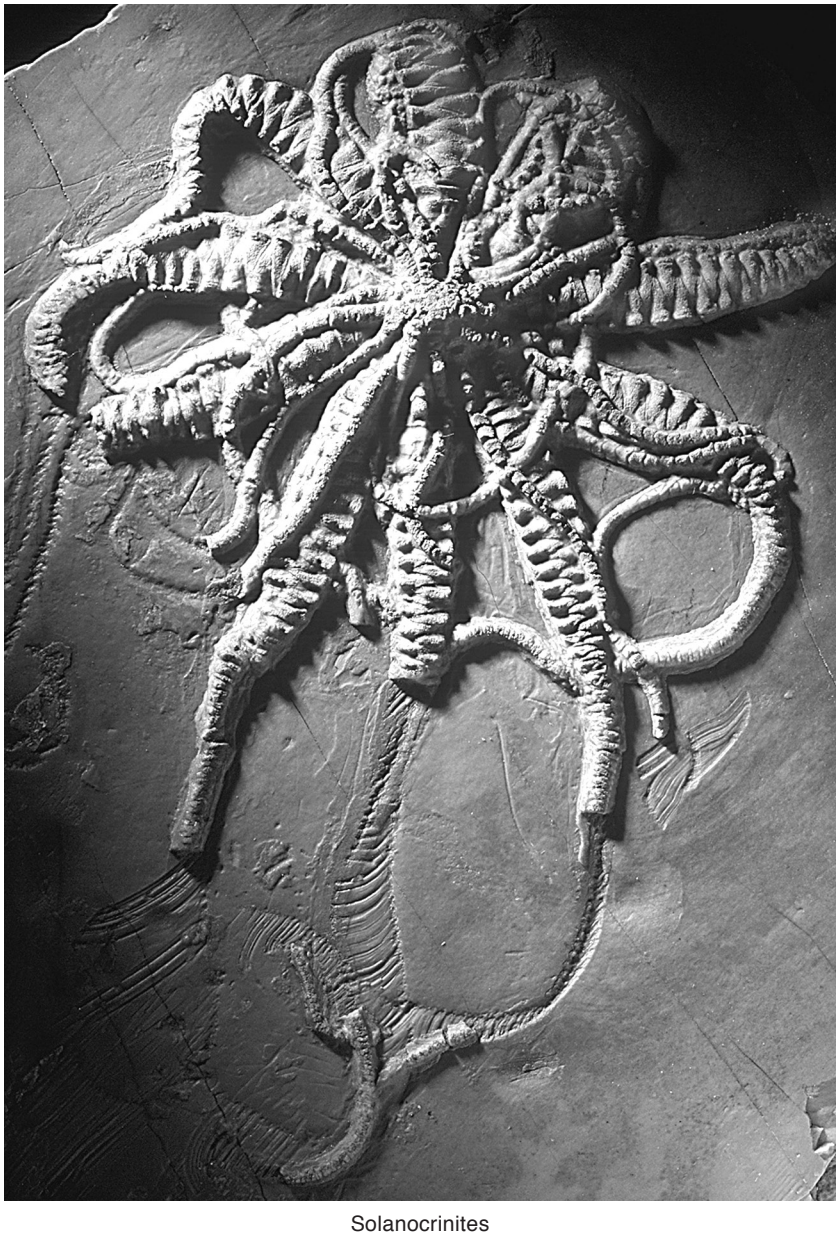


FIG. 38. Solanocrinitidae (p. 76–77).



Solanocrinites

FIG. 39. Solanocrinitidae (p. 76–77).

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

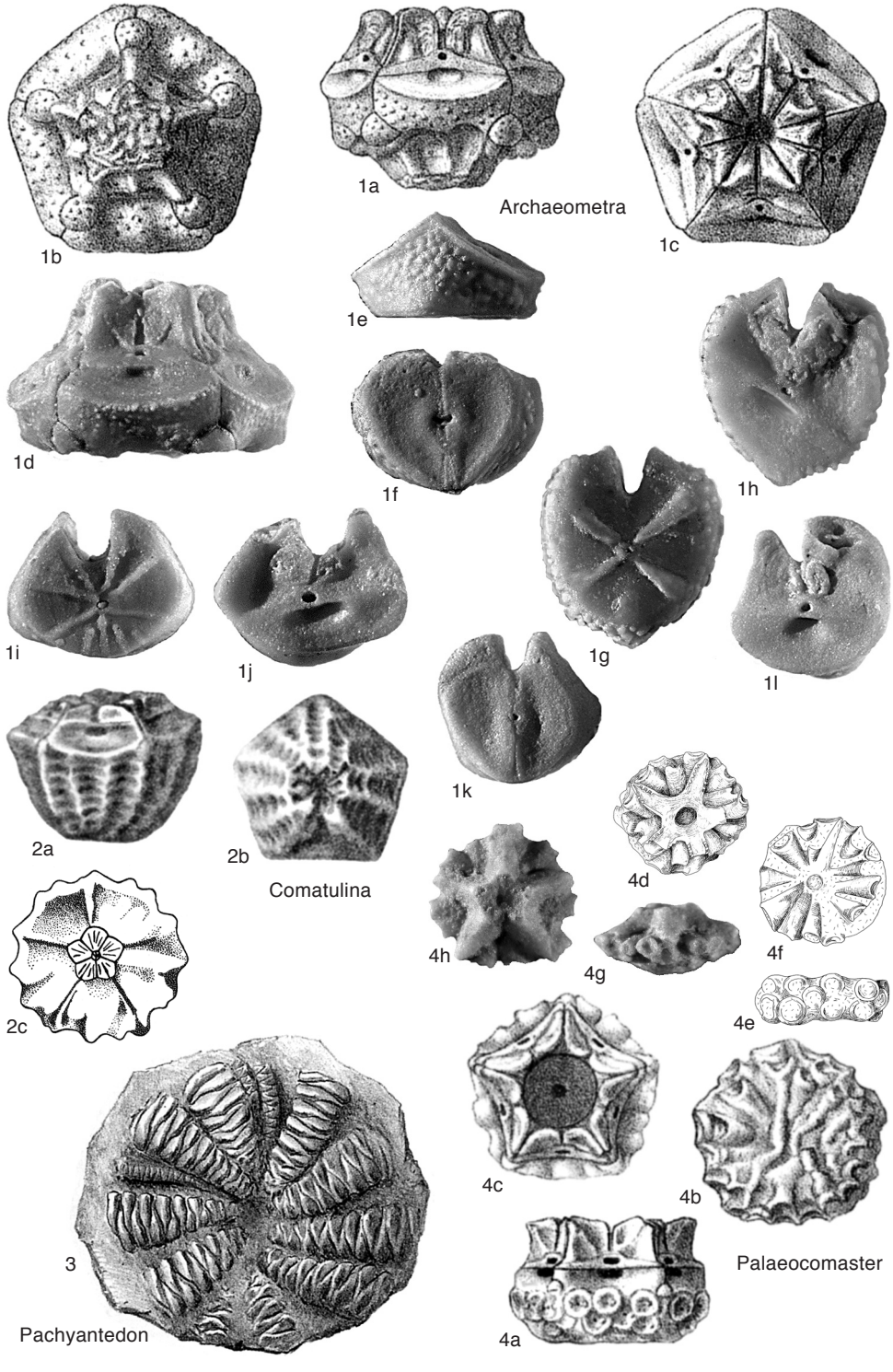


FIG. 40. Solanocrinitidae (p. 77–81).

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

Family DECAMERIDAE Rasmussen, 1978

[Decameridae Rasmussen, 1978, p. 877]

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

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

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

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

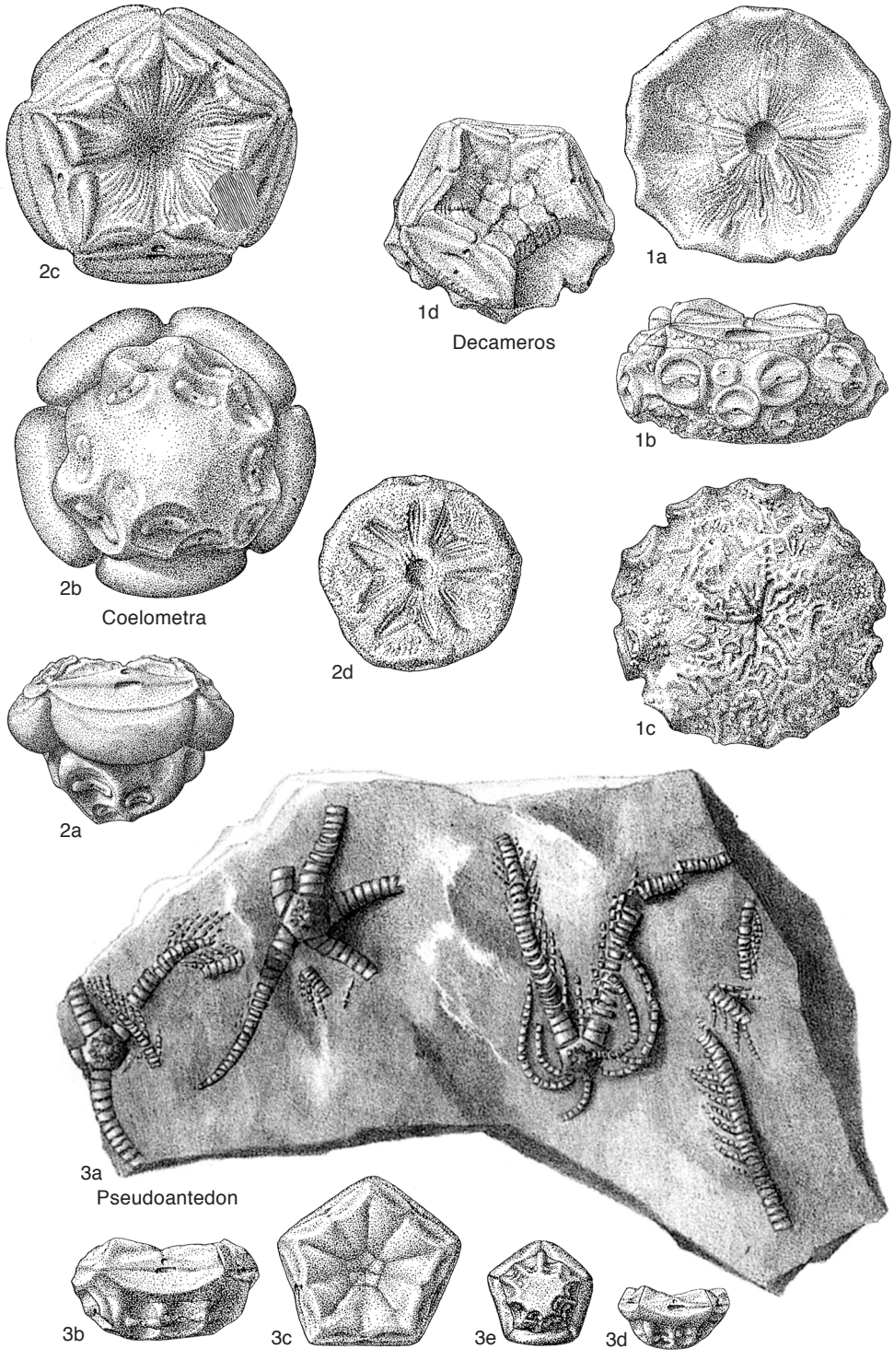


FIG. 41. Decameridae (p. 81).

Family THIOLLIERICRINIDAE A. H. Clark, 1908

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

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

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

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

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

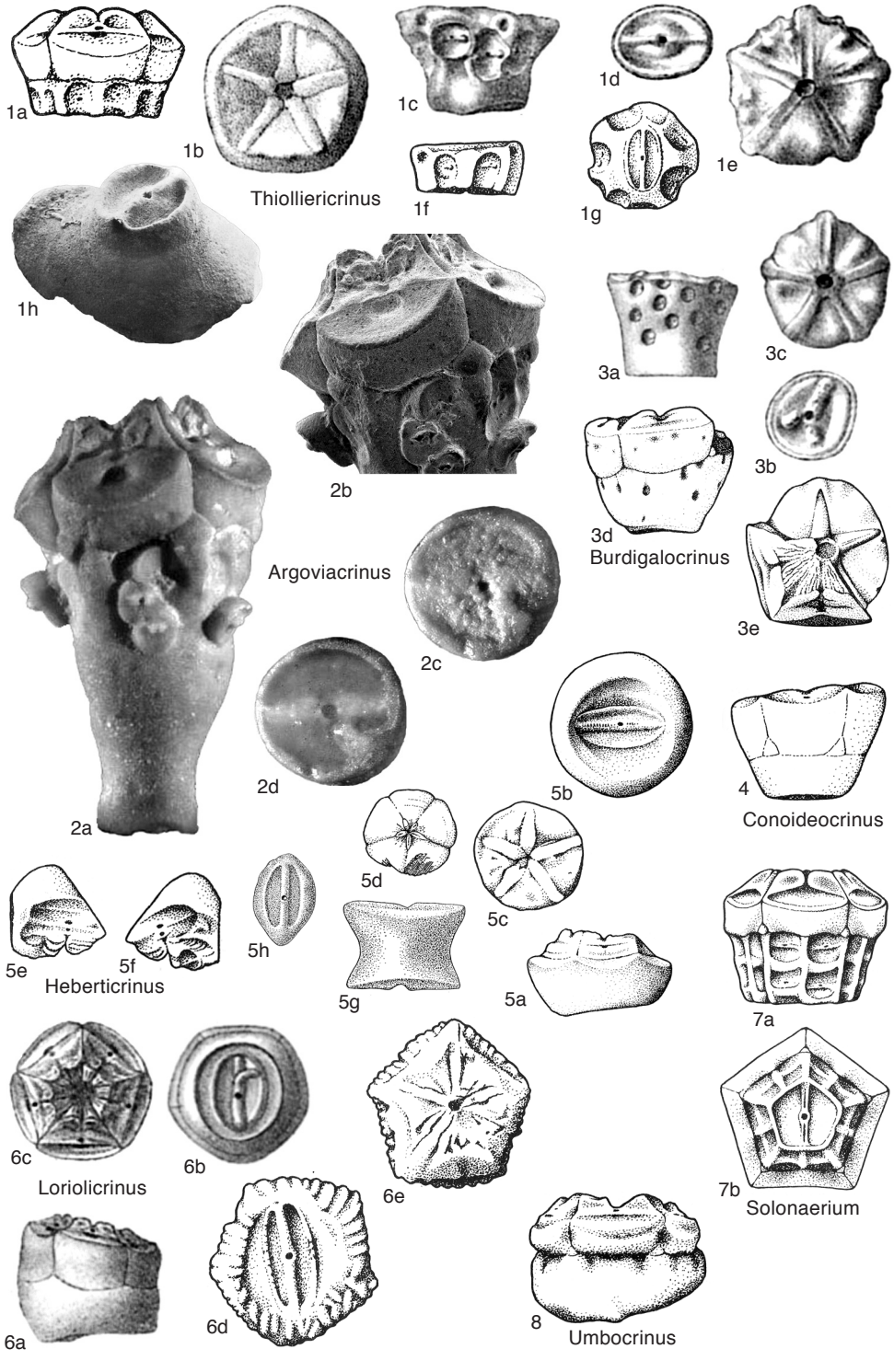


FIG. 42. Thiollericrinidae (p. 83–85).

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

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

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

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

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

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

Superfamily COMASTEROIDEA A. H. Clark, 1908

[*nom. correct.* Hess & Messing, herein, *pro* Comasteracea Rasmussen, 1978, p. 881, *nom. correct. pro* Comasterida Gislén, 1924, p. 229 (established as a superfamily although named a tribe), *nom. transl. ex* family Comasteridae A. H. Clark, 1908h, p. 135]

Centrodorsal thick to thin discoidal or pentagonal, rarely stellate; aboral apex broad, cirrus-free, flat or slightly convex or concave, sometimes with narrow, radiating, interradial impressions (also in fossil Notocrinoidea); dorsal star absent, but center of aboral apex sometimes depressed; centrodorsal cavity less than 30 percent of centrodorsal diameter, larger in very small specimens; adoral surface with interradial furrows for basals, but no radial pits or coelomic impressions. Cirrus sockets generally rather large, without distinct ornament, crowded around centrodorsal margin in 1 to 3 irregular tiers, never forming vertical columns. Some species of *Comatula*, *Comanthus*, *Comaster*, *Phanogenia,* and *Capillaster* with centrodorsal thin, reduced, commonly not projecting below radials and bearing few or no cirri. Basal rosette; basals rod shaped, commonly exposed interradially. Subradial clefts may be present, especially in large specimens. Radials typically with low exposed surface, commonly concealed midradially or barely exposed interradially; rarely completely concealed; well exposed and trapezoidal in species with reduced centrodorsal; well exposed with tongue-like extensions separating bases of adjacent rays in paedomorphic *Comatilia*. Radial articular facet parallel to oral-aboral axis or nearly so and with shallow fossae. Interarticular ligament fossae large, high and wide, generally

higher than aboral ligament fossa and separated by broad and shallow midradial furrow, which is commonly constricted between muscle fossae. Adoral border of interarticular fossae straight or slightly curved, horizontal or slightly sloping. Adoral muscle fossae low, always smaller than interarticular ligament fossae, forming narrow bands along horizontal adoral edge. Radial cavity large, with a spongy calcareous filling in living specimens. Rays divided at least at primibrachial 2, commonly up to several times more and producing as many as 180 undivided arms. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2, or modified synarthry either relatively featureless or resembling syzygies. True syzygies present only in *Comatula*. First pinnule on secundibrachial 2 (when series composed of 4 ossicles). Pinnulation incomplete only in *Comatilia*, which lacks several pinnules after the first pair. Oral pinnules slender, flagellate, of numerous short pinnulars. Distal pinnulars of at least some oral pinnules bearing a comb formed by peg- or bladelike teeth, 1 or 2 per pinnular. Similar combs present elsewhere only in some Heliometrinae (Antedonoidea). Middle and distal pinnules commonly extremely spiny. Arms arising farthest away from the eccentrically placed mouth (=posterior) commonly shorter than those arising closest to mouth, sometimes lacking ambulacral groove but with better developed gonads. Mouth typically displaced off center or marginal, and anal papilla central or subcentral on disk (commonly less so in juveniles); mouth central or subcentral in *Phanogenia*, *Palaeocomatella*, *Aphanocomaster*, *Comissia*, *Rowemissia,* and *Comatilia*. [The more or less marginal mouth and the modified posterior arms and specialized pinnules indicate that this is a specialized group among comatulids. Comasteridae resemble Solanocrinitoidea in their discoidal centrodorsals, large, cirrus-free, aboral apex, distinct cirrus sockets, rod-shaped basals, steep radial articular facet with low muscle fossae, and large radial cavity. Rasmussen (1978) transferred several Jurassic and Cretaceous species recorded under the genera *Actinometra* (=*Comatula*) and *Palaeocomaster* to Solanocrinitoidea.] *Paleogene (Eocene)–Holocene.*

Family COMASTERIDAE A. H. Clark, 1908

[Comasteridae A. H. Clark, 1908h, p. 135] [=Actinometridae Bather, 1899, p. 923]

Characters as for superfamily. [The family name Comatuladae Fleming, 1828, p. 494 (=Comatulidae d'Orbigny, 1852 in 1850–1852, p. 138), based on *Comatula,* was used for all comatulids as in the order Comatulida A. H. Clark, 1908h. A. H. Clark (1908h) erected the family Comasteridae to accommodate species in the genus *Actinometra* Müller. During the following 2 decades, he established 3 subfamilies and 20 genera and subgenera, an output that culminated in a massive monograph (A. H. Clark, 1931 in 1915–1950) still critical to any taxonomic study of the family. A. M. Clark and Rowe's (1971) key to shallow Indo-western Pacific members of the family is based chiefly on A. H. Clark (1931 in 1915–1950). In 1986, Rowe and others (1986) and Hoggett and Rowe (1986) revised the Comasteridae, emphasizing different diagnostic features than recognized by A. H. Clark (1931 in 1915–1950); notably the pinnule comb form. Their results have proven to be a very useful guide to the identification of Indo-western Pacific reef-dwelling species (Messing, 1994, 1998). Messing (1995a, 1995b, 1998) described 1 new species and 2 new genera, discovered new diagnostic characters for 2 other genera, and reassigned several species to different genera. This new information altered the characteristics of several abundant and widespread genera and led Messing (2001) to prepare a new dichotomous, artificial (nonphylogenetic) key that remains chiefly based on Hoggett and Rowe (1986). Morphological characteristics have not yet been examined in detail using phylogenetic techniques. For example, Hoggett and Rowe (1986) placed *Comaster* (now *Phanogenia*) and *Comanthus* in separate subfamilies based on different distributions of syzygies, although both share

uniquely similar modified oral pinnule combs that occur at intervals to near the arm tip, a combination of features unknown in any other comasterid. In addition, recent classifications (Hoggett & Rowe, 1986; Messing, 2001) rest on characters that occur only in taxa with more than 10 arms, so that a quarter of the genera cannot be assigned to a subfamily. Several genera listed under Comasteridae in Rasmussen (1978, p. 883) have been removed from the family (*Comatonia* and *Microcomatula* to Antedonidae) (Messing, 1981; Hoggett & Rowe, 1986) or synonymized (*Comanthoides* under *Cenolia*) (Rowe & others, 1986). Rasmussen (1978) also incorrectly included the antedonid *Ctenantedon* in the Comasteridae. The molecular phylogenetic reconstruction of White and others (2001) of the family based on 30 species in 15 genera returned most but not all morphologically defined genera examined; support for subfamilies was less clear. Of the 19 extant families of comatulids, the Comasteridae ranks second only to Antedonidae in numbers of species and breadth of distribution. Of the 95 species currently recognized, approximately 65 occur on Indo-western Pacific coral reefs and adjacent deeper waters; 11 are endemic to southern China–Japan, 10 to southern temperate Australia–New Zealand, 8 to the tropical western Atlantic, and 1 to the northeastern Atlantic. Approximately 20 species are restricted to depths below 100 m, and 10 of these occur only below 200 m (Messing, 2001). Comasterids dominate the modern coral reef crinoid fauna and typically account for more than half the crinoid species (and most of the individuals) present in tropical shallow-water surveys in both the Indo-western Pacific and western Atlantic (Meyer, 1973; Messing, 1994, 1998, 2001).] *Paleogene (Eocene)–Holocene.*

Subfamily COMASTERINAE A. H. Clark, 1908

[*nom. transl.* A. H. Clark, 1909h, p. 175, *ex* Comasteridae A. H. Clark, 1908h, p. 135] [=Actinometridae Bather, 1899, p. 923, *sensu* Jaekel, 1918, p. 74; =Comanthinae Hoggett & Rowe, 1986, p. 124, *partim*]

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

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

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

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

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

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

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

Subfamily COMATULINAE Fleming, 1828

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

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

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

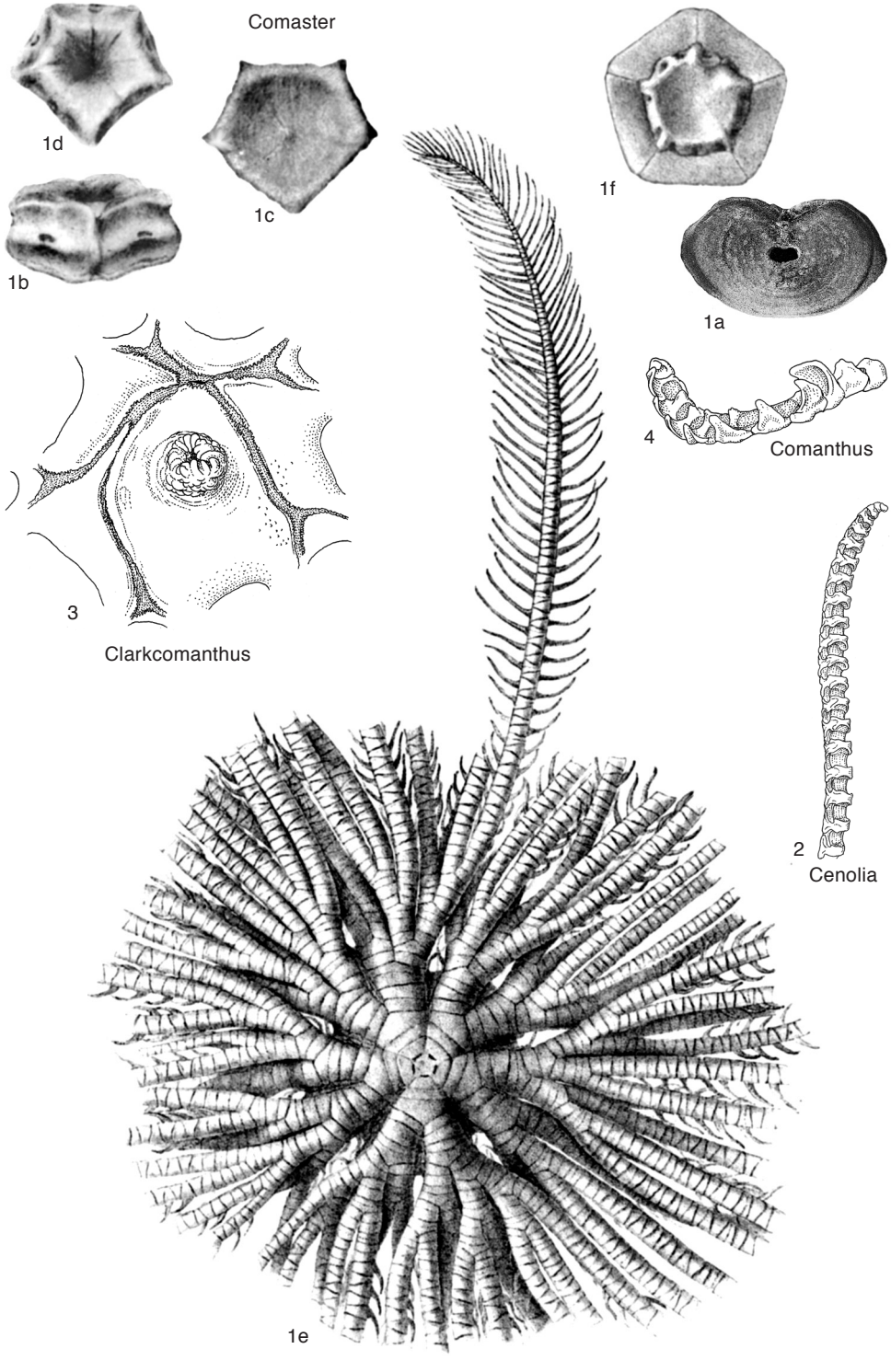


FIG. 43. Comasteridae (p. 87–88).

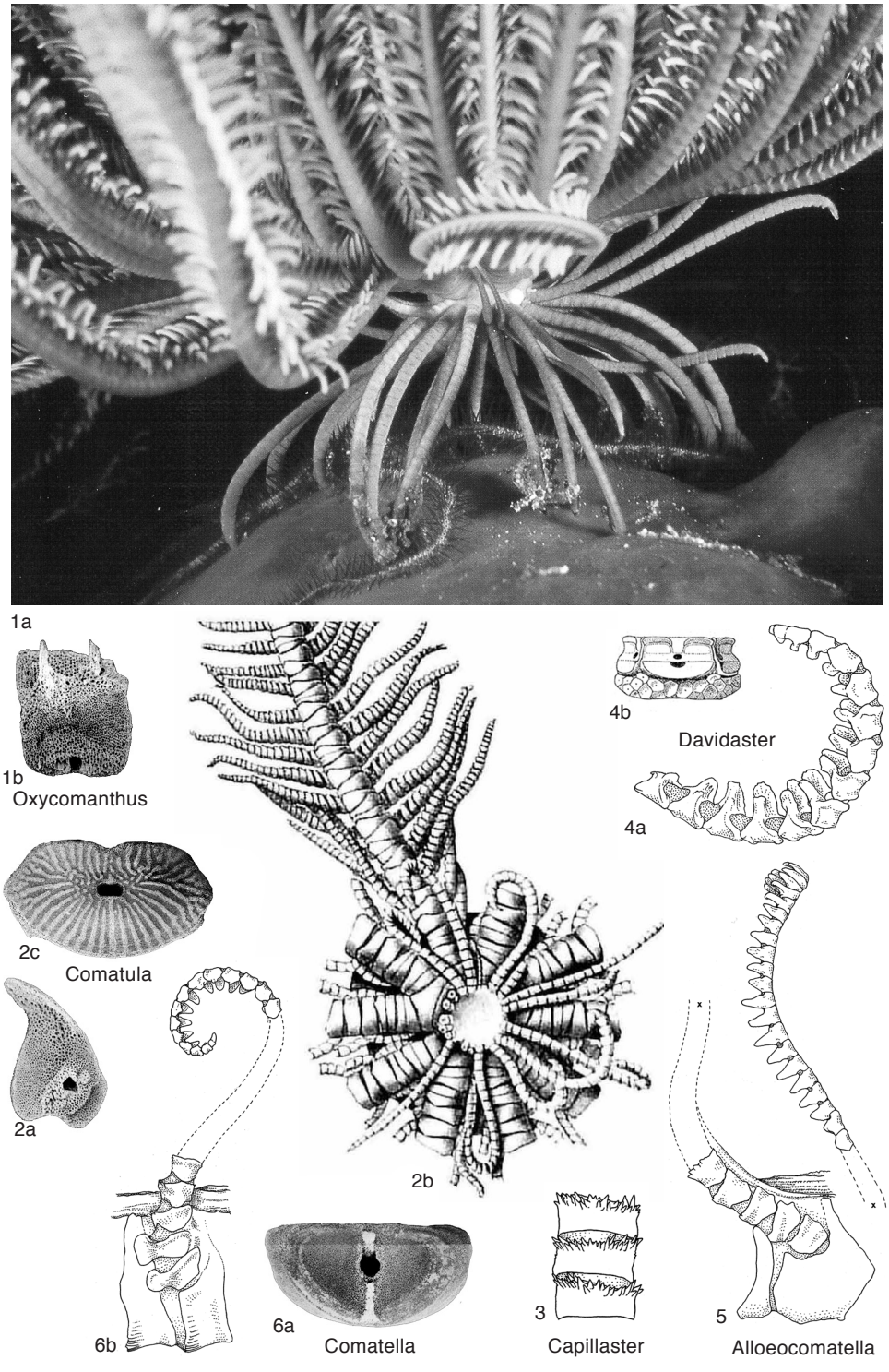


Fig. 44. Comasteridae (p. 88–94).

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

Subfamily CAPILLASTERINAE A. H. Clark, 1909

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

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

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

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

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

Subfamily PHANOGENIINAE White & others, 2001

[Phanogeniinae White & others, 2001, p. 136] [=Comasterinae Hoggett & Rowe, 1986, p. 124, *partim*]

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

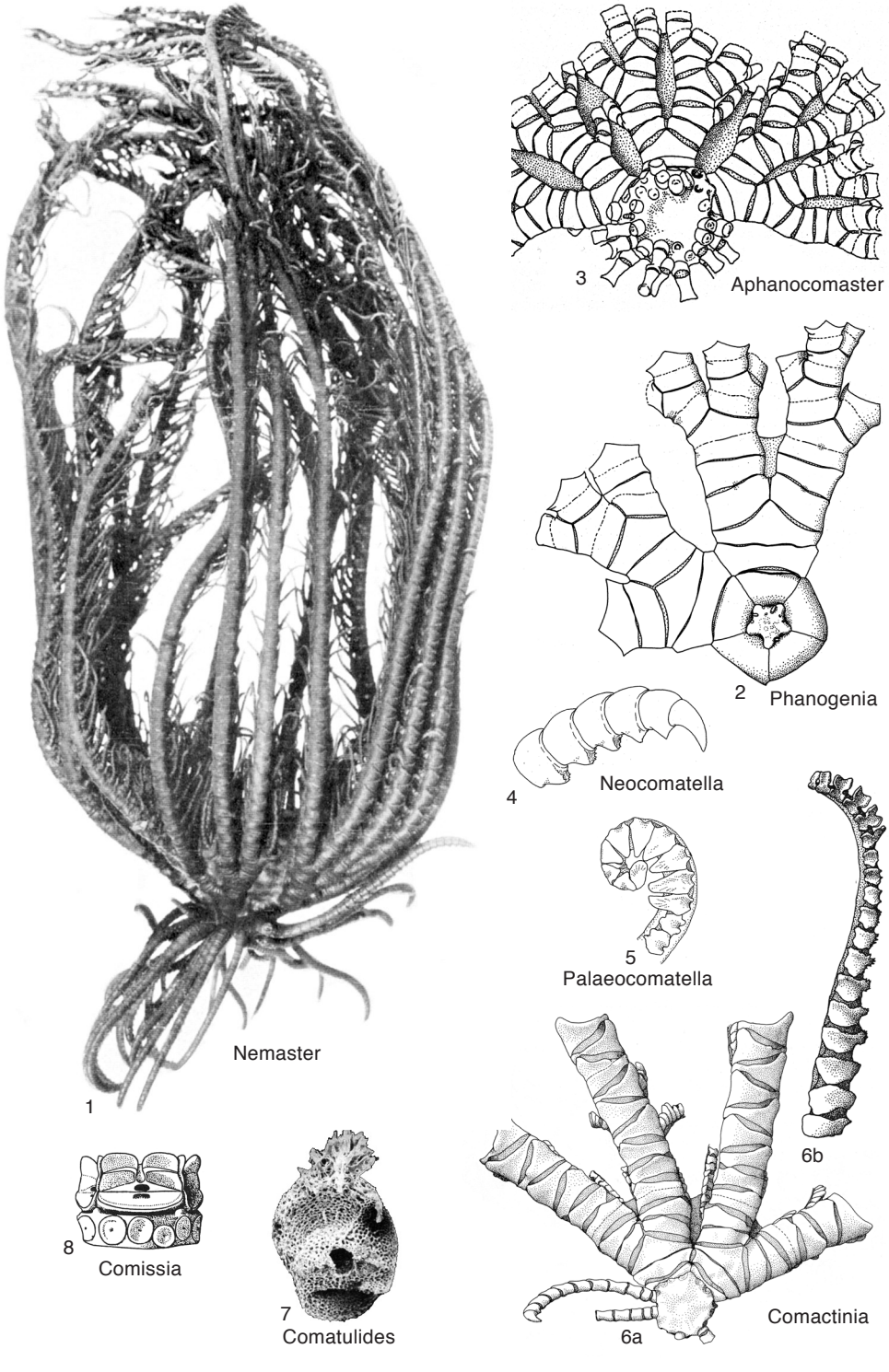


FIG. 45. Comasteridae (p. 91–95).

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

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

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

Aphanocomaster MESSING, 1995b, p. 657 [**Comaster pulcher* A. H. CLARK, 1912d, p. 22; OD]. Cryptosynarthry between primibrachials 1 and 2. Two or 4 secundibrachials consisting of 1 or 2 synarthrial pairs, rarely 4 brachials with syzygy between brachials 3 and 4. Two or 4 tertibrachials joined by synarthry, syzygy, 2 synarthrial or syzygial pairs, or a synarthry followed by a syzygy. Arms up to 39, arising from secundibrachials typically with syzygy between brachials 3 and 4; arms arising from tertibrachials with syzygy between brachials 1 and 2 and 3 and 4 (rarely only one syzygy). Comb teeth single, triangular or spade shaped, confluent with exterior side of pinnulars; initial tooth sometimes slightly twisted but not oriented transversely. Mouth

central. [Messing (1995b) erected this genus to accommodate the holotype of *Comaster pulcher,* because the unique and variable arrangement of brachitaxes (including tertibrachials composed of 2 successive synarthrial or syzygial pairs) is unknown elsewhere in the Comasteridae, and because pinnule combs do not resemble those diagnostic of *Comaster* (now *Phanogenia*).] *Holocene:* tropical western Pacific Ocean (littoral to sublittoral).——Fig. 45,*3*. **A. pulcher* (Clark); aboral view of centrodorsal and proximal part of 3 rays, Indonesia, holotype, UA U.Cri.-2114, ×3.5 (Messing, 1995b, courtesy of the *Bulletin of the Biological Society of Washington*).

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

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

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

Subfamily UNCERTAIN

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

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

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

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

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

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

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

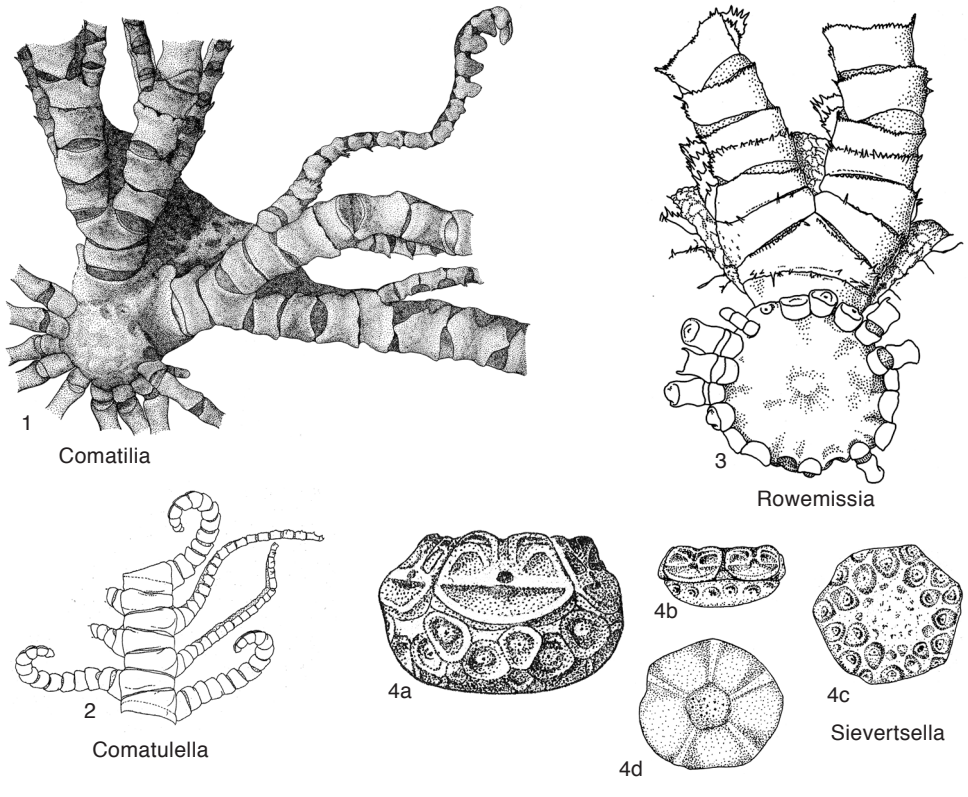


FIG. 46. Comasteridae (p. 95–96).

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

Superfamily UINTACRINOIDEA Zittel, 1879

[*nom. transl.* HESS & MESSING, herein, *pro* Uintacrinidae ZITTEL, 1879 in 1876–1880, p. 345, 375] [=Uintacrinida BROILI in ZITTEL, 1921, p. 186, *nom. transl.* SIEVERTS-DORECK in MOORE, LALICKER, & FISCHER, 1952, p. 614; =suborder Innatantes A. H. CLARK, 1909h, p. 174]

Large, subspheroidal calyx of thin, polygonal plates without column or cirriferous centrodorsal. Second primibrachials axillary, no further division. Arms composed of low, disk-shaped brachials, semicircular to almost circular in section. Syzygy between primibrachials 1 and 2 and secundibrachials 1 and 2, generally between secundibrachials 3 and 4, with intervals increasing from 3 to more than 6 in succeeding brachials; other arm articulations muscular, with adoral muscle fossae smaller than interarticular ligament fossae. Complete pinnulation beginning on abaxial side of secundibrachial 2. [Based on a cladistic analysis, MILSOM, SIMMS, and GALE (1994) considered *Uintacrinus* and *Marsupites* to be closely related to the Comasteridae, and, thus, classified in the superfamily Comasteroidea. However, comasterids and *Uintacrinus* share no uniquely apomorphic features, with the exception of an eccentric mouth and a more or less central anus (the tegmen is unknown in *Marsupites*). Most comasterids have a synarthry

(flat in some forms; e.g., *Phanogenia*) between primibrachials 1 and 2 and secundibrachials 1 and 2. The globose calyx of *Uintacrinus* and *Marsupites* appears to be an autapomorphy and an adaptation to an exceptional environment, the soupy sediment of the American Niobrara Chalk and the English Chalk. No other crinoid is adapted to a similar situation. MILSOM, SIMMS, and GALE (1994) assigned both genera to a single family, Marsupitidae. However, the only synapomorphies linking the 2 genera are the size of the calyx and the arm structure. *Uintacrinus* and *Marsupites* differ in their calyces and do not overlap stratigraphically. Therefore, they are placed in separate families, although *Marsupites* probably evolved from *Uintacrinus*. According to GALE and others (2008, p. 143), the successive species and subspecies of the superfamily spanning the Santonian–Campanian interval were short ranged (mean duration of 200 kyr) and occur synchronously in precisely the same order on a global scale.] *Upper Cretaceous (Santonian–lower Campanian).*

Family UINTACRINIDAE Zittel, 1879

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

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

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

Family MARSUPITIDAE d'Orbigny, 1852

[Marsupitidae D'ORBIGNY, 1852 in 1850–1852, p. 138; *emend.*, SIMMS, 1988a, p. 284]

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

Marsupites MANTELL in MILLER, 1821, p. 135 [**M. ornatus;* M; =*Encrinites testudinarius* VON SCHLOTHEIM, 1820, p. 339; =*M. milleri* MANTELL, 1822, p. 184; =*Sitularia triangulariformis* CUMBERLAND, 1826, p. 21; =*M. mantelli* BRONN, 1848 in 1848–1849, p. 705; =*M. laevigatus* FORBES in DIXON, 1850, p. 343; =*M. americanus* SPRINGER, 1911, p. 158; =*M. lamberti* BESAIRIE, 1936, p. 203] [=*Sitularia* CUMBERLAND, 1826, p. 21 (type, *S. triangulariformis*, M); =*Marsupiocrinites* DE BLAINVILLE, 1830, p. 244, *nom. van.*, *non* PHILLIPS in MURCHISON, 1839, p. 672]. Characters as for family. [The name *Marsupites* was taken by MILLER (1821) from a manuscript by MANTELL published in 1822. The name *Marsupium* KOENA, recorded by AGASSIZ (1836, p. 194) is presumably a *nomen vanum*, origin untraced.] *Upper Cretaceous (Santonian):* England, France, Germany, Poland, Kazakhstan, Turkmenistan, Crimea, Algeria, Gulf Coast, USA, Canada, Australia,

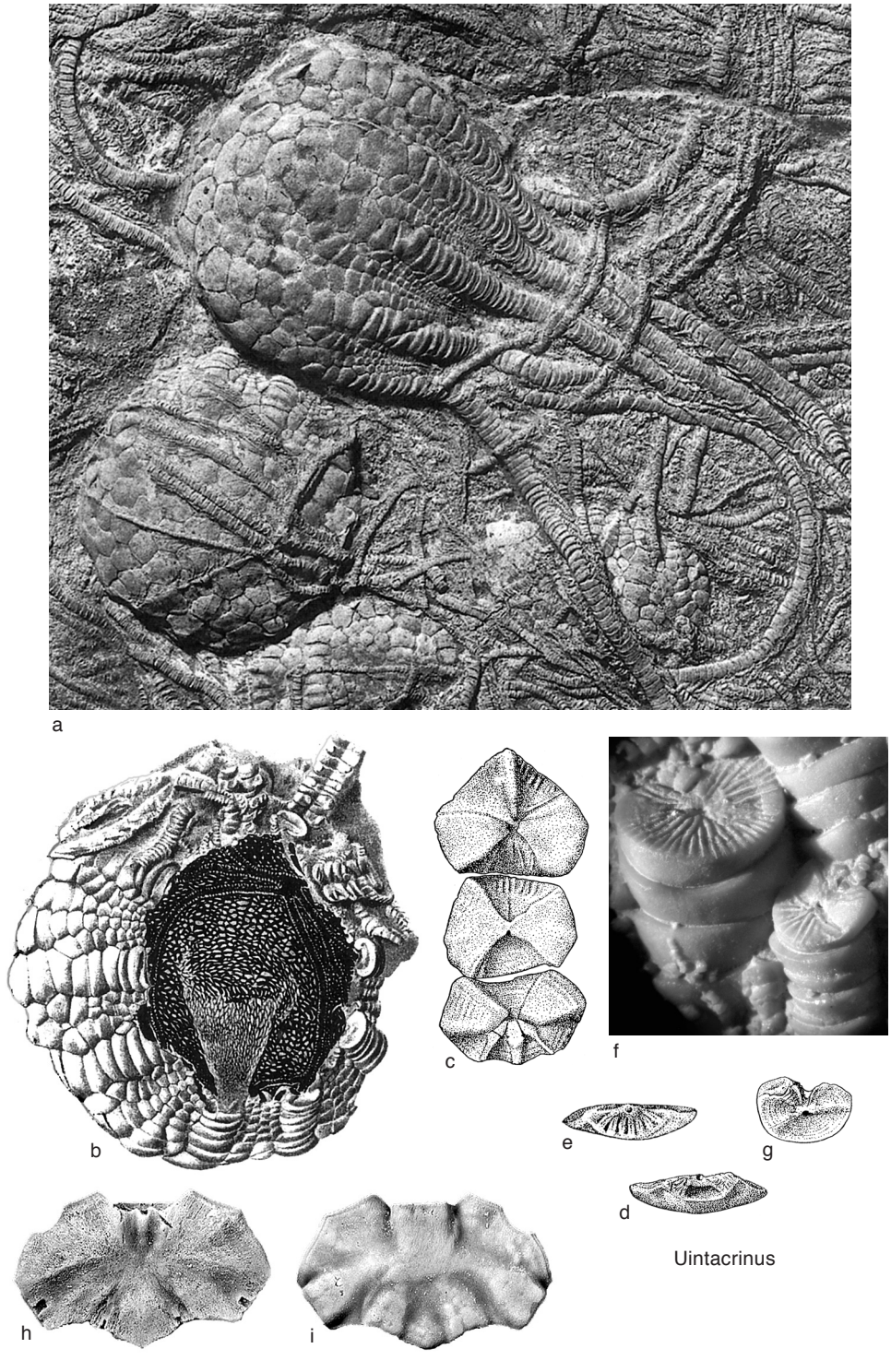


Fig. 47. Uintacrinidae (p. 97).

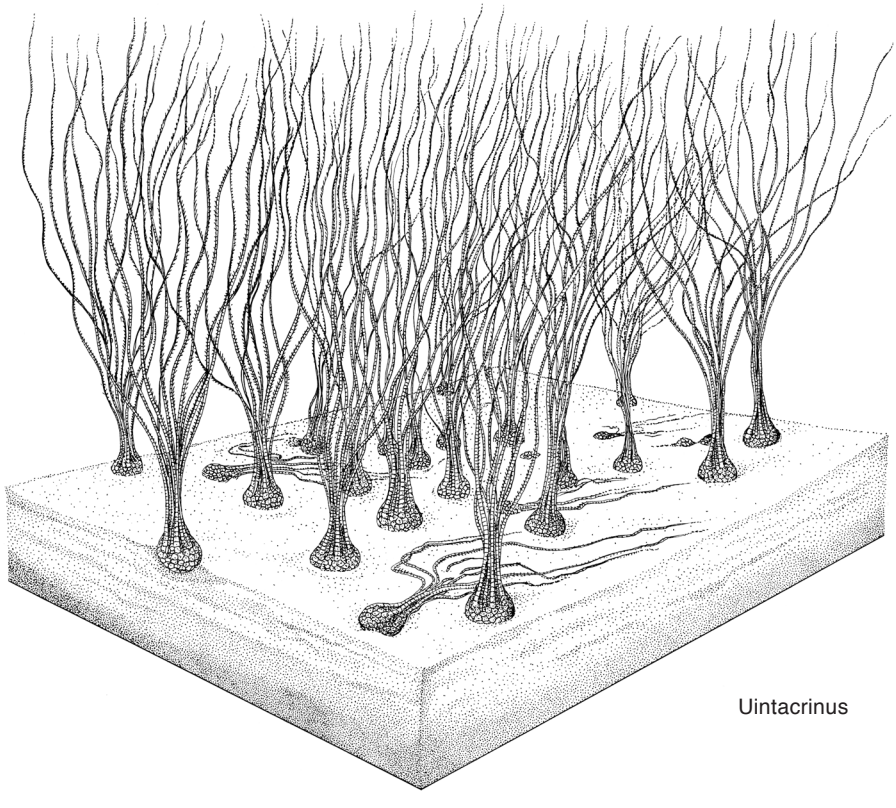


FIG. 48. Uintacrinidae (p. 97).

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

Superfamily MARIAMETROIDEA A. H. Clark, 1909

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

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

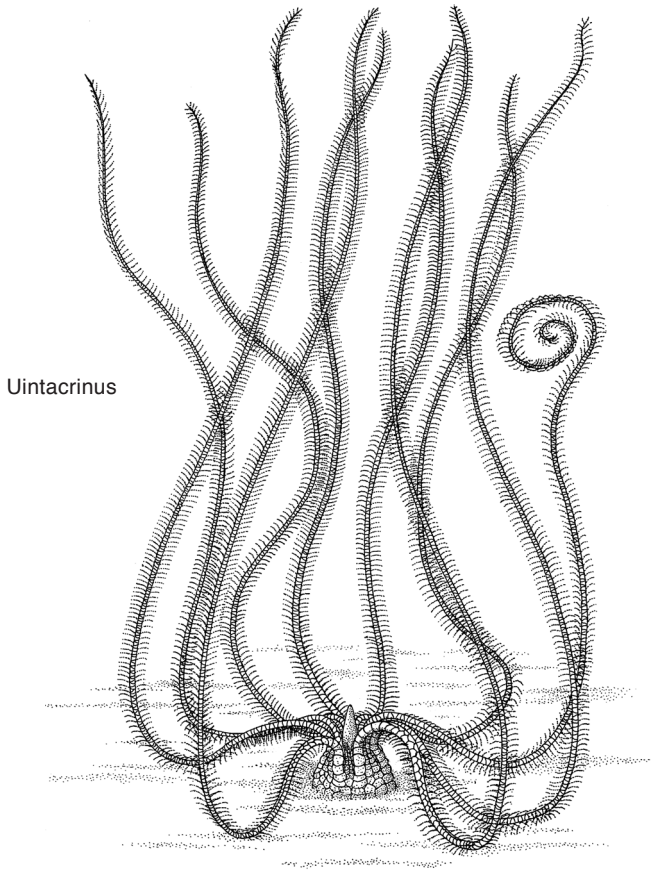


Fig. 49. Uintacrinidae (p. 97).

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

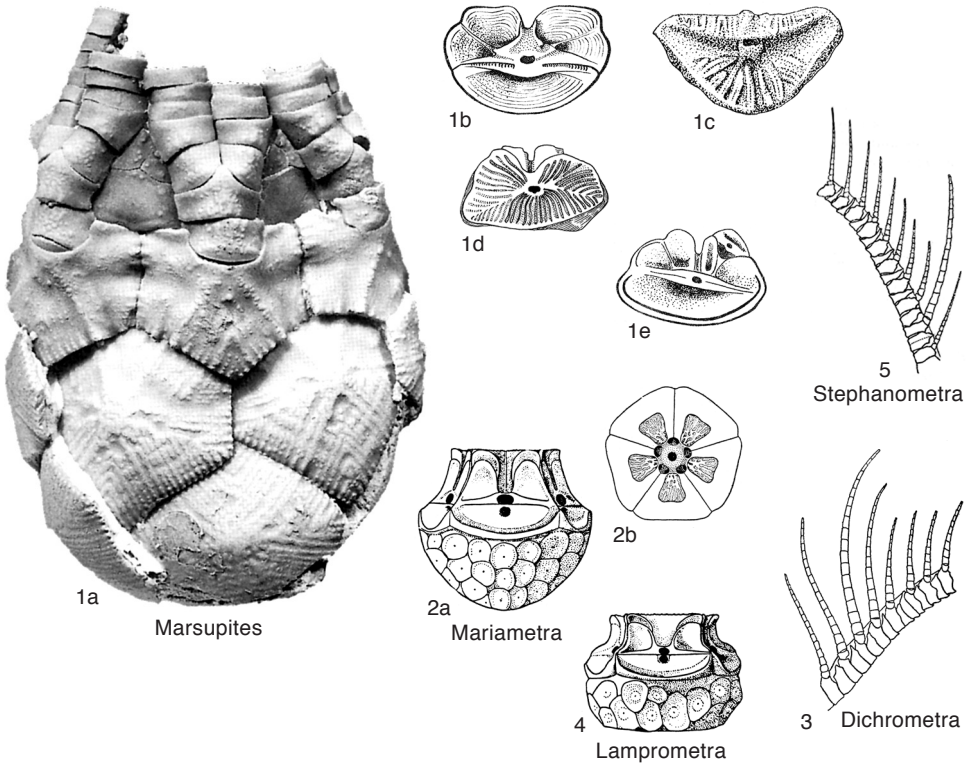


FIG. 50. Marsupitidae and Mariametridae (p. 97–102).

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

Family MARIAMETRIDAE A. H. Clark, 1909

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

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

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

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

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

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

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

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

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

Family COLOBOMETRIDAE A. H. Clark, 1909

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

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

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

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

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

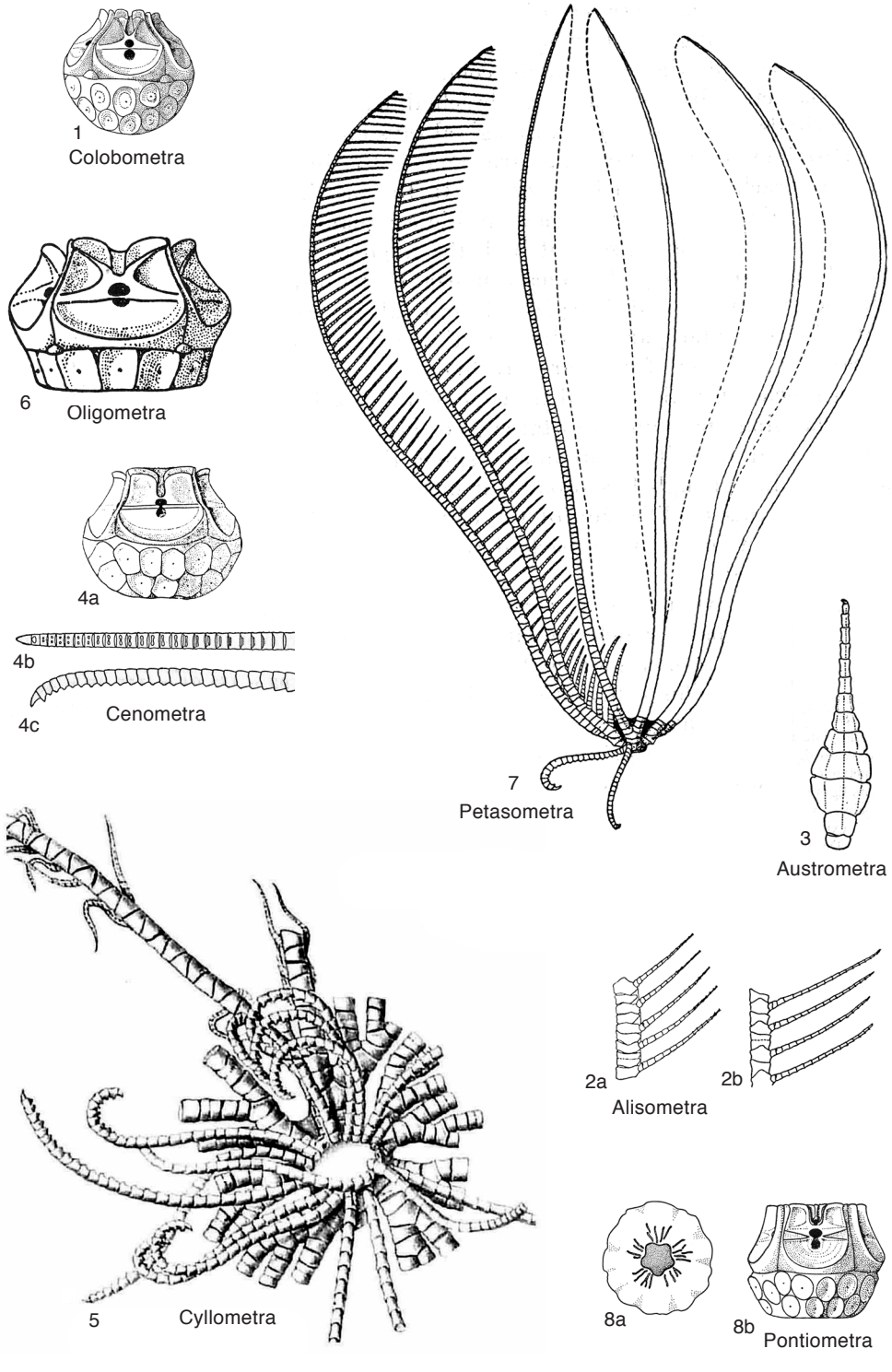


Fig. 51. Colobometridae (p. 102–105).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Petasometra A. H. Clark, 1912h, p. 25 [**Antedon clarae* Hartlaub, 1890, p. 174; OD]. Cirri with aboral transverse ridge on proximal segments, becoming median spine distally. Arms 10 to 22; brachitaxes distal to primibrachials of 4 ossicles. First interior pinnule absent; first and second

exterior pinnules similar. *Holocene:* western Pacific Ocean (littoral to sublittoral).——Fig. 51,*7. *P. clarae* (Hartlaub); lateral view, ×1 (A. H. Clark, 1921 in 1915–1950).

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

Family EUDIOCRINIDAE A. H. Clark, 1907

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

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

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

Family HIMEROMETRIDAE A. H. Clark, 1908

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

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

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

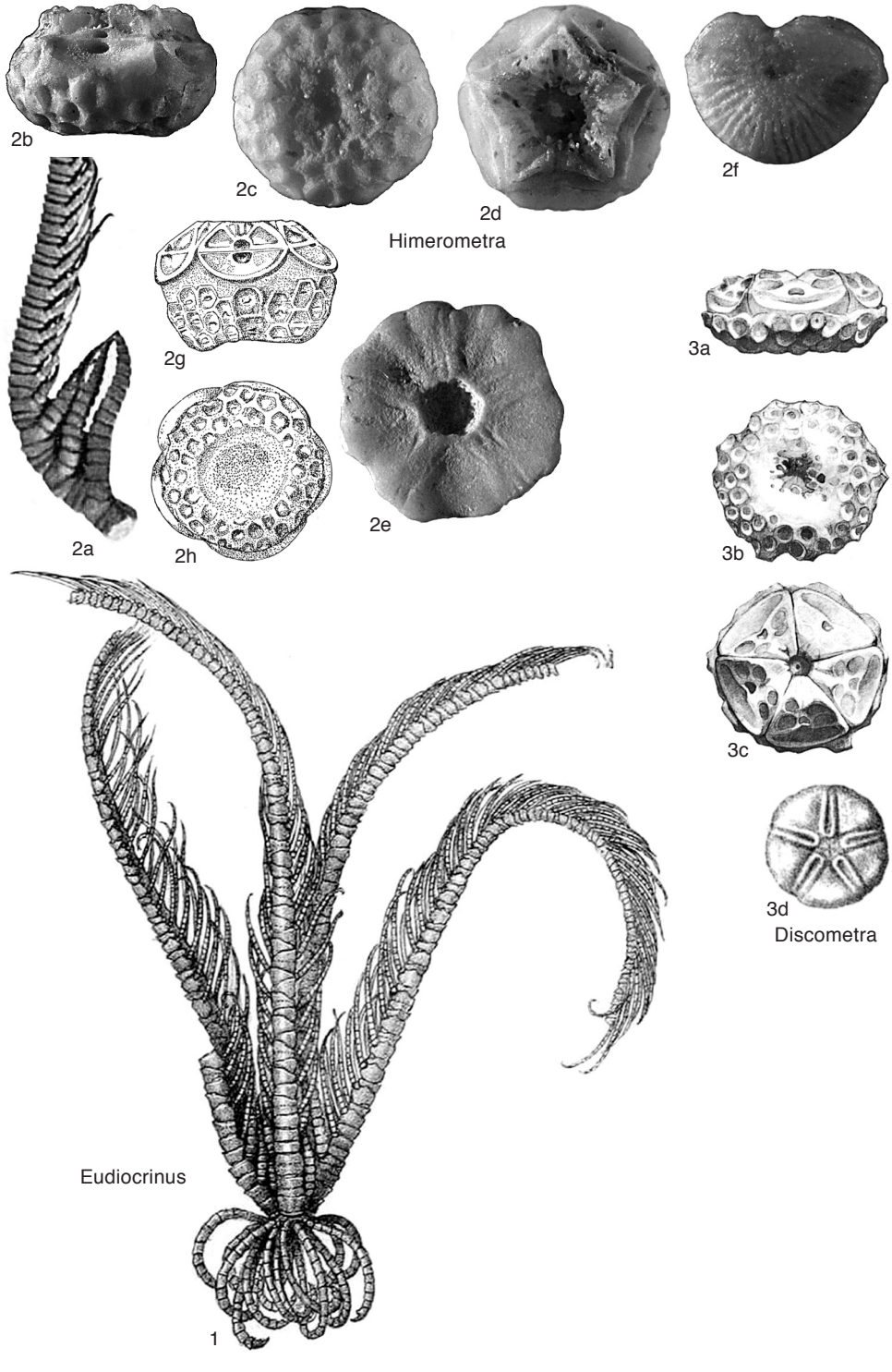


FIG. 52. Eudiocrinidae and Himerometridae (p. 105–107).

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

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

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

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

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

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

Family ZYGOMETRIDAE A. H. Clark, 1908

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

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

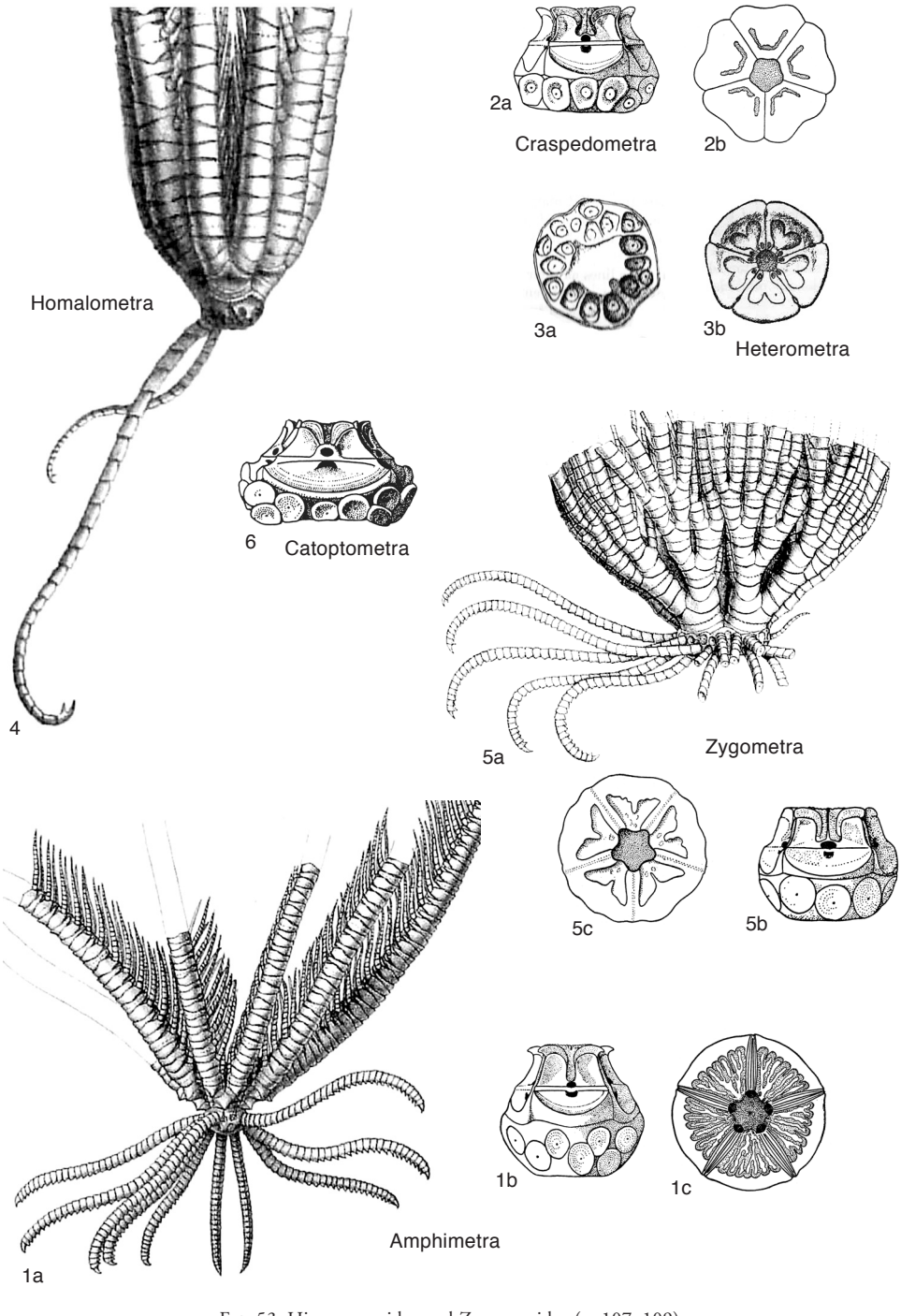


FIG. 53. Himerometridae and Zygometridae (p. 107–109).

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

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

Superfamily TROPIOMETROIDEA A. H. Clark, 1908

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

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

Family TROPIOMETRIDAE A. H. Clark, 1908

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

Centrodorsal large, thick discoidal to low columnar with large, flattened, cirrus-free aboral area. Cirrus sockets large, without distinct ornament, arranged irregularly around margin but tending to form 15 or 20 short columns. Cirri stout, rather short, without aboral spines. Cirrals 20 to 40, short, generally wider than long. Distal cirrals may be laterally compressed. No dorsal star. Shallow radial depressions at edge of centrodorsal cavity may be indicated. Rod-shaped basals not united around center, tapering outward and rarely exposed on surface. Exposed surface of radials low and outward sloping, or concealed. Radial articular facet steep and wide, meeting along interradial suture. Adoral muscle fossae large and wide, approximately twice as high as interarticular ligament fossae and separated from these by a ridge almost parallel to the

fulcral ridge. Radial cavity wide; no central plug. Brachials wider than high. Primibrachial series of 2 ossicles, the first low and wide, and the second an axil; 10 arms only. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Syzygy between secundibrachials 3 and 4 and with intervals of generally 4 to 9 muscular articulations. Pinnules without distinct ambulacral covering plates. *Holocene.*

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

Family ASTEROMETRIDAE Gislén, 1924

[Asterometridae Gislén, 1924, p. 231]

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

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

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

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

Family CALOMETRIDAE A. H. Clark, 1911

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

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

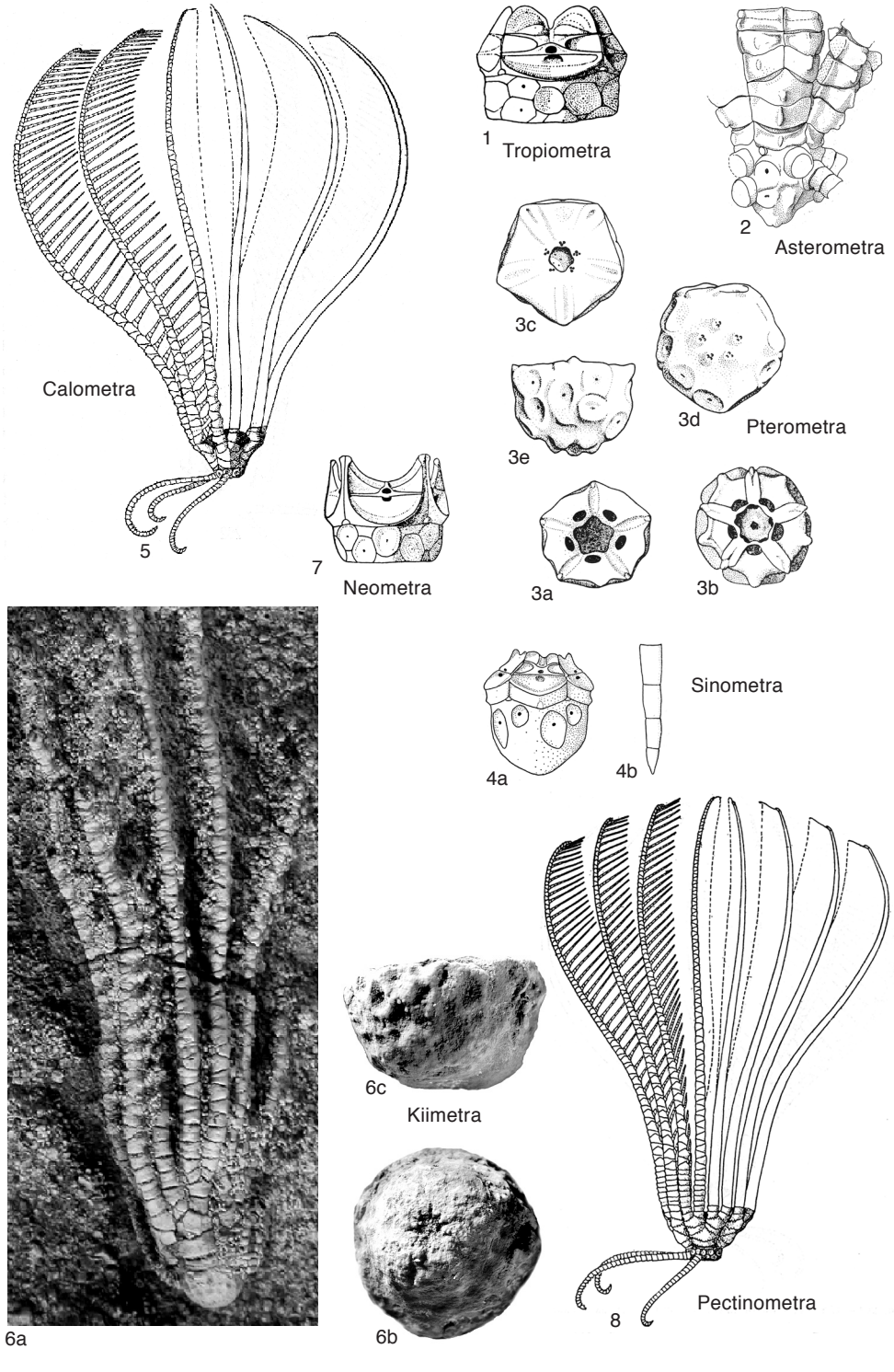


FIG. 54. Tropiometridae, Asterometridae, and Calometridae (p. 110–112).

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

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

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

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

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

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

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

Family CHARITOMETRIDAE A. H. Clark, 1909

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

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

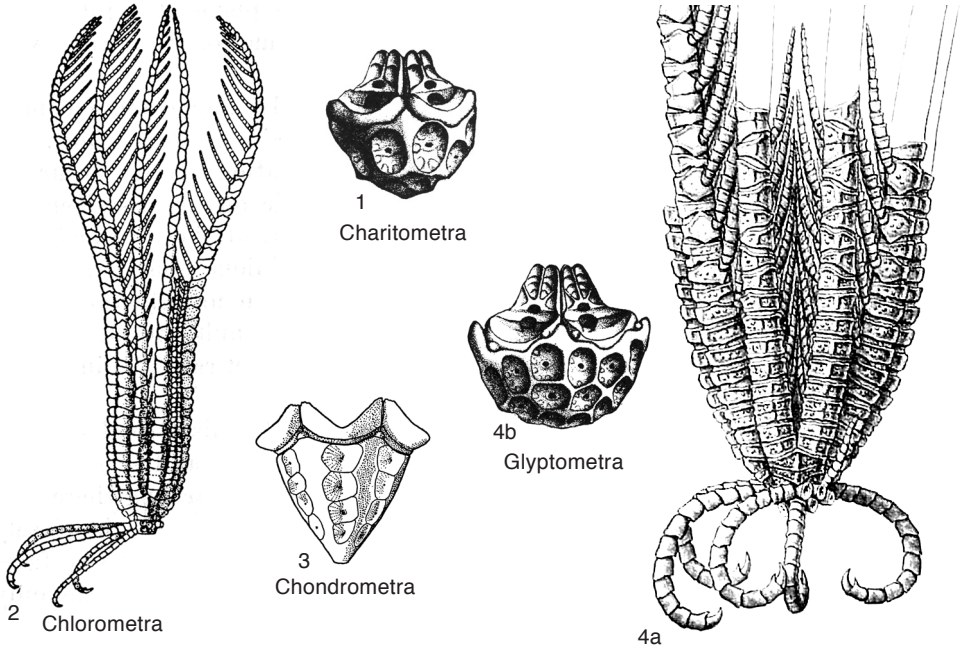


FIG. 55. Charitometridae (p. 113–115).

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

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

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

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

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

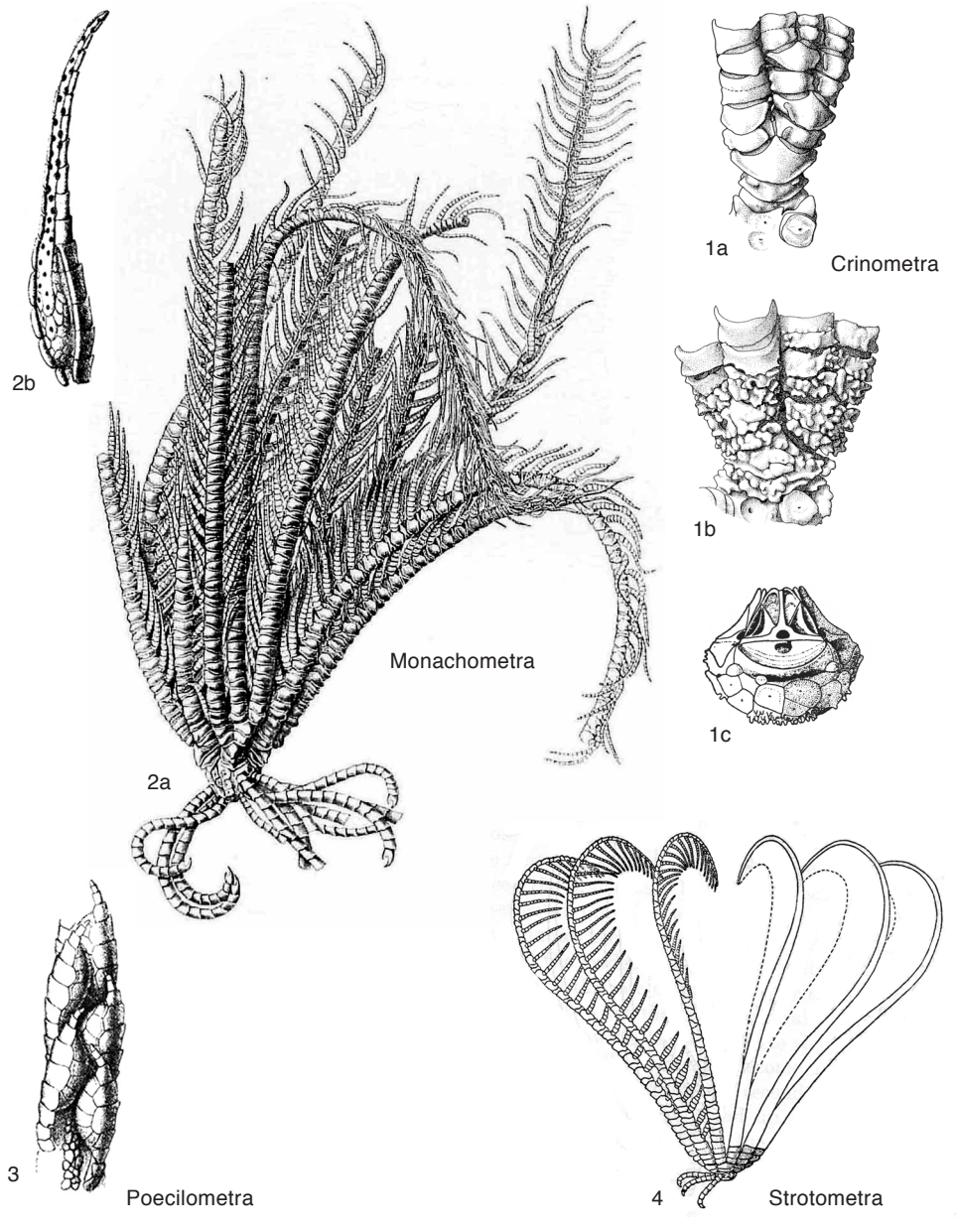


FIG. 56. Charitometridae (p. 113–115).

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

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

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

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

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

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

Family CONOMETRIDAE Gislén, 1924

[Conometridae Gislén, 1924, p. 159]

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

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

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

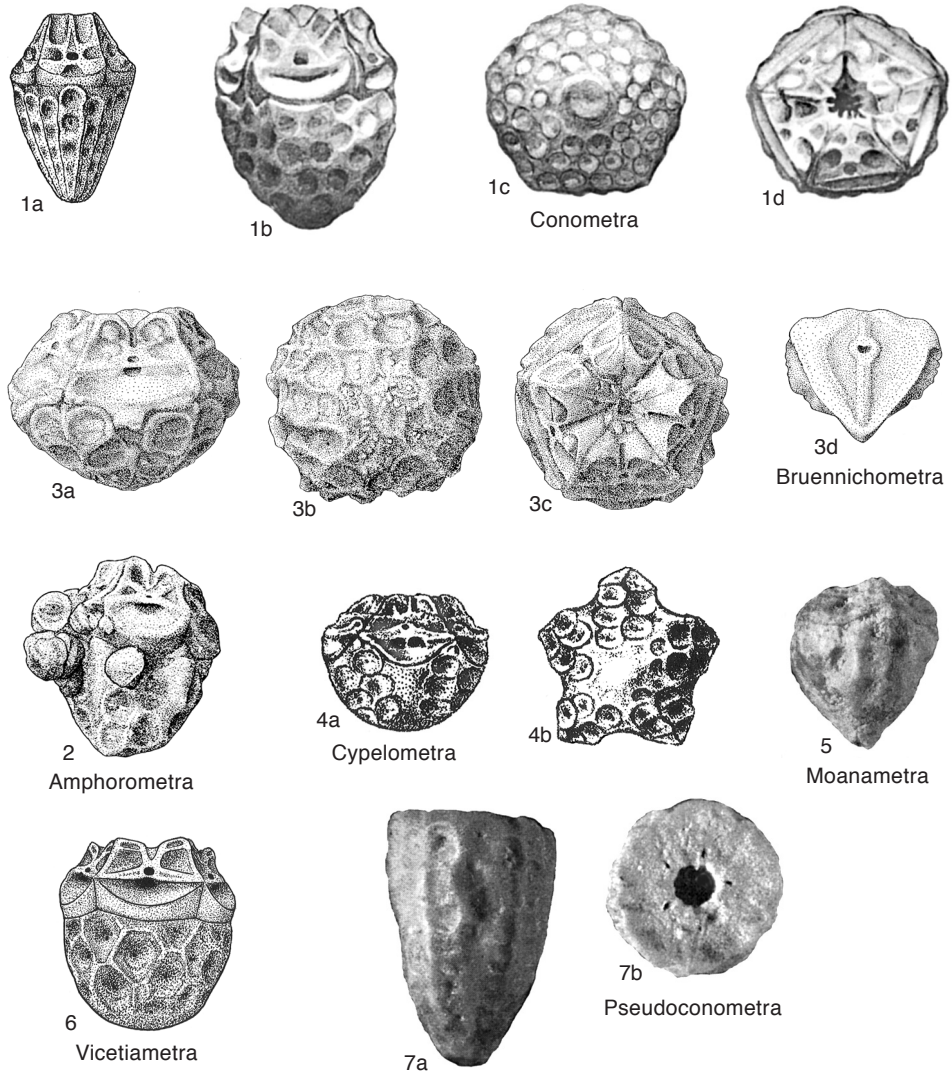


FIG. 57. Conometridae and Pseudoconometridae (p. 115–117).

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

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

a, lateral, *b*, aboral, *c*, distal, MGUH 8992, ×7; *d*, distal view of primibrachial 1, MGUH 8993, ×7 (Rasmussen, 1961).

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

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

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

Family PSEUDOCONOMETRIDAE Eagle, 2001

[Pseudoconometridae Eagle, 2001, p. 83]

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

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

Family PTEROCOMIDAE Rasmussen, 1978

[Pterocomidae Rasmussen, 1978, p. 894]

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

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

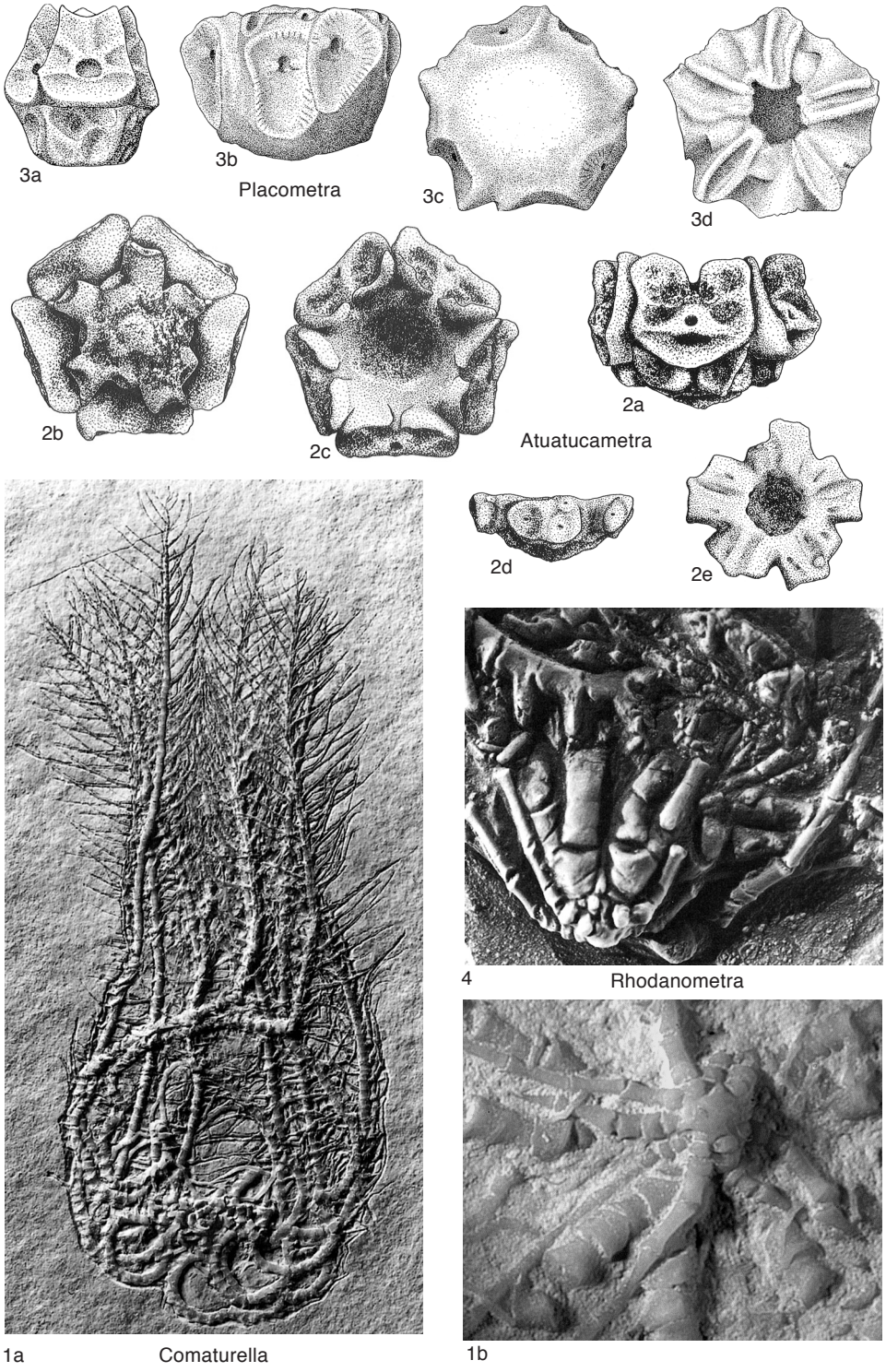


Fig. 58. Pterocomidae (p. 117–119).

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

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

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

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

Family PTILOMETRIDAE A. H. Clark, 1914

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

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

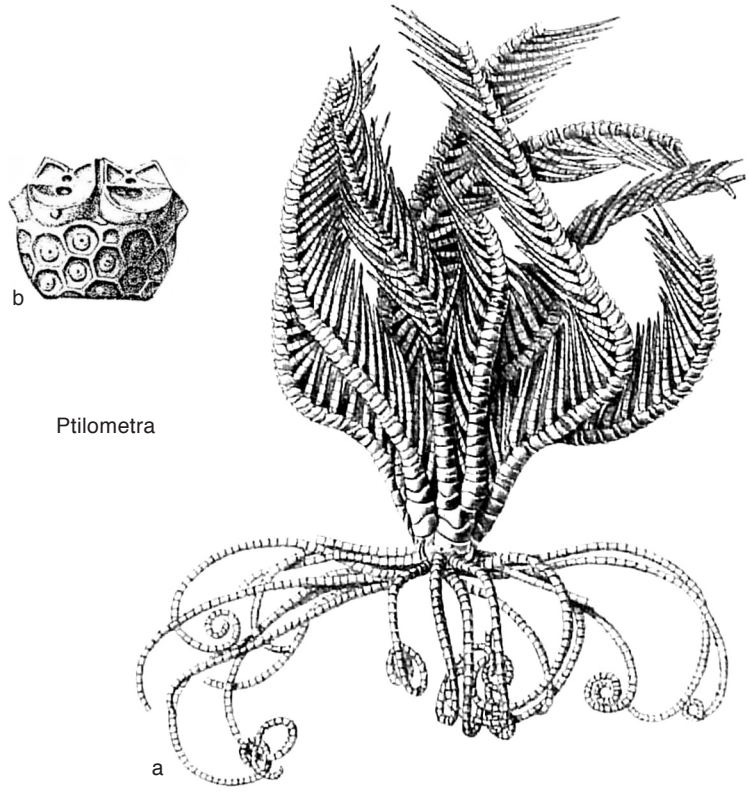


FIG. 59. Ptilometridae (p. 120).

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

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

Family THALASSOMETRIDAE A. H. Clark, 1908

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

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

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

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

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

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

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

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

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

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

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

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

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

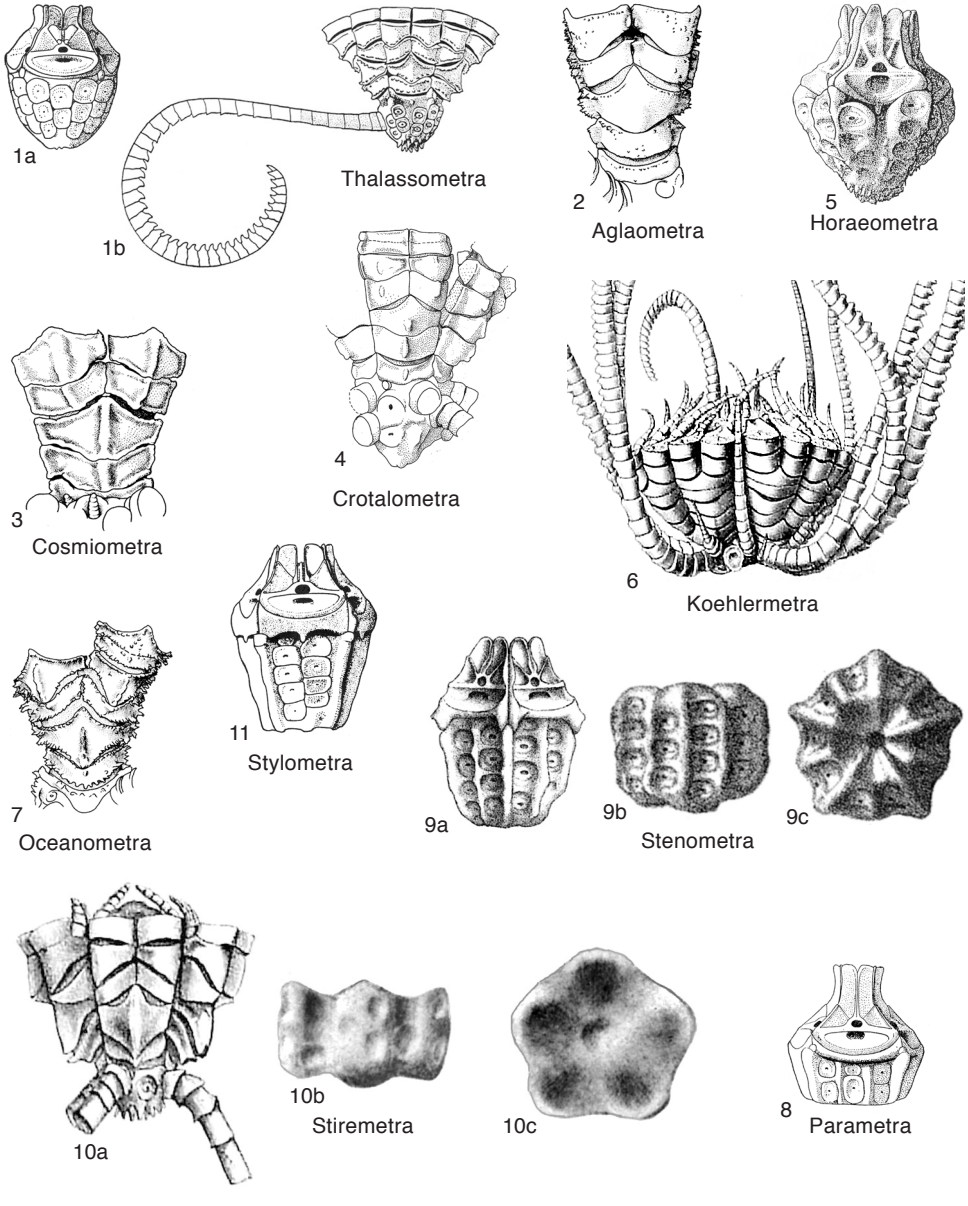


FIG. 60. Thalassometridae (p. 121–124).

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

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

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

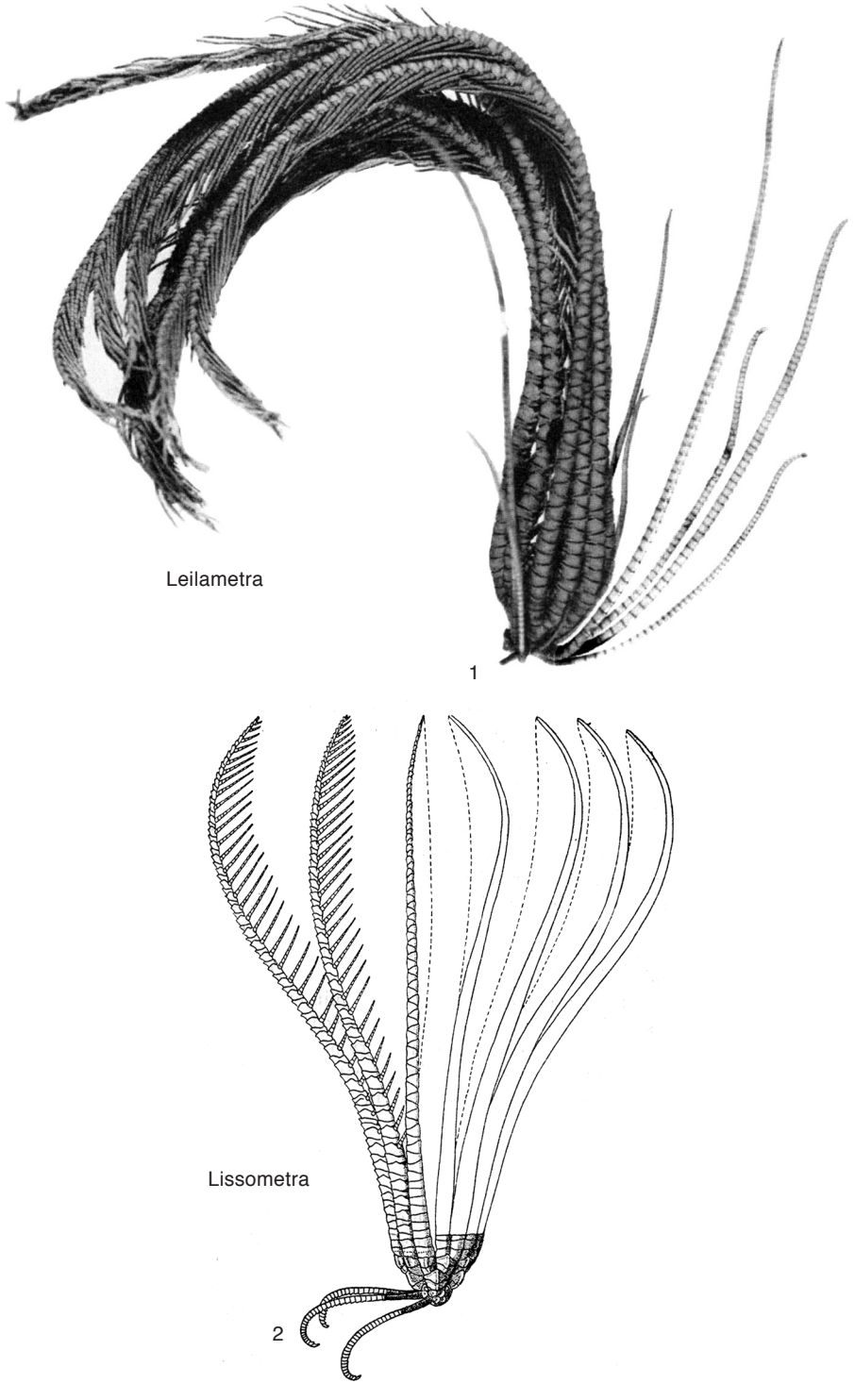


FIG. 61. Thalassometridae (p. 121).

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

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

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

Superfamily NOTOCRINOIDEA Mortensen, 1918

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

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

Family NOTOCRINIDAE Mortensen, 1918

[Notocrinidae Mortensen, 1918, p. 10]

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

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

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

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

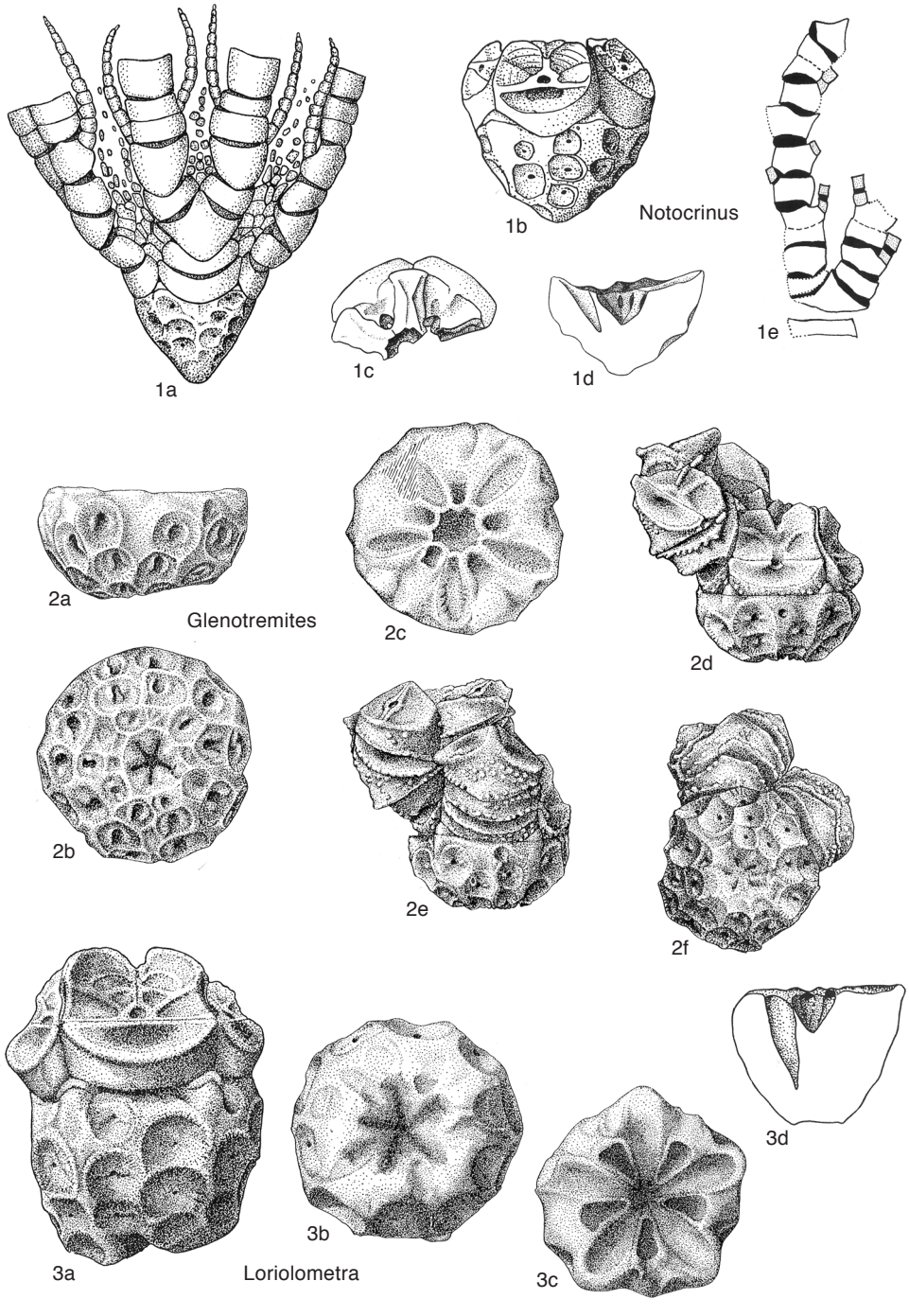


FIG. 62. Notocrinidae (p. 125–127).

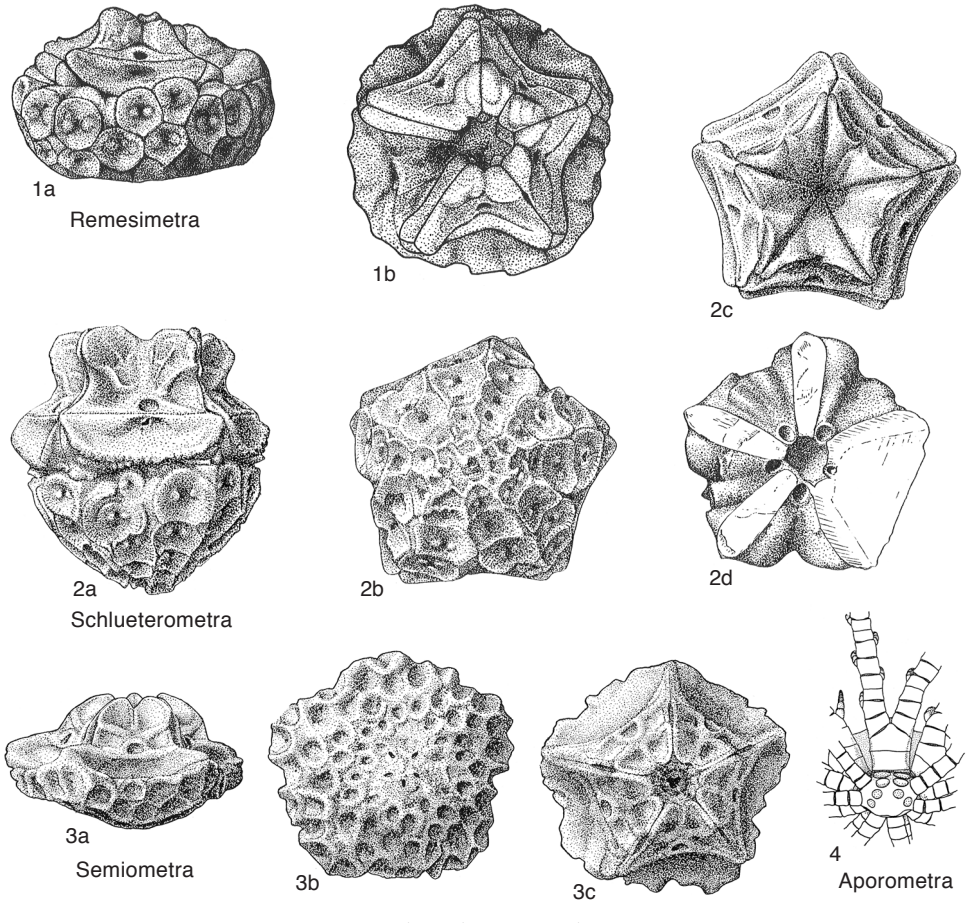


FIG. 63. Notocrinidae and Aporometridae (p. 127–128).

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

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

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

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

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

Family APOROMETRIDAE H. L. Clark, 1938

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

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

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

Superfamily ANTEDONOIDEA Norman, 1865

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

Centrodorsal variable, discoidal or hemispherical to rounded subconical, conical, or columnar. Cirrus sockets generally small and numerous, closely placed, ranging from irregular alternating rows to indistinct columns, and 10 to 20 distinct columns in Zenometridae. Sockets without distinct sculpturing. Basals commonly transformed to a rosette with rod-shaped radiating portions ranging from absent through reduced to distinct in *Nanometra* and Heliometrinae, and broad, tongue-shaped, and exposed interradially in some Zenometridae. Centrodorsal cavity moderate, approximately 30 percent of centrodorsal diameter in most Antedoninae, Thysanometrinae, Heliometrinae, and Isometrinae, and large to very large in Perometrinae, Bathymetrinae, Zenometridae, and Pentametrocrinidae. Small radial pits may be present in adoral surface of centrodorsal in some specimens of *Antedon* only. Radials 10 (5 radials and 5 pararadials) in *Promachocrinus* and *Thaumatocrinus*, but 5 in all other Antedonoidea as

well as in other comatulids. Adoral muscle fossae forming pair of high, thin flanges almost parallel to oral-aboral axis that meet midradially at approximately a 90 degree angle. Radial cavity narrow or funnel shaped, without central plug. Arms undivided in Pentametrocrinidae and divided at primibrachial 2 in Antedonidae. Synarthry between brachials 1 and 2 commonly embayed. Syzygy between brachials 3 and 4, generally between brachials 9 and 10, and distal at short intervals. Distal brachials strongly wedge shaped. Pinnules cylindrical to flattened, not carinate. Mouth central. *Lower Cretaceous (Albian)–Holocene.*

Family ANTEDONIDAE Norman, 1865

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

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

Subfamily ANTEDONINAE Norman, 1865

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

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

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

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

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

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

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

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

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

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

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

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

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

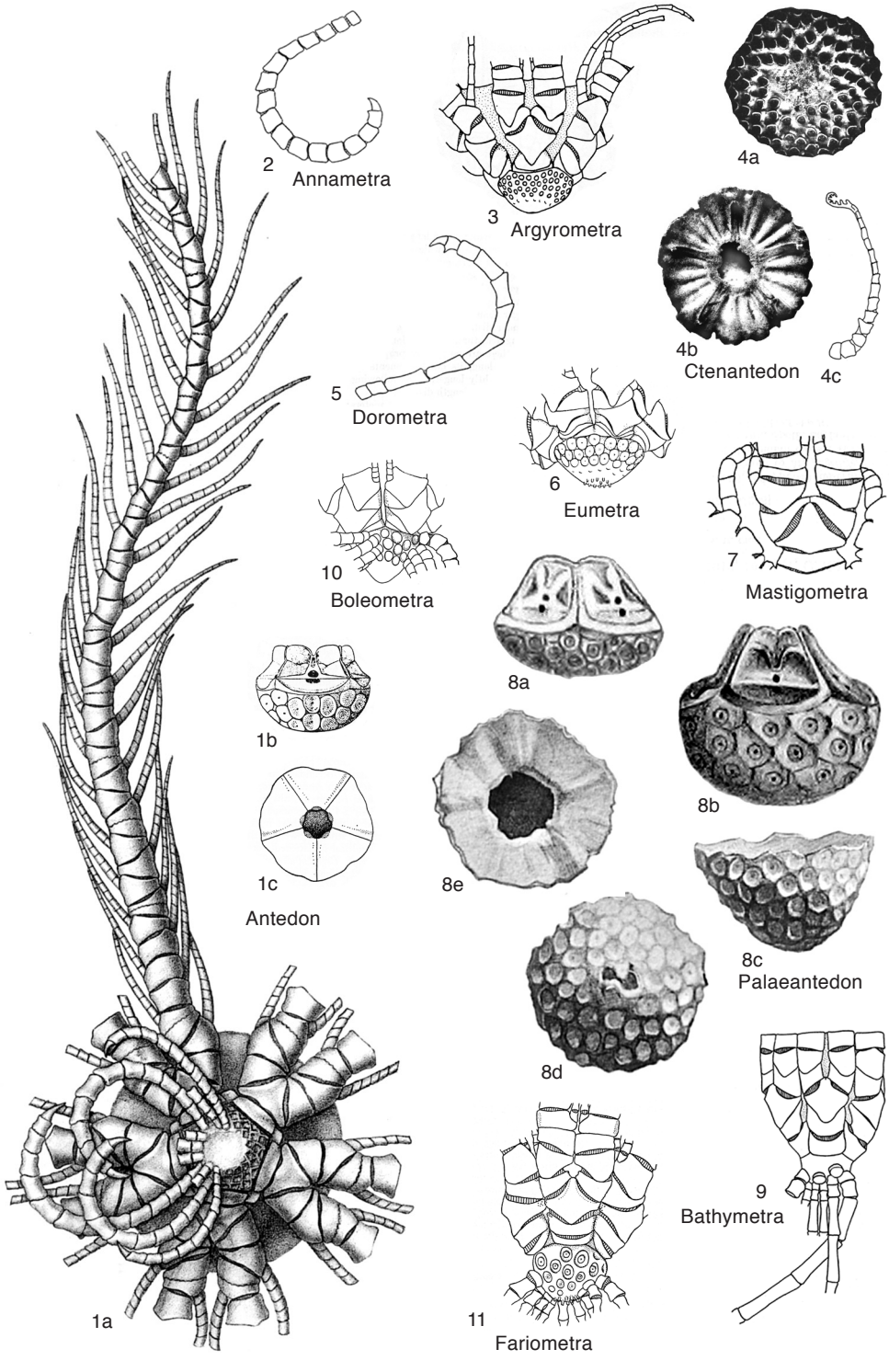


FIG. 64. Antedonidae (p. 130–132).

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

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

Subfamily BATHYMETRINAE A. H. Clark, 1909

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

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

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

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

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

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

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

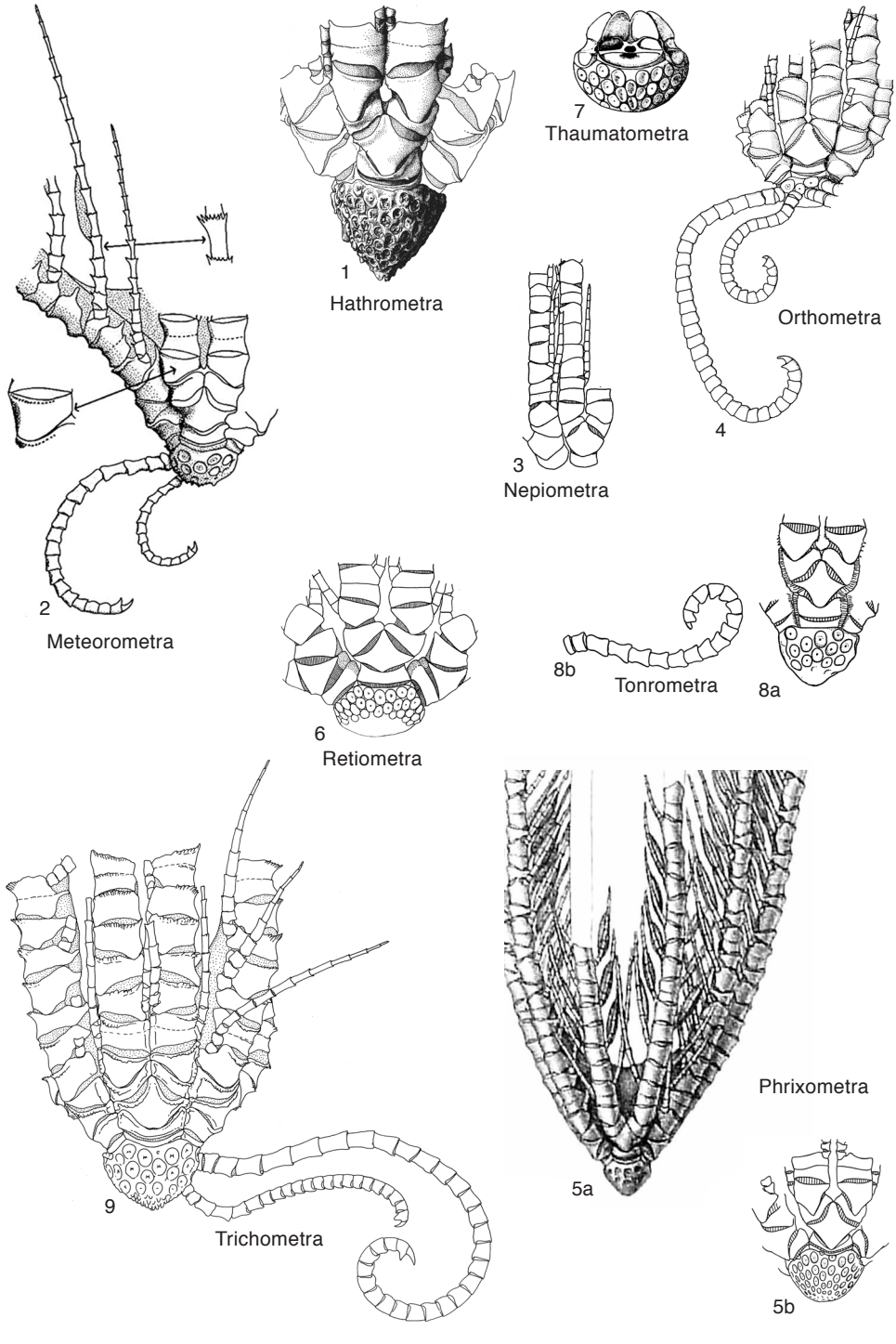


FIG. 65. Antedonidae (p. 132–134).

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

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

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

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

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

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

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

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

Subfamily HELIOMETRINAE A. H. Clark, 1909

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

Centrodorsal rounded, commonly with cirrus-free aboral apex, to low hemispherical with small, flattened, or concave cirrus-free aboral apex or deep aboral pit. Cirrus sockets numerous, crowded, commonly regularly alternating, forming 4 to 7 circles. Centrodorsal cavity moderate. Shallow radial pits or furrows may be present at edge of centrodorsal cavity in *Florometra*. Cirri 30

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

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

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

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

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

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

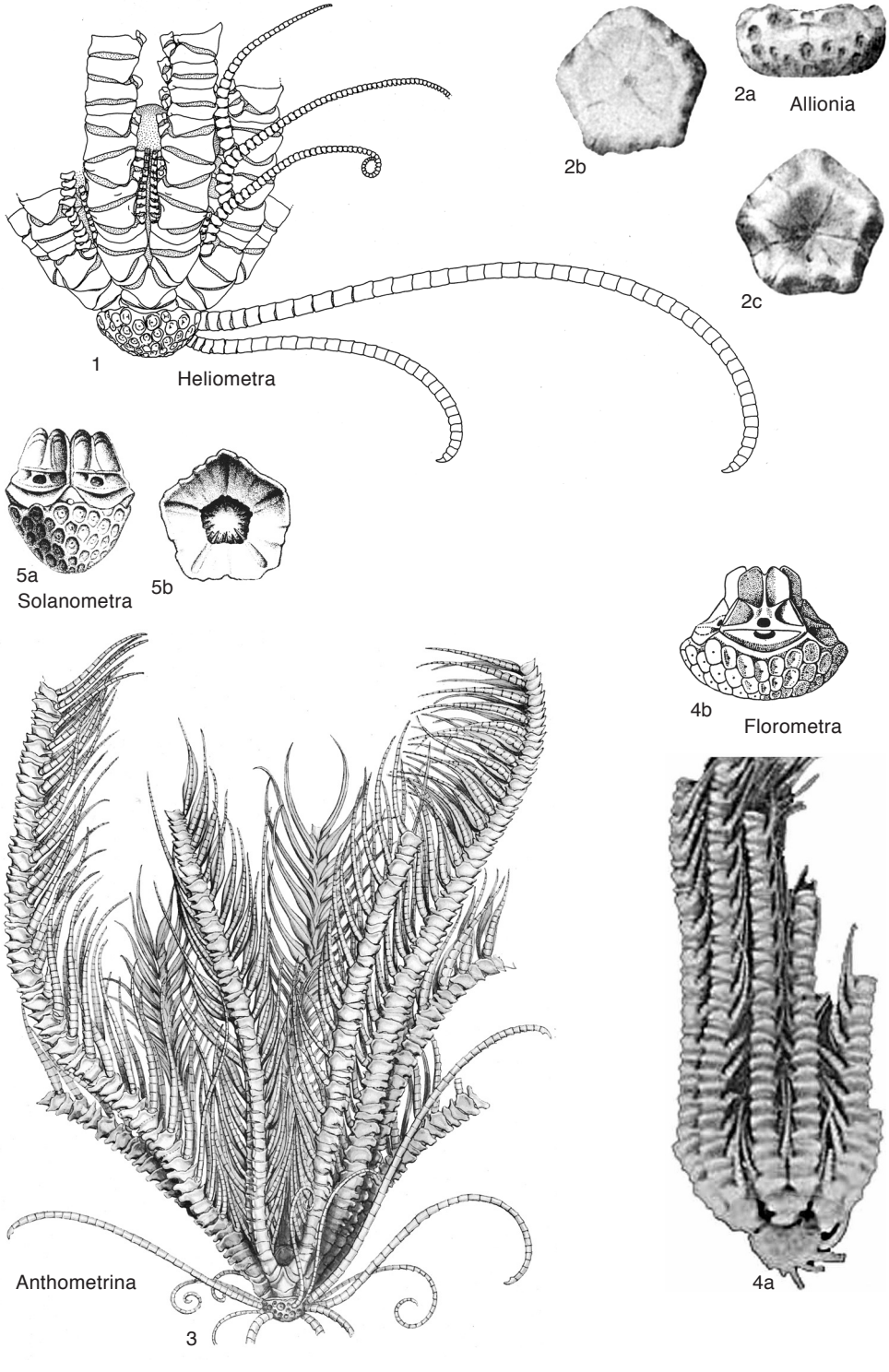


FIG. 66. Antedonidae (p. 135–137).

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

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

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

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

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

Subfamily ISOMETRAINAE A. H. Clark, 1917

[*nom. nov.* Fet & Messing, 2003, p. 293–296, *pro* Isometrinae A. H. Clark, 1917a, p. 127, *non* Kraepelin, 1891 (Arachnida, Scorpiones); ICZN, 2005]

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

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

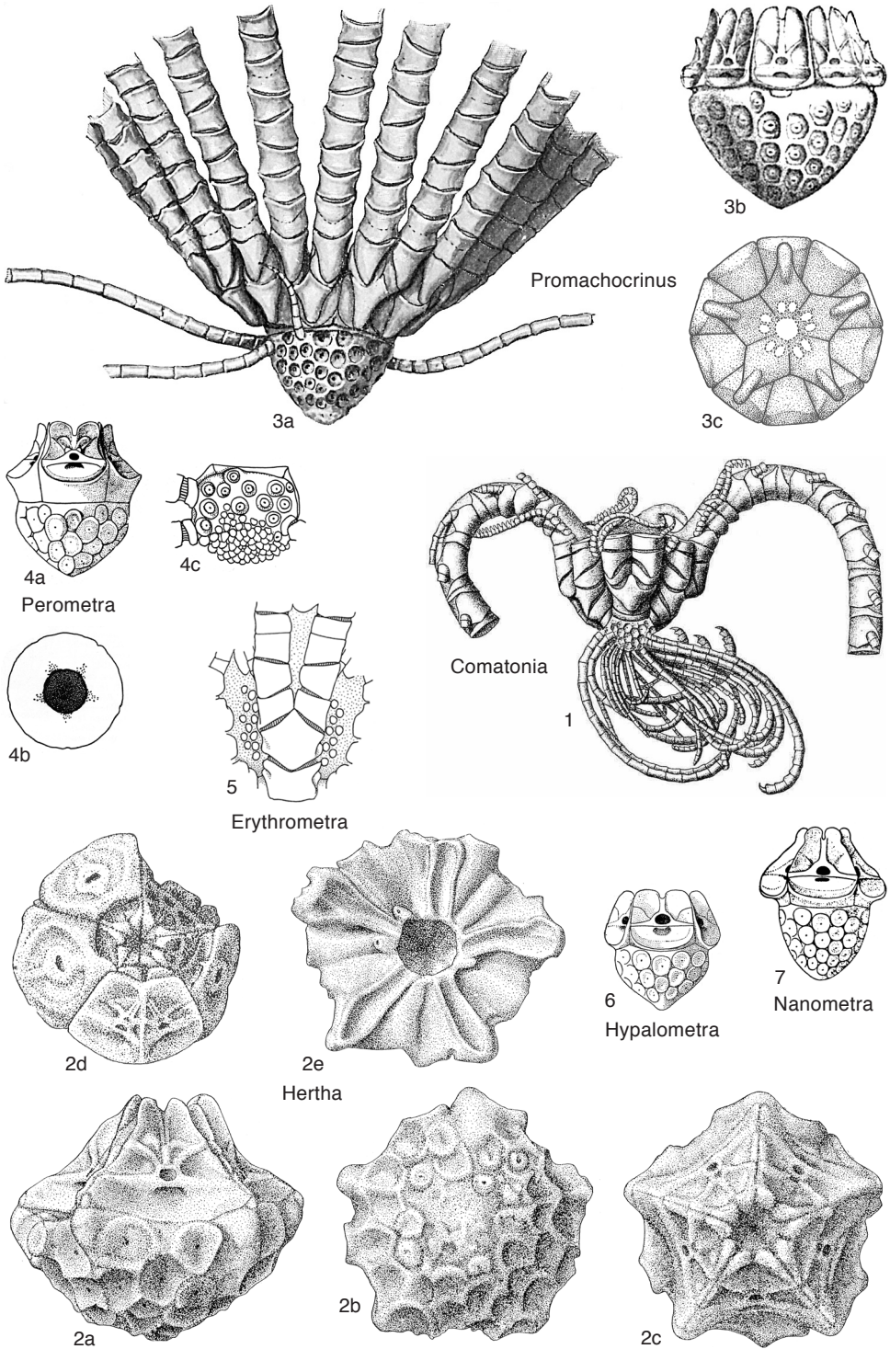


FIG. 67. Antedonidae (p. 135–139).

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

Subfamily PEROMETRINAE A. H. Clark, 1909

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

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

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

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

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

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

Subfamily THYSANOMETRINAE A. H. Clark, 1909

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

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

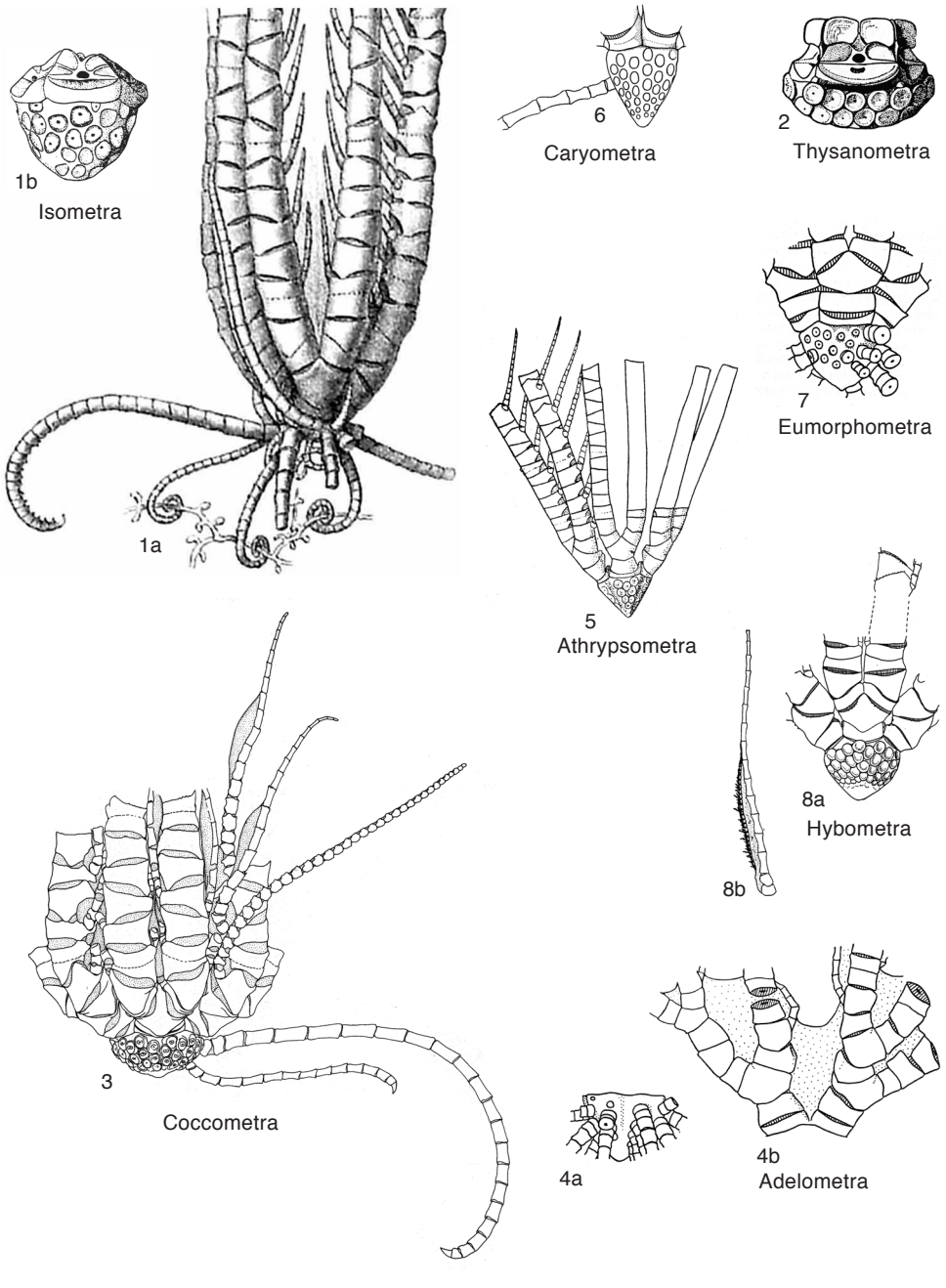


FIG. 68. Antedonidae (p. 137–143).

narrow, subtriangular, separated from interarticular ligament fossae by oblique ridge. Radial cavity in *Thysanometra* moderate to rather large, in *Coccometra* narrow. Arms 10, divided at primibrachial 2. Primibrachial 1 low, sides commonly converging and overhung by proximal part of primibrachial 2. Synarthry between brachials 1 and 2

flat to embayed. First pinnule long, flagellate, composed of 30 to 40 usually short pinnulars. Second pinnule resembles those following. *Holocene.*

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

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

Subfamily UNCERTAIN

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

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

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

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

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

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

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

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

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

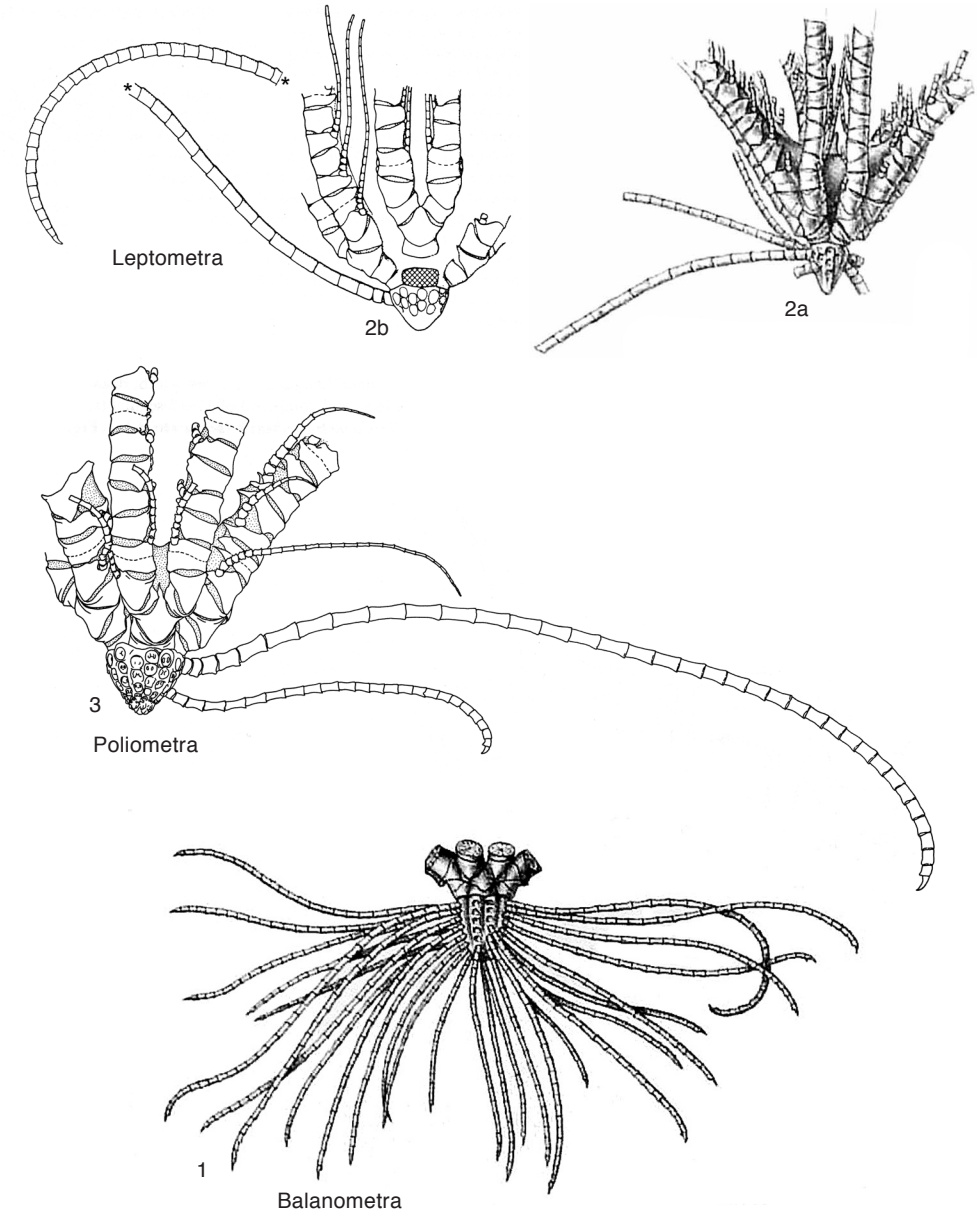


FIG. 69. Antedonidae (p. 141–143).

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

Hybometra A. H. CLARK, 1913d, p. 54 [**H. senta*; OD]. Centrodorsal conical, slightly wider than high, with sockets in 20 columns, not separated

into radial groups; interradial columns of 4 sockets each; the radial ones abbreviated toward apex. Second pinnule very long, third pinnule much shorter, distal pinnules longer, with ambulacral spines. *Holocene:* western and ?southeastern Atlantic Ocean (sublittoral).——Fig. 68,*8a–b*. **H. senta*; *a,* centrodorsal with base of crown, *b,* eighteenth pinnule, Brazil, holotype, BMNH 93476, ×2.5 (Clark & Clark, 1967).

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

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

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

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

Family PENTAMETROCRINIDAE A. H. Clark, 1908

[Pentametrocrinidae A. H. Clark, 1908h, p. 134] [=Thaumatocrinida Haeckel, 1896, p. 469; =Thaumatocrinidae Bather, 1899, p. 923; =Decametrocrinidae Minckert, 1905, p. 494; =Thaumatocrininae Jaekel, 1918, p. 74]

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

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

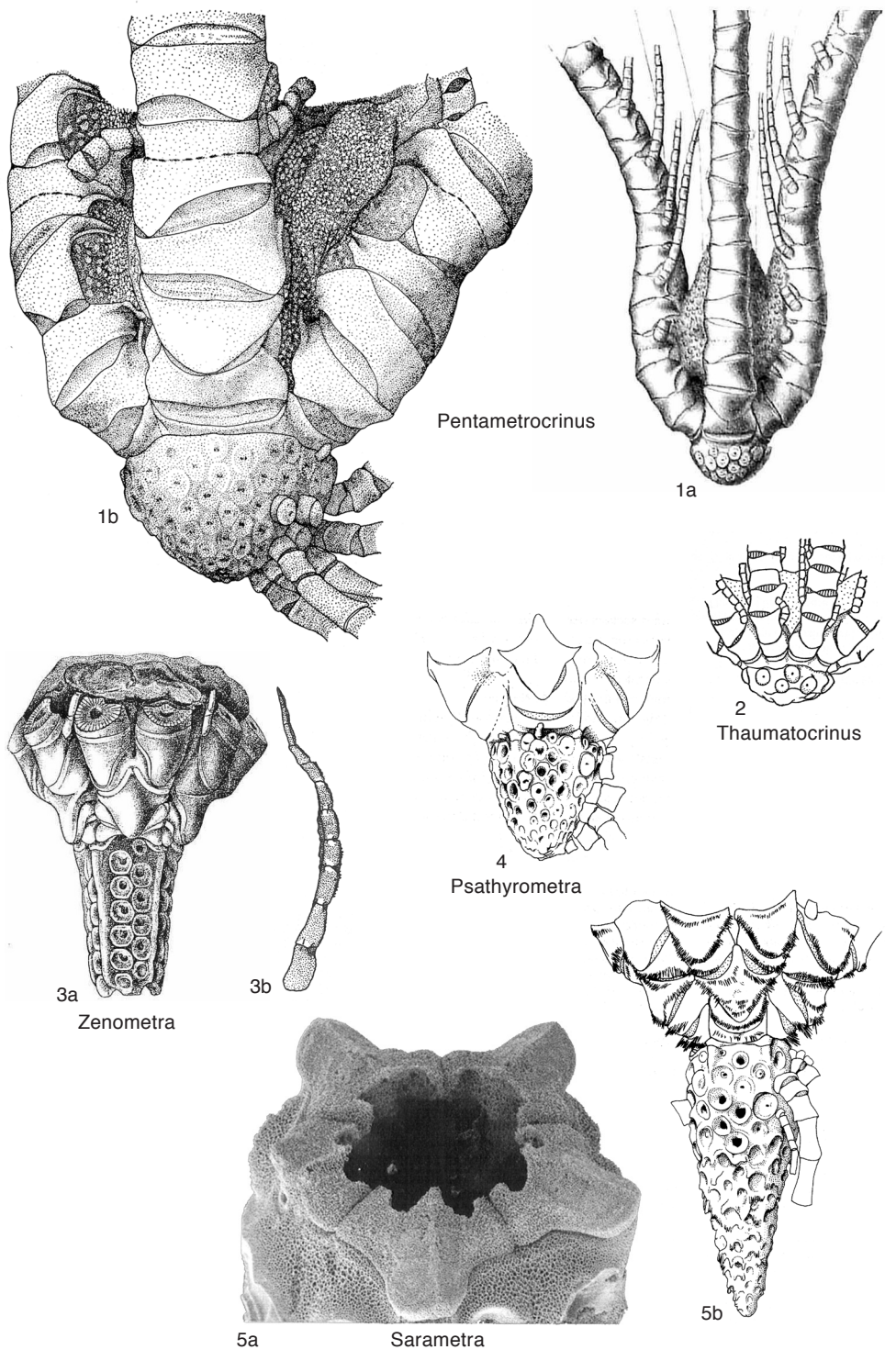


FIG. 70. Pentametrocrinidae and Zenometridae (p. 143–145).

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

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

Family ZENOMETRIDAE A. H. Clark, 1909

[*nom. transl.* Messing & White, 2001, p. 159, *ex* Zenometrinae A. H. Clark, 1909h, p. 176]

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

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

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

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

Superfamily UNCERTAIN
Family JAEKELOMETRIDAE Hess, new family

[Jaekelometridae Hess, herein] [type genus, *Jaekelometra* Gislén, 1924, p. 162]

Centrodorsal low to high convex conical. Cirrus sockets with more or less distinct fulcral ridge or tubercles but no projecting lateral margin, in 10 columns commonly separated by interradial or radial ridge or space. Adoral side of centrodorsal flat or concave, with increasing concavity during growth. Centrodorsal cavity rather narrow to moderate, radial depressions or pits in suture between basals may continue in centrodorsal as radial pits. Interradial furrows distinct, indistinct, or absent. Basals large, forming a high complete circlet visible externally, united as thin plates in bottom of large, deep, radial cavity, and covering adoral side of the centrodorsal except for narrow, central

perforation. Radials and primibrachials thin, with aboral crest. Brachials in type species large, high, slightly recumbent, with median crest. Radial articular facet low and wide, almost triangular, with very low and indistinct interarticular ligament fossae and rather low, very wide muscle fossae. Radial cavity large. *Upper Cretaceous (Campanian)–Paleogene (Danian).*

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

Family ATOPOCRINIDAE Messing, new family

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

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

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

Superfamily and Family UNCERTAIN

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

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

Suborder BOURGUETICRININA Sieverts-Doreck, 1953

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

[Hans Hess]

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

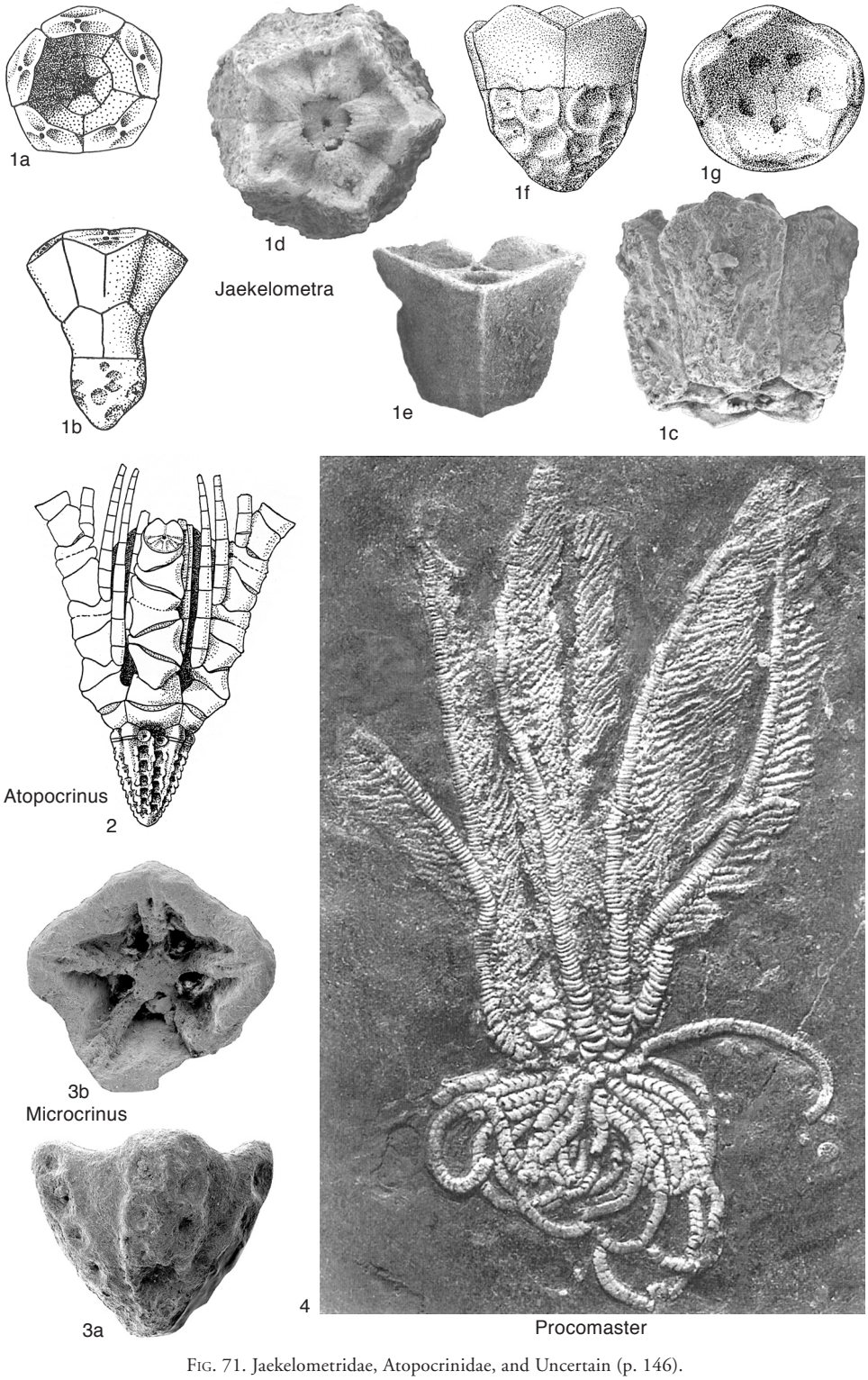


FIG. 71. Jaekelometridae, Atopocrinidae, and Uncertain (p. 146).

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

Family BOURGUETICRINIDAE de Loriol, 1882

[*nom. correct.* Carpenter, 1884a, p. 6, 23, *pro* Bourgueticrinidées de Loriol, 1882 in 1882–1889, p. 64; *emend.*, Gislén, 1924, p. 206]

Bourgueticrinina with 5 undivided rays. Cup mostly elongate, cylindrical to spindle shaped, composed of a proximale superposed by basals and radials of equal or nearly equal height, or high basals and shorter radials (proximale undifferentiated or absent in *Conocrinus*). Radial articular facet wide, with large muscle fossae, surrounding narrow axial canal. Articulation between brachials 1 and 2 cryptosynarthrial or synostosial (possibly muscular in *Dunnicrinus mississippiensis*). First pinnule abaxial on brachial 4. Discrete sutures in proximale of some specimens indicate derivation by fusion of a few disk-shaped proximal columnals; articular facet at base of proximale wide, circular in cross section and joined to topmost columnal by synostosis, or elliptical and joined by synarthry; uppermost free columnals cylindrical

and slightly shorter than more distal ones, or elliptical in section and similar to more distal columnals; synarthrial articulation with proximale and full size of uppermost free columnal in many specimens indicate that the formation of new columnals below the proximale is restricted to juveniles; form and size of columnals changing during growth and varying through a single column (cylindrical, barrel shaped, or with elliptical section at ends and constricted medially). Branched radicular cirri present on some distal columnals. *Upper Cretaceous (Cenomanian)–Holocene.*

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

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

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

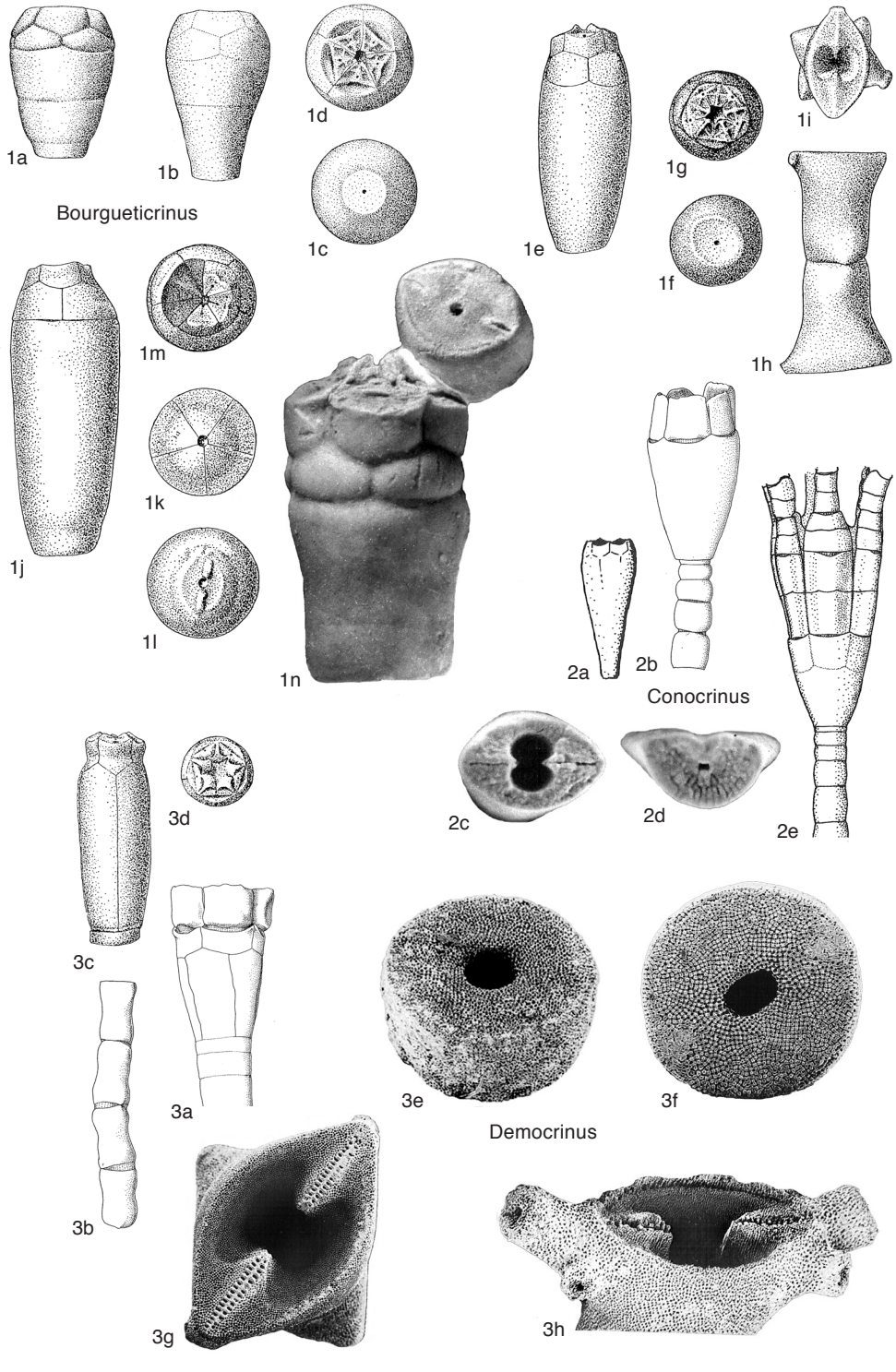


FIG. 72. Bourgueticrinidae (p. 149–151).

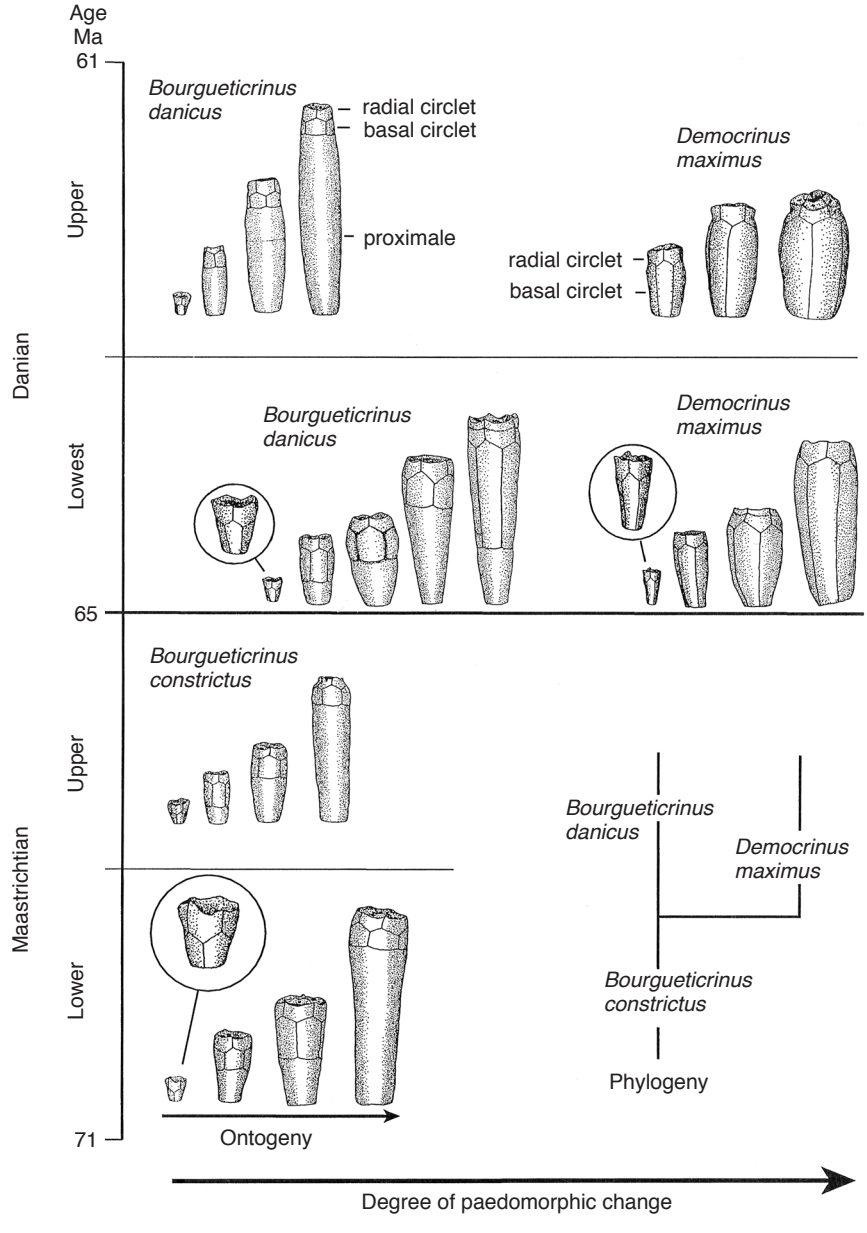


FIG. 73. Bourgueticrinidae (p. 149).

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

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

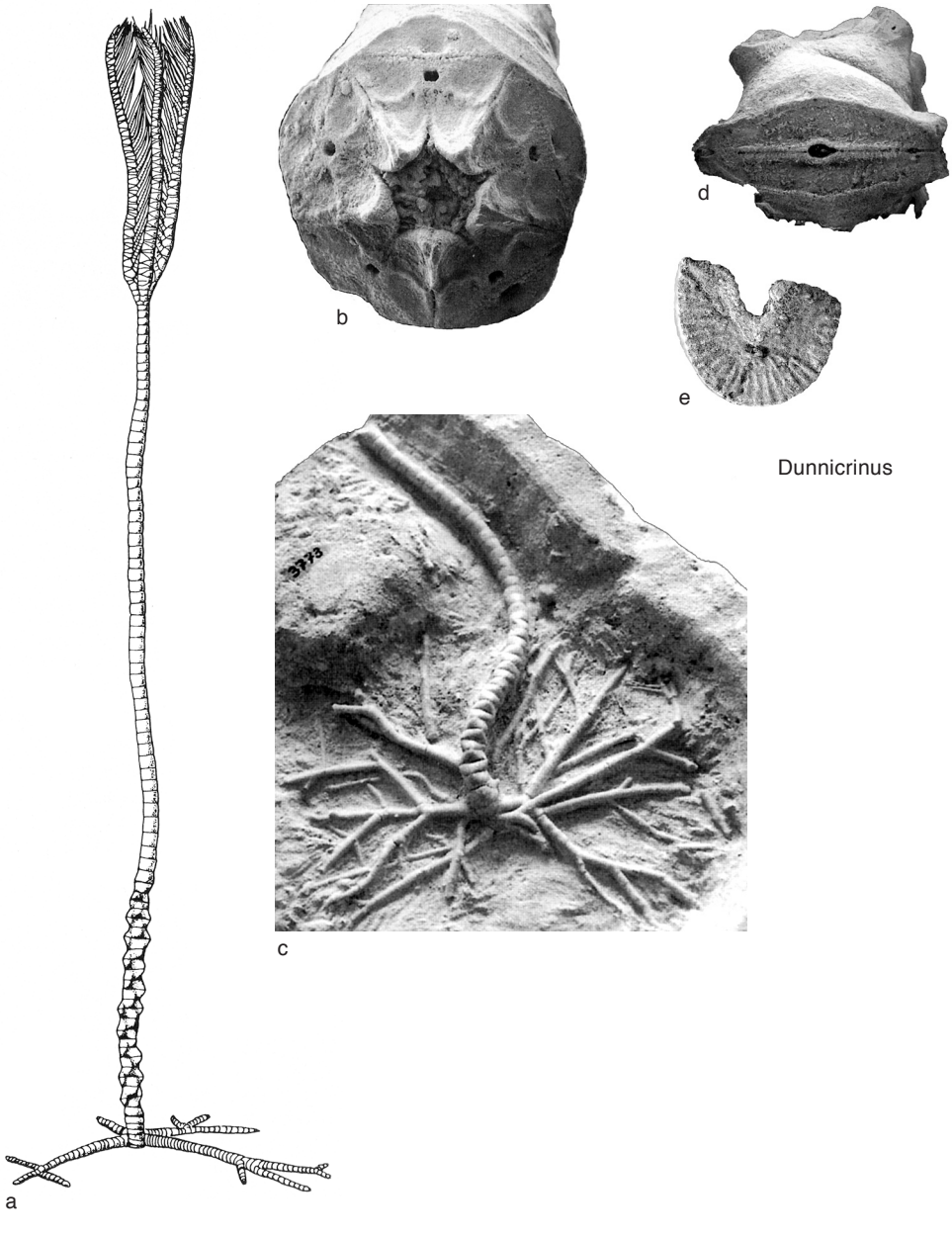


FIG. 74. Bourgueticrinidae (p. 151–153).

sized basals and radials separated by distinct sutures. Base circular, corresponding to top of column. Most fossil specimens broken along suture between basals and radials. Radial articular facet with steep, high, and narrow muscle fossae; radial cavity narrow. Arms 5, undivided, exceptionally with 4, 6, or 8 rays (JAGT, 1999a, p. 119). Brachials rounded aborally, strongly wedge shaped with oblique muscular articulations distal to brachial 2. Cryptosynarthry between brachials 1 and 2 in *D. aequalis* (possibly muscular in *D. mississippiensis*), other articulations muscular and cryptosyzygial to syzygial, distributed randomly (JAGT, 1999a). Pinnulation complete; first

pinnule on brachial 2; each pinnule with approximately 25 pinnulars, equal in length and diameter, and with straight muscular articulations. Proximalmost columnals generally thin; new, extremely thin columnals introduced immediately below basal circlet during juvenile growth, first appearing externally midradially below interbasal sutures, thus resembling infrabasals. After formation of new columnals has ceased in adults, the uppermost columnal grows to a size equal to other columnals, similar in diameter, but in some specimens higher, thus approaching the proximale of *Bourgueticrinus*. Proxistele with cylindrical to slightly barrel-shaped columnals, height similar to diameter, circular to slightly elliptical in section and with articulations almost synostosial in the few uppermost columnals, at least in juvenile specimens. Distal columnals stout, similar to *Bourgueticrinus*, with narrow lumen, elliptical in section and joined by synarthries. Distalmost column bearing branched radicular cirri. [JAGT (1999a, p. 129) noted that *Mesocrinus suedicus* CARPENTER (1881b), Campanian, may be assignable to *Dunnicrinus* based on brachial morphology; unfortunately, there is not enough material known to be certain about this.] *Upper Cretaceous (Maastrichtian):* Netherlands, USA (Mississippi).——FIG. 74*a*. **D. mississippiensis*; reconstruction, Maastrichtian, USA, ×0.5 (Moore, 1967).——FIG. 74*b–e*. *D. aequalis* (D'ORBIGNY, 1841 in 1840–1841), Maastrichtian, Netherlands; *b,* distal view of cup, MHMM 1997101-1, ×10; *c*, radix with part of column, MHMM MD 3773, ×0.7; *d*, proximal facet of columnal from dististele, MHMM 1997102-1, ×5; *e*, distal facet of brachial with syzygy, MHMM 1997100-3, ×10 (Jagt & others, 1998).

Family BATHYCRINIDAE Bather, 1899

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

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

Subfamily BATHYCRININAE Bather, 1899

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

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

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

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

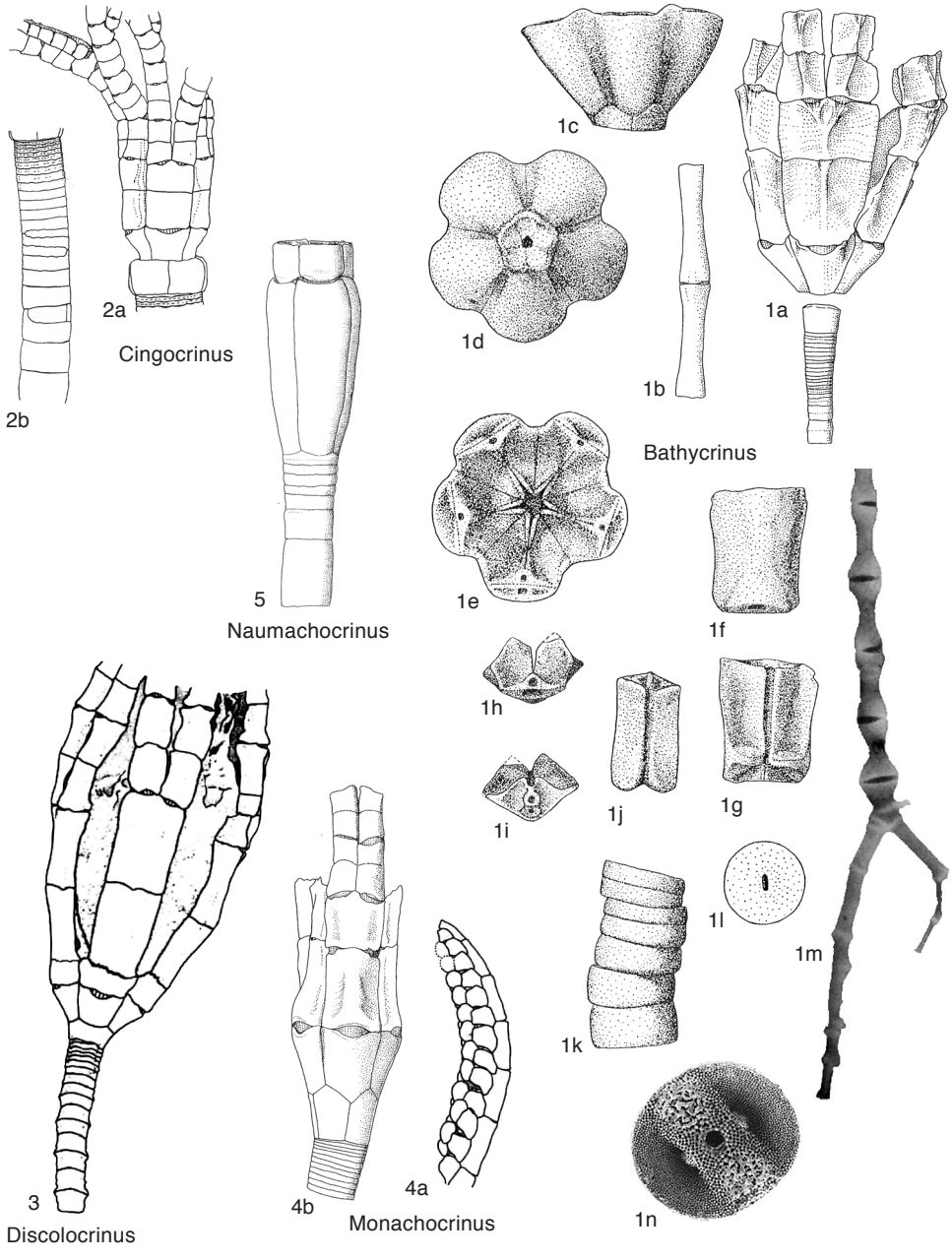


FIG. 75. Bathycrinidae (p. 153–155).

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

Monachocrinus A. H. CLARK, 1917b, p. 390 [**M. sexradiatus*; OD]. No angular boundary between basals and radials. Circlet of unfused basals approximately as high as wide; radial circlet of similar height, widening upward. Generally more than 10 proximal columnals, thin and disk shaped. [A. H. CLARK (in ZITTEL, 1913, p. 230) recorded

and characterized the genus and included it (A. H. Clark, 1915b) in a key to the genera of the Bourgueticrinidae. Seven species were indicated, but not by name. A. H. Clark (1915a in 1915–1950) assigned *Bathycrinus caribbeus* A. H. Clark (1908g) and *B. paradoxus* A. H. Clark (1909g) to this genus. He diagnosed it (A. H. Clark, 1917b, p. 390) and briefly described the type species, *M. sexradiatus*, but later offered a full description of the type as a new species (A. H. Clark, 1923b, p. 19). According to Jagt (1999a, p. 131), none of the Santonian–Maastrichtian species tentatively assigned by Rasmussen (1961) to *Monachocrinus* belongs in this genus. According to Roux (1977b, p. 28), *M. recuperatus* is the most typical of the genus. According to Mironov (2008, p. 148) pinnules with rows of large covering plates bordering the ambulacral groove are characteristic of bathycrinids.] *Holocene:* worldwide (bathyal, abyssal in temperate and tropical seas).——Fig. 75,*4a*. **M. sexradiatus*; lateral view of pinnule with covering plates, northern Atlantic at 2075 m, syntype, CM Cri-65, ×15 (Mironov, 2008).——Fig. 75,*4b*. *M. recuperatus* (Perrier, 1883); proximal column and base of crown, holotype, MNHN EcPh26, ×5 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

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

Subfamily CALEDONICRININAE Mironov, 2000

[Caledonicrininae Mironov, 2000, p. 721]

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

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

Family PHRYNOCRINIDAE A. H. Clark, 1907

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

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

Subfamily PHRYNOCRININAE A. H. Clark, 1907

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

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

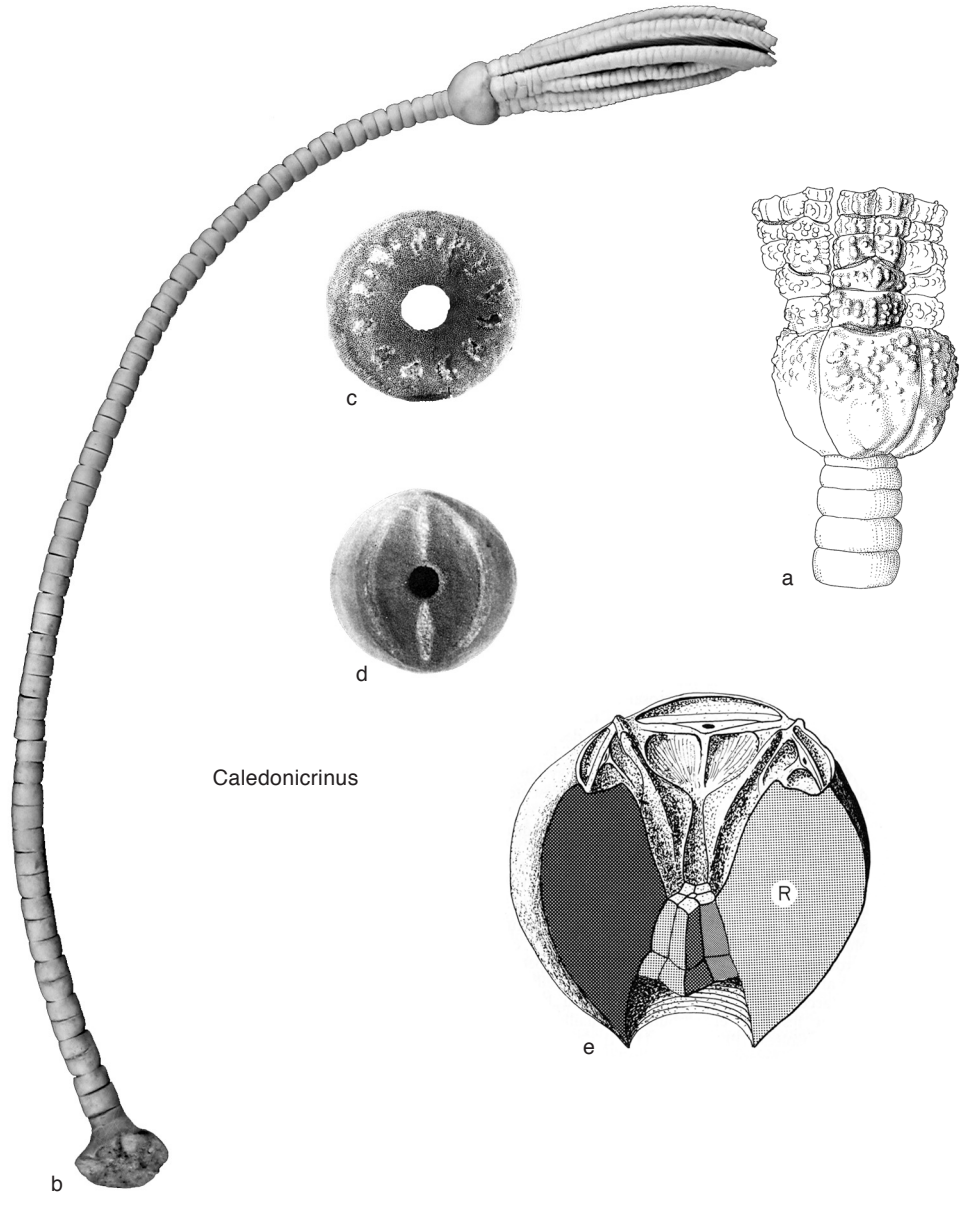


FIG. 76. Bathycrinidae (p. 155).

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

Subfamily PORPHYROCRININAE A. M. Clark, 1973

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

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

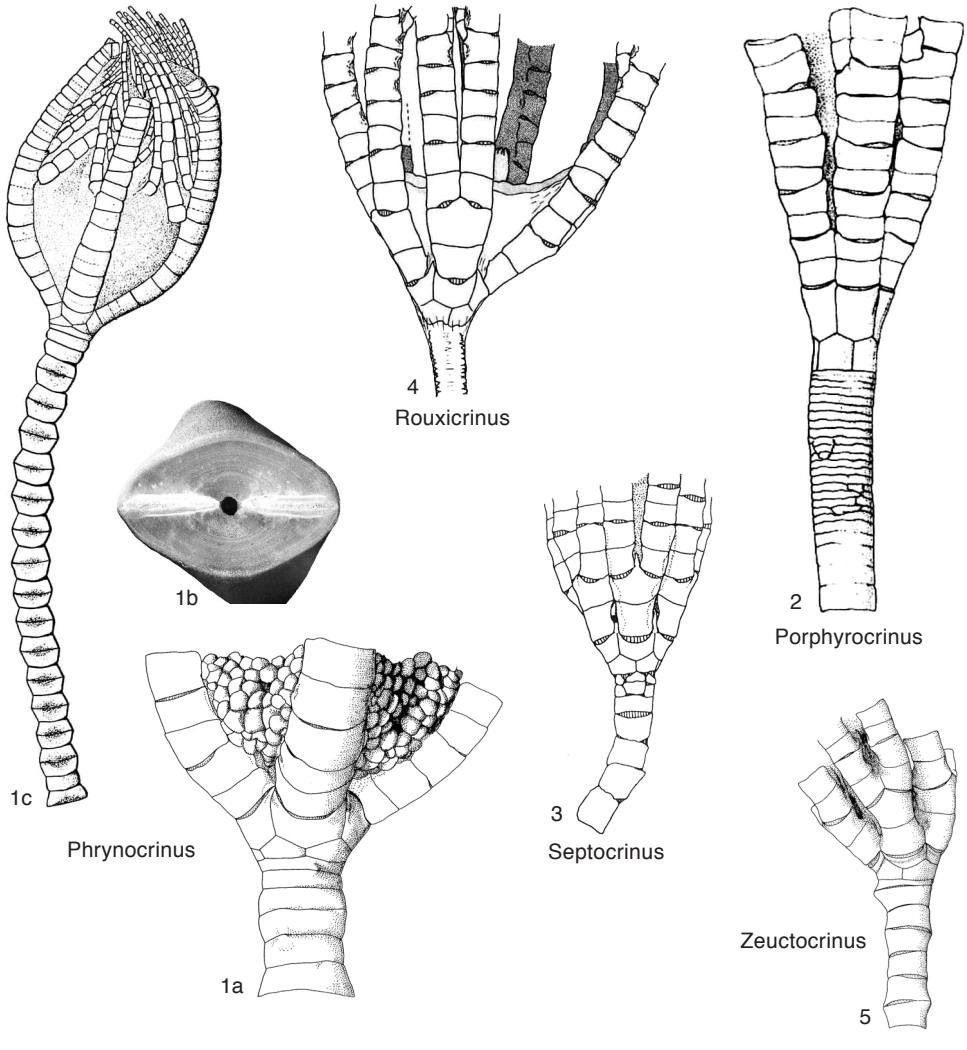


FIG. 77. Phrynocrinidae and Septocrinidae (p. 156–158).

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

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

Family SEPTOCRINIDAE Mironov, 2000

[Septocrinidae MIRONOV, 2000, p. 721]

Cup conical; 5 basals and 5 radials almost equal in height. Synostosis between primibrachials 1 and 2. Arms 10, divided at primibrachial 2. Tegmen incompletely covered by primibrachials 1 and 2. Proximal synostoses in most cases between secundibrachials 1 and 2 and 3 and 4, then at variable

intervals. First pinnule from brachials 6 to 12, commonly 10. Pinnulars semicircular in cross section, without cover or lateral plates. Large, rodlike spicules in ambulacra. Column attached by radicular cirri in *Septocrinus* (unknown in *Zeuctocrinus*). *Holocene.*

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

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

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

Suborder GUILLECRININA Mironov & Sorokina, 1998

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

[Hans Hess]

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

Family GUILLECRINIDAE Mironov & Sorokina, 1998

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

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

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

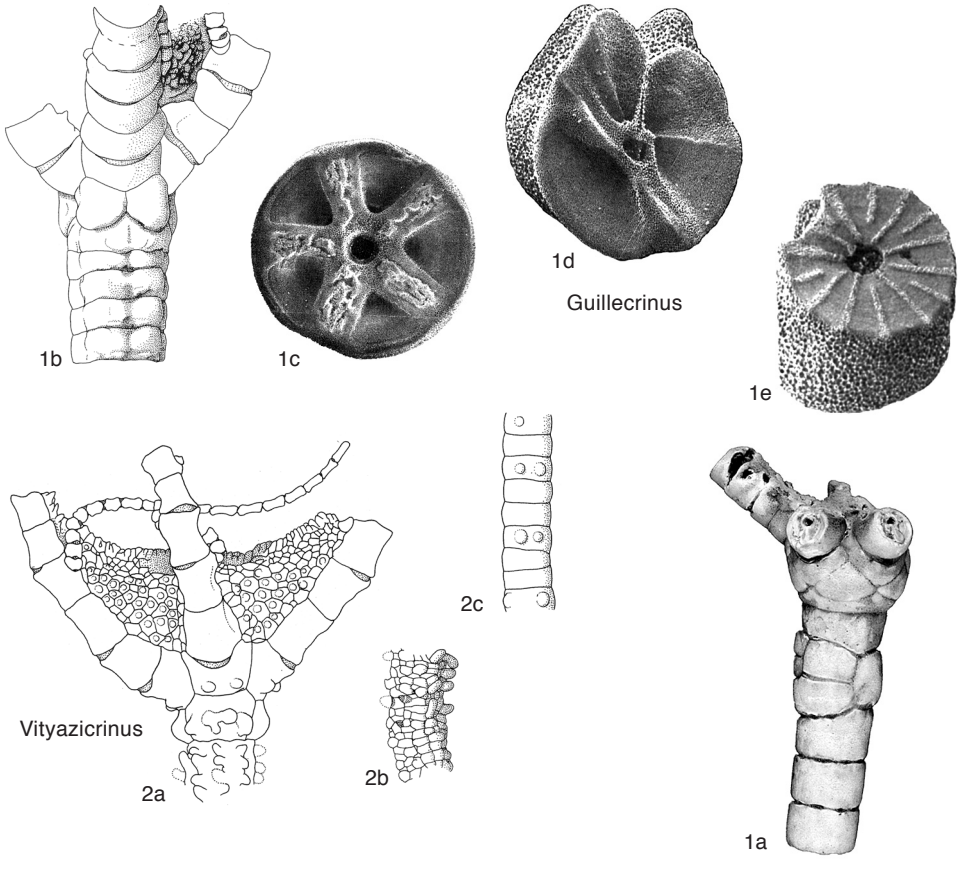


FIG. 78. Guillecrinidae (p. 158–159).

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

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