MILLERICRINIDA Hans Hess

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Order MILLERICRINIDA Sieverts-Doreck, 1952

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

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

Family MILLERICRINIDAE Jaekel, 1918

[Millericrinidae JAEKEL, 1918, p. 69]

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

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



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

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

- Ailsacrinus TAYLOR, 1983, p. 42 [*A. abbreviatus; M]. Cup bowl shaped to conical with small basals and commonly with irregularly developed, tiny accessory plates between basals. Synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2. Arms with frequent syzygies. First pinnule on secundibrachial 2. Pinnules differentiated into oral and distal series; short, oral pinnules without groove and cover plates but an adoral transverse ridge, and more elongate distal pinnules with groove and cover plates. Column reduced, tapering distally and terminating in a rounded columnal; incomplete lenticular columnals may be present. No holdfast. [The genus includes A. prattii (GRAY, 1828), with a column of highly variable length, of 1 to more than 66 columnals (TAYLOR, 1983, p. 43).] Middle Jurassic (Bathonian): England.-FIG. 79,2a-b. *A. abbreviatus; a, syzygial facet of brachial, syntype, BMNH E68080, ×9 (Taylor, 1983); b, base of crown with top columnal, topotype, NMB M10531, ×3.2 (Hess, new).—FIG. 79,2c. A. prattii (GRAY); column and base of crown, CAMSM J.33695, ×2.5 (Taylor, 1983)
- Angulocrinus ROLLIER, 1911, p. 4 [*Millericrinus nodotianus D'ORBIGNY, 1841 in 1840-1841, p. 59; SD RASMUSSEN, 1978, p. 819]. Cup truncated conical, not tumid, increasing in diameter upward from edge of enlarged uppermost columnal, which is more or less included as a rounded to 5-sided proximale in cup with a 5-sided pyramidal proximal facet toward the basals. Synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2. Proximal part of column 5-sided with columnals that may alternate in height and diameter. Mesistele mostly cylindrical, commonly ornamented with tubercles, spines, or strands of stereom attached to each other; attachment by radicular cirri as creeping roots or runners along the substrate but also by terminal root. Columnal articular facets with radiating crenulae commonly arranged in 5 groups, especially in proximal part of column. Crenulae may, in some species, be restricted to a marginal zone of facet. [ROLLIER (1911) based this genus on the cup of Millericrinus regularis D'ORBIGNY and M. nodotianus D'ORBIGNY as figured by DE LORIOL (1883 in 1882-1889). RASMUSSEN (1978, p. 819) designated M. nodotianus as the type of the genus, because it was the only species based on specimens with a preserved cup by D'ORBIGNY (1841 in 1840-1841). DE LORIOL (1884 in 1882–1889, pl. 116, 1c) found small, concealed infrabasals in specimens of A. orbignyi. Numerous species from Oxfordian strata assigned by D'ORBIGNY (1841 in 1840-1841) and DE LORIOL (1878, 1883-1884 in 1882-1889) to Millericrinus are based on columns only. Most of them appear to belong to Angulocrinus; in view of the heteromorphic nature and high variability of the columns, a number of these species may well be identical.] Middle Jurassic (Callovian)-Upper Jurassic (Kimmeridgian): France, Germany, Portugal, Switzerland, Crimea.—FIG. 79,3a-g.

*A. nodotianus (D'ORBIGNY); *a*-*b*, cup, *a*, lateral, *b*, distal, Oxfordian, France, Dijon Museum, ×1; *c*-*d*, proximal column with proximale, *c*, lateral, *d*, proximal, Oxfordian, France, ×1 (de Loriol, 1883 in 1882–1889); *e*-*f*, column, *e*, lateral, *f*, facet, Oxfordian, France, NMB M10608, ×4 (Hess, new); *g*, crown and proximal column, base of crown with sutures poorly preserved; there are 2 primibrachials and probably 5 secundibrachials, Oxfordian, Switzerland, ETH 5431, ×1 (Rollier, 1911).—FIG. 79,3*b*. *A. horridus* (D'ORBIGNY, 1841 in 1840–1841); proximal view of primibrachial 2, Oxfordian, France, ×2 (de Loriol, 1883 in 1882–1889, as *Millericrinus beaudouini* DE LORIOL).

- Liliocrinus ROLLIER, 1911, p. 6 [*Millericrinus polydactylus D'ORBIGNY, 1841 in 1840–1841, p. 41; SD RASMUSSEN, 1978, p. 819]. Cup low conical to bowl shaped, not tumid, increasing in diameter upward from edge of rather wide, uppermost columnal. Basals and radials large. Radial articular facet low and wide. Synostosis with marginal crenulae between primibrachials 1 and 2, synarthry between secundibrachials 1 and 2. Column cylindrical, proximal columnals slightly increasing in diameter toward cup, not 5-sided. Columnal articular facets covered by radiating crenulae not separated in groups. Proximal articular facet of uppermost columnal more or less pyramidal or conical to almost flat. Attachment by root. [ROLLIER (1911) based this genus on Apiocrinites rosaceus (VON SCHLOTHEIM, 1823 in 1822-1823) as figured by GOLDFUSS (1831 in 1826-1844, pl. 56,3) and QUENSTEDT (1858, pl. 87,20), and on Millericrinus polydactylus D'ORBIGNY as figured by DE LORIOL (1884 in 1882-1889, pl. 109). Because DESOR (1845, p. 217) demonstrated that the identity of the first recorded species is ambiguous, RASMUSSEN (1978, p. 819) designated M. polydactylus as the type species. Most specimens from the Upper Jurassic of France and Switzerland described as Apiocrinites rosaceus belong to Liliocrinus munsterianus (D'ORBIGNY), the best documented species of the genus. DE LORIOL (1884 in 1882-1889, pl. 110,2a) showed small, concealed infrabasals in specimens of L. polydactylus.] Middle Jurassic (Bathonian)–Upper Jurassic (Kimmeridgian): England, France, Germany, Switzerland.-–Fig. 80,1a-b. *L. polydactylus (D'ORBIGNY), Oxfordian, France; a, crown, $\times 0.8$; b, proximal column with cup, MNHN R62602, ×1 (de Loriol, 1884 in 1882-1889).-FIG. 80, 1c-g. L. munsterianus (D'ORBIGNY, 1841 in 1840-1841), Oxfordian, Switzerland; c-e, cup with a primibrachial 1 still attached and a primibrachial 2 in the radial cavity, c, lateral, d, proximal, e, distal, NMB M10602, ×1; *f*–*g*, column, *f*, lateral, *g*, facet, NMB M10609, ×1.3 (Hess, new).
- Orbignycrinus BIESE, 1935 in 1935–1937, p. 478, nom. nov. pro Cupulocrinus ROLLIER, 1911, p. 7, non D'ORBIGNY, 1850 in 1850–1852, p. 23, 46 [*Millericrinus cupuliformis D'ORBIGNY, 1841 in 1840– 1841, p. 51; SD SIEVERTS-DORECK in RASMUSSEN, 1978, p. 822]. Cup smooth, bowl shaped, almost



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

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

Pomatocrinus DESOR, 1845, p. 217 [*Encrinites mespiliformis VON SCHLOTHEIM, 1820, p. 332; M]. Cup large, globe shaped, thick walled, composed of very large basals, smaller radials, and a rather large proximale surrounding an almost spherical central cavity. Sutures distinct. All cup plates with flat, slightly rough facets. No trace of infrabasals. Radial articular facet large, wide, meeting along interradial sutures; articulation with distinct fulcral ridge, aboral and interarticular ligament fossae, and small adoral muscle fossae. Primibrachials meet laterally. Arms divided at primibrachials 2 and more distally; first pinnule on secundibrachial 2. Synarthries between primibrachials 1 and 2 and secundibrachials 1 and 2. Proximalmost columnal 5-sided, forming aboral pole of spherical cup, and continued as high, 5-sided, truncated pyramid inside basal circlet to bottom of central cavity; underside has a concave, circular, articular facet to receive finely granulated proximal facet of next columnal, which together with a few succeeding, very low columnals form very short, slightly conical transition to cylindrical column. Columnal articular facets with fine, radiating crenulae, closely placed, not in separate groups; crenulae may be modified to granules in central area. [KOENIG (1825, pl. 11,129) introduced this genus name in the combination P. jaegeri in the second part of Icones Fossilium Sectiles, which was never published; but it was distributed to a few people. The specimen figured by KOENIG but undescribed has never been identified. It resembles E. mespiliformis, although this species was figured on the same plate as Symphytocrinus? mespiliformis. AGASSIZ (1836, p. 195) recorded Pomatocrinus as one of several synonyms of Apiocrinus; DESOR (1845) first used the name for Encrinites mespiliformis. ROLLIER (1911, p. 6) used the name Pomatocrinus for one of his subgroups of Millericrinus. QUENSTEDT (1858, p. 715), described Apiocrinites mespiliformis as resembling the fruit of medlar (Mespilus); the name Mespilicrinus therefore was considered suitable, but it was not established

for this genus. QUENSTEDT (1858, p. 198, 514) also used the name Mespilocrinites. He used Mespilocrinus in later publications (QUENSTEDT, 1876, pl. 104,138-152, pl. 105,1-4, 8-12; 1885, p. 931, fig. 344, pl. 73,40-44) for species of Cyclocrinus, but this name was preoccupied by DE KONINCK and LE HON (1854). Genus is closely similar to a group of Apiocrinites except for the unmodified radial articular facet and proximal brachials. It differs from Orbignycrinus in column and proximale.] Lower Jurassic-Upper Jurassic: Germany, France, Poland, Portugal, Spain, Switzerland, Russia.-FIG. 80,3a-c. *P. mespiliformis (VON SCHLOTHEIM); cup, a, lateral, b, proximal, c, distal, Upper Jurassic, Portugal, ×1 (de Loriol, 1891).-—FIG. 80,3d. P. magnificus (D'ORBIGNY, 1850 in 1850-1852); crown and proximal column, Oxfordian, France, lectotype, MNHN B11439, ×0.75 (de Loriol, 1883 in 1882-1889).

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

Family APIOCRINITIDAE d'Orbigny, 1840

[nom. correct. RASMUSSEN, 1978, p. 822, pro Apiocrinidae D'ORBIGNY, 1840 in 1840–1841, p. 1]

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



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

- Apiocrinites MILLER, 1821, p. 17 [*A. rotundus; SD D'ORBIGNY, 1840 in 1840-1841, p. 20; = Encrinites parkinsoni von Schlotheim, 1820, p. 332] [=Apiocrinus AGASSIZ, 1836, p. 195, nom. van.]. Cup typically globe or pear shaped to ovoid; greatest diameter at basal or radial circlet. Primibrachials meet laterally, with or without a few small, polygonal, interradial plates. Synarthry or synostosis with marginal crenulae between primibrachials 1 and 2, synarthry between secundibrachials 1 and 2. All or most secundibrachials free. Arms divided at primibrachial 2, and in some species, further divided once or twice with variable interval. First pinnule on secundibrachial 2. Proximal column of thin, discoidal columnals increasing gradually in diameter to form long, smoothly conical transition from column to cup. Proximal columnals typically with flat proximal articular facet and concave distal facet, leaving empty central space between columnals. Proximal facet of uppermost columnal with 5 radiating ridges separating facets facing basals. [By emendation, D'ORBIGNY (1840 in 1840-1841) left A. rotundus (=A. parkinsoni) as only the original species maintained in the restricted genus Apiocrinus. Several species generally referred to Apiocrinites have a hemispherical to almost spherical cup and a very short conical proximal column. In some species, only a single, 5-sided proximale with convex to pyramidal proximal facet included in the aboral side of the cup are known as in Pomatocrinus, but these have insufficiently known, presumed modified, and reduced articulations in the radials and proximal brachials. These species may perhaps belong to Pomatocrinus or may be intermediate in the evolution from Pomatocrinus toward Guettardicrinus.] Lower Jurassic-Lower Cretaceous: England, France, Germany, Hungary, Italy, Poland, Spain, Switzerland, Yugoslavia, Russia, Algeria, Mexico.-FIG. 81,2a-b. *A. parkinsoni (VON SCHLOTHEIM), Bathonian; a, crown, France, ×0.75; b, proximal view of topmost columnal with facets to basals, England, ×0.6 (de Loriol, 1882 in 1882–1889).-–Fig. 81,2c-j. A. roissyanus D'ORBIGNY, 1841 in 1840-1841, France; c, branched column, Oxfordian, NMB M9607, ×0.8 (Hess, 1975); d, distal view of part of cup with facets of radial and primibrachial 1, Oxfordian, NMB M10610, ×1.6; e, facet of columnal from mesistele, Oxfordian, NMB M10571, ×3 (Hess, new); f-g, juvenile specimen, f, cup with proximal arms and tegmen, $\times 1$, g, tegmen, Kimmeridgian, ×2.5 (de Loriol, 1887); h, distal view of top columnal and 2 reduced columnals, Oxfordian, NMB 2, ×1.5; i, proximal view of primibrachial 2 (synarthry), Oxfordian, NMB M10568, ×5; j, secundibrachial (syzygy), Oxfordian, NMB M10569, ×6 (Hess, new).
- Guettardicrinus D'ORBIGNY, 1840 in 1840–1841, p. 14 [*G. dilatatus; M] [=Guettardocrinus BRONN, 1851 in 1851–1856, p. 123, nom. null.]. Cup very large, as large as 76 mm in diameter, hemispherical

to almost spherical. Uppermost columnal with low, conical proximal facet just reaching central cavity and with low ridges separating flat or slightly convex, feebly crenulate synostosial joint facets toward basals. Basals and radials rather low and wide. Radials and proximal brachials separated by several small, polygonal, interradial plates, variable in number. Brachials through second secundibrachials included in structure of cup, all stout and connected by modified, generally synostosial articulations with feeble granulation on joint faces. Proximal column of thin columnals increasing rapidly in diameter to form short, smoothly conical transition from column to cup. Upper Jurassic (Oxfordian): France, Switzerland.——FIG. 81,3a-c. *G. dilatatus, Kimmeridgian, France; a, cup, lectotype herein, MNHN B11466, ×0.7; b, distal view of radial circlet, paralectotype, MNHN A25646, ×0.75; c, aboral view of proximal column with basals and radials, ×0.8 (de Loriol, 1882 in 1882-1889).

Family NEODADOCRINIDAE Hess, 2006

[Neodadocrinidae HESS, 2006, p. 47]

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

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

- Neodadocrinus MANNI & NICOSIA, 1990a, p. 363 [*N. tokayi; M]. Cup small, of variable height. Radial articular facet narrow, occupying entire width of adoral side; muscle fossae almost parallel to oral-aboral axis; one axial canal only. Primibrachials compact, joined by synostosis. [Columnals and secundibrachials are unknown. MANNI and NICOSIA (1990a) inferred the presence of an infrabasal circlet (fused infrabasals) from the nerve canals at the proximal surface of the basals of N. tokayi. Nerve canals are visible only on the distal surface in N. brevis, however, and there is no indication of an infrabasal circlet (HESS, 2006).] Lower Jurassic (Sinemurian–Pliensbachian): Switzerland, Turkey.——FIG. 82, 1a-b. *N. tokayi; reconstructed cup, a, lateral, b, distal, Turkey, ×7 (Manni & Nicosia, 1990a).—FIG. 82, 1c-h. N. brevis HESS, Pliensbachian, Switzerland; c, cup, holotype, NMB M10152, ×8; d, adoral view of basal, syntype, NMB M10161, ×10; e-h, radial, e, proximal, f, aboral, g, adoral, h, distal, paratype, NMB M10156, ×8 (Hess, 2006).
- Pustulocrinus HESS, 2006, p. 48 [*P. iguana; M]. Cup low and wide. Pinnules mostly fused. Brachials and pinnulars with crest; all plates with strong, irregular pustules. *Lower Jurassic (Pliensbachian):*

Switzerland.——FIG. 82,2*a*–*n*. **P. iguana*; *a*–*b*, cup, *a*, distal view of part of basal circlet on topmost columnal, *b*, proximal view of radial circlet, holotype, NMB M10493, ×5; *c*–*f*, radial, *c*, aboral, *d*, adoral, *e*, proximal, *f*, distal, paratype, NMB M10259, ×7.5; *g*–*i*, primibrachial 1, *g*, aboral, *h*, adoral, *i*, distal, paratype, NMB M10270, ×7.5; *j*, aboral view of primibrachial 2, syntype, NMB M10274, ×10; *k*, proximal view of secundibrachial 2, paratype, NMB M10280, ×10; *l*–*m*, secundibrachial, *l*, lateral, *m*, adoral, paratype, NMB M10288, ×10 (Hess, 2006).

Family BANGTOUPOCRINIDAE Stiller, 2000

[Bangtoupocrinidae STILLER, 2000, p. 39]

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

Subfamily BANGTOUPOCRININAE Stiller, 2000

[Bangtoupocrininae STILLER, 2000, p. 42]

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

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



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

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

Subfamily SILESIACRININAE Stiller, 2000

[Silesiacrininae STILLER, 2000, p. 47]

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

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

Family UNCERTAIN

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

proximal, JME PL 1993/51, \times 3; *h-i*, radial, *h*, aboral, *i*, adoral, JME PL 1993/34, \times 2.6; *j-l*, radial circlet, *j*, lateral, *k*, proximal, *l*, distal, JME PL 1993/40, \times 3; *m*, columnal facet, NMB M10492, \times 2 (Jäger, 1993).

- Carinacrinus HESS, 2006, p. 55 [*C. hagdorni; M]. Cup unknown. Brachials triangular in cross section with smooth surface and aboral keel. Proximal and distal brachial articular facets at an angle to each other, either both muscular or one muscular and one synostosial. Large pinnule socket with fulcral ridge parallel to adoral furrow; no pinnule socket in approximately half the brachials with synostosial facet. Column unknown. Lower Jurassic (Pliensbachian): Switzerland.—FIG. 83,2a-e. *C. hagdorni; a-c, secundibrachial, a, lateral, b, adoral, c, distal, holotype, NMB M10252, ×10; d, lateral view of secundibrachial, syntype, NMB M10250, ×10; e, proximal view of secundibrachial with synostosis, syntype, NMB M10251, ×10 (Hess, 2006).
- Catinicrinus HESS, 2006, p. 56 [*C. jaegeri; M]. Cup unknown. Primibrachials connected by synostosial facets. Saddle-shaped brachials with smooth surface, constricted body and large facets, with or without pinnule sockets. Brachial articular facets muscular, synostosial, or syzygial with 2 ridges arranged in a V shape. Distal brachials elongate, with articular facets at an angle to the ossicle and a protruding pinnule socket. Distal facets of many brachials with one muscle fossa on lappet articulating with spoon-shaped muscle fossa on proximal side of following brachial. Axils with proximal muscle fossae indicate arm branching distal to primibrachials. Column unknown. Lower Jurassic (Pliensbachian): Switzerland.-FIG. 83,3a-h. *C. jaegeri; a-c, secundibrachial, a, aboral, b, adoral, c, distal, holotype, NMB M10312, ×10; d-e, secundibrachial, d, proximal (syzygy), e, adoral, paratype, NMB M10307, ×10; f, adoral view of distal secundibrachial, paratype, NMB M10316, ×10; g, aboral view of distal secundibrachial, paratype, NMB M10317, ×10; h, aboral view of primibrachial 1, paratype, NMB M10496, ×6 (Hess, 2006).
- Rotacrinus HESS, 2006, p. 57 [**R. canalis*; M]. Cup unknown. Brachials disk shaped, with parallel facets and broad, adoral furrow bordered by sharp ridges; facets oblique and straight muscular, syzygial with 2 to 4 V-shaped or crosslike culmina, and synostosial with or without pinnule socket. Column unknown. *Lower Jurassic (Pliensbachian):* Switzerland.——FIG. 84, *1a-d. *R. canalis; a-c,* epizygal secundibrachial, *a,* proximal, *b,* adoral, *c,* distal, holotype, NMB M10333, ×7; *d,* distal view of secundibrachial without pinnule socket, paratype, NMB M10337, ×7 (Hess, 2006).
- Serracrinus HESS, 2006, p. 58 [*S. planus; M]. Cup unknown. Brachials typically wide and low, rectangular to triangular in adoral or aboral view. Aboral surface with spines that increase in size laterally. Brachials with or without pinnule socket. Facets muscular and synostosial; muscular facets



FIG. 83. Uncertain (p. 169).



FIG. 84. Uncertain (p. 169-171).

with small, drop-shaped muscle fossae bordering adoral furrow. Column unknown. *Lower Jurassic* (*Pliensbachian*): Switzerland.——FIG. 84,2*a*-*e*. **S. planus*; *a*-*c*, secundibrachial, *a*, adoral, *b*, proximal, *c*, distal, holotype, NMB M10341, ×7; *d*, aboral view of secundibrachial, paratype, NMB M10347, ×7; *e*, proximal view of secundibrachial (synostosis), syntype, NMB M10349, ×10 (Hess, 2006). Souticrinus NICOSIA, 1991, p. 398 [*S. farinacciae; M]. Small compact cup with proximale, contiguous basals and radials. Radial cavity deep and narrow. Radial articular facet small, inward sloping; aboral ligament pit wide; adoral muscle fossae small. Column cylindrical. Lower Jurassic (Sinemurian): Turkey.——FIG. 84,3a-c. *S. farinacciae; reconstructed cup, a, lateral, b, proximal, c, distal, ×3 (Nicosia, 1991).

HYOCRINIDA Hans Hess

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Order HYOCRINIDA Rasmussen, 1978

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

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

such columnals appears to be questionable. The species was transferred by MIRONOV and SOROKINA (1998b) to *Cratecrinus (Excavocrinus)* of uncertain affinity.] *Holocene*.

Family HYOCRINIDAE Carpenter, 1884

[Hyocrinidae CARPENTER, 1884a, p. 217]

Characters as for order. Holocene.

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

Hyocrinus THOMSON, 1876, p. 47 [*H. bethellianus; M]. Basals 3 or fused, forming a circlet without distinct sutures. Width of distal radial articular facet 33 to 44 percent of upper width of radial. No lateral spines or flattened projections on proximal brachials and pinnulars. Second and third nonmuscular articulations between brachials 3 and 4 and 5 and 6. First pinnule typically on brachial 6, rarely on 5. In middle part of arm, successive series of 2 or 3 brachials united by synostosis, never successive muscular articulations. Expansion of genital pinnules with one row of H-shaped plates, but shape of cover plates very variable and useful at species level only (ROUX, 2004, fig. 7). Cover plates consisting of 2 or 3 pairs corresponding to each pinnular. Tegmen typically low, sometimes inflated. Oral plates typically large, forming high oral cone where tegmen low. Anal cone low. Columnal symplexies with 6 to 10 crenular units of one crenula each, or more in larger species like H. biscoitoi (number of crenular units and crenulae unknown in H. giganteus). Holocene: Southern Ocean, Indian Ocean, Pacific Ocean (bathyal and abyssal).---FIG. 85, 1a-b. *H. bethellianus; a, proximal column and crown, Crozet Islands at approximately 3000 m, holotype, BMNH (18)85.3.30.31, ×1.7 (Thomson, 1876); b, adoral view of cup with tegmen, ×10 (Carpenter, 1884a, pl. 6,4).-FIG. 85,1c. H. biscoitoi ROUX, 2004; complete specimen, length of crown 25 cm, 35 pinnules on each side, East Pacific Rise at 2410 m, holotype, MNHN EcPh90 (Roux, 2004).-FIG. 85,1*d–e. H. cyanae* BOURSEAU & others, 1991; *d*, proximal column and base of crown, *e*, portion of mesistele, southwestern Pacific, MNHN EcPs244, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

- Anachalypsicrinus A. M. CLARK, 1973b, p. 269 [*A. nefertiti; M]. Three basals with distinct sutures. Width of distal radial articular facet 40 to 50 percent of upper width of radial. Second nonmuscular articulation between brachials 4 and 5, third between brachials 6 and 7; nonmuscular articulations irregularly distributed along middle arm. Consecutive muscular articulations commonly 1 or 2, maximum 4. First pinnule on brachial 5. Expansion of genital pinnules with one row of H-shaped plates. Cover plates of 2.5 to 3.5 pairs corresponding to each pinnular. Tegmen low. Anal cone low. Oral cone large and high. Columnal symplexies with 9 to 12 crenular units of 1 to 5 crenulae each. Holocene: northern Atlantic Ocean (lower bathyal).-FIG. 86,1a. *A. nefertiti; proximal column and base of crown, northeastern Atlantic, holotype, BMNH 1972.12.5, ×1.5 (Roux, Messing, & Améziane, 2002; courtesy of the Bulletin of Marine Science).----FIG. 86,1b. A. atlanticus (ROUX, 1990); facet of distal columnal, Newfoundland at 1850-1875 m, holotype, NMNH ED-319, ×15 (Roux, 1990, under Ptilocrinus, species transferred to Anachalypsicrinus by Mironov & Sorokina, 1998b).
- Belyaevicrinus MIRONOV & SOROKINA, 1998b, p. 58 [*B. latipinnulus; M]. Structure of cup unknown. Second nonmuscular articulation between brachials 4 and 5; middle part of arm with 2 or series of 3 brachials united by synostosis. Maximum number of consecutive muscular articulations 1. Brachials do not become narrower at inner margin of arms. First pinnule on brachial 6. Fewer than 10 (approximately 5) pinnules on one side of arm. Expansion of genital pinnules wide and well developed; 2 rows of genital plates on one side of pinnule. Interradial fossae of tegmen not equal in height; tegmen reaching brachial 3 in interrays BC and CD, but only brachial 1 in interray AE. Tegminal interradial plates tend to be arranged in median row. Columnal symplexies with 7 crenular units of 1 or 2 straight crenulae each. Holocene: Indian Ocean, Southern Ocean (abyssal).—FIG. 85,2a-c. *B. latipinnulus; a, highest part of tegmen at interradius BC, $\times 4$, *b*, anal cone, $\times 4$, *c*, proximal part of arm, Antarctica at approximately 5600 m, holotype, ZMM C-21, ×3 (Mironov & Sorokina, 1998b).
- Calamocrinus AGASSIZ, 1890, p. 165, emend., ROUX, 2004, p. 606 [*C. diomedae; M]. Basals fused or with a few inconspicuous sutures, aboral side of basal circlet flanged. Arms irregularly branching, first branching between brachials 8 to 15, additional branching more distally. Second synostosis between brachials 5 and 6. Maximum number of consecutive muscular articulations approximately 9. Distribution of nonmuscular articulations along middle arm irregular. First pinnule on brachial 4. Expansion of genital pinnules with

numerous, imbricated, small plates, never in rows (ROUX, 2004, fig. 7e). Tegmen inflated, with welldeveloped anal cone. Columnal symplexies with 7 to 16 crenular units of 1 to 4 crenulae, depending on columnal diameter. *Holocene:* eastern Pacific Ocean (bathyal).——FIG. 86,2. **C. diomedae*; proximal column and base of crown, USNM E47881, ×2 (Roux, Messing, & Améziane, 2002; courtesy of the *Bulletin of Marine Science*).

- Dumetocrinus MIRONOV & SOROKINA, 1998a, p. 413 [*Ptilocrinus antarcticus BATHER, 1908, p. 296; SD MIRONOV & SOROKINA, 1998a, p. 413]. Basals fused, aboral side of basal circlet flanged. Arms 5, exceptionally branching at brachial 4. Second nonmuscular articulation between brachials 5 and 6. Maximum number of consecutive muscular articulations 16. Middle portion of arm with brachials as wide as proximal brachials. First pinnule on brachial 4. Three rows of genital plates on one side of pinnule; the median row consisting of H-shaped plates. Large, laterally flattened projections on pinnulars. Tegmen inflated. Oral plates of moderate size. Anal cone slightly lower than oral cone. Tegminal plates connected with first 5 brachials. All or most proximal columnals compound. In mesistele, 11 or 12 crenular units of 1 or 2 crenulae each; in dististele, numerous (approximately 33) long crenulae weakly grouped into crenular units. Holocene: Southern Ocean (bathyal).——FIG. 86,3. *D. antarcticus (BATHER); Southern Ocean at approximately 480 m, holotype, ×1.5 (Bather, 1908).
- Feracrinus MIRONOV & SOROKINA, 1998a, p. 410, emend., AMÉZIANE & ROUX, 2011, p. 138 [*F. aculeatus; M] [=Ptilocrinus A. H. CLARK, 1907b, p. 551 (type, P. pinnatus, M), sensu lato, partim, ROUX, MESSING, & AMÉZIANE, 2002, p. 822; = Camaecrinus MIRONOV & SOROKINA, 1998b, p. 21, nom. nov. pro Ailsacrinus MIRONOV & SOROKINA, 1998a, p. 404-405 (type, Ailsacrinus peripterus MIRONOV & SOROKINA, 1998a, OD), non TAYLOR, 1983]. Basals fused or basal circlet with 1 to 3 sutures. Arms moderately narrow. Width of distal radial articular facet 74 to 81 percent of upper width of radial. Second nonmuscular articulation between brachials 5 and 6; synostoses occur regularly after brachial 7. Distal arm with fewer than 5 successive muscular articulations in juveniles and at most 22 in large adult specimens. First pinnule on brachial 4. Proximal part of genital pinnules with one row of lateral plates on each side, rarely joined by stereom bridges over gonad in H-shaped plates. Cover plates of distal pinnules with short, terminal, fingerlike projection; outer perpendicular spine or tubercle absent. Tegmen low to inflated. Oral plates of moderate size. Anal cone lower or higher than oral cone. Tegminal plates connected with brachials 1 to 4. Columnal symplexies with 6 to 10 crenular units of 1 to 3 crenulae each. [AMÉZIANE and ROUX (2011) pointed out that Feracrinus and Ailsacrinus (the latter renamed Camaecrinus by MIRONOV & SOROKINA, 1998b) are based on 3 specimens, each attributed to a different species.



FIG. 85. Hyocrinidae (p. 173-174).

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

- Gephyrocrinus KOEHLER & BATHER, 1902, p. 68, emend., ROUX & BOHN, 2010, p. 429 [*G. grimaldii; M]. Interbasal sutures absent, aboral border of basal circlet flanged. Arms 5, exceptionally branching at brachial 4. Lateral spines or flattened projections on proximal brachials and pinnulars absent. Second nonmuscular articulation between brachials 5 and 6, rarely 4 and 5. In middle and distal arm, regular pattern with successive brachial pairs united by synostosis and separated by a muscular articulation. Rarely, series of 3 brachials united by synostosis. First pinnule on brachial 4, rarely 5. Expansion of genital pinnules with numerous small plates, never in rows. Tegmen moderately inflated. Anal cone higher than oral cone. Columnal symplexies with 6 to 8 crenular units of 1 to 3 crenulae each. Holocene: northeastern Atlantic and Pacific Oceans -FIG. 86,5a-b. *G. grimaldii; a, (bathyal).proximal column and base of crown; b, portion of mesistele, northern Atlantic, MNHN EcPs245, ×4 (Roux, Messing, & Améziane, 2002; courtesy of the Bulletin of Marine Science).
- Laubiericrinus Roux, 2004, p. 598 [*L. pentagonalis; M]. Three interbasal sutures. Width of distal radial articular facet 71 to 77 percent of upper width of radial. First pinnule on brachial 5. Second nonmuscular articulation between either brachials 3 and 4 or 4 and 5; beyond brachial 5, synostoses alternating with muscular articulations. Welldeveloped cylindrical anal cone shorter than oral cone. Proximal columnals weakly pentagonal; columnal symplexies with 5 crenular units of 1

(juvenile) to 3 (adult) crenulae. *Holocene:* southwestern Pacific Ocean (lower bathyal).——FIG. 87,*1a-c. *L. pentagonalis*, North Fiji Rise at 2765 m, holotype, MNHN EcPs10269; *a*, holdfast, ×4; *b*, facet of proximal columnal, ×20; *c*, facet of distal columnal, ×20 (Roux, 2004).

- Ptilocrinus A. H. CLARK, 1907b, p. 551 [*P. pinnatus; M]. Basals 3 or fused. Synostoses distributed irregularly in middle part of arm; maximum number of consecutive muscular articulations 17. Some brachials cuneate and not reaching inner margin of arm. First pinnule on brachial 4, rarely 5. More than 10 pinnules on each side of arm. Expansion of genital pinnules high or inconspicuous. Genital plates in 1 to 5 rows on one side of pinnule. Tegmen from moderate to high, interradial fields of tegmen equal in height. Proximal columnals commonly in one piece. Columnal facets with 6 to 10 crenular units of 1 to 3 crenulae each. [The genus was subdivided by MIRONOV and SOROKINA (1998b) into 2 subgenera, Ptilocrinus s. str. with P. pinnatus as type species, and Chambersaecrinus MIRONOV & SOROKINA (1998b, p. 52), with P. brucei VANEY (1908, pl. 24,70) as type species. Following ROUX (2004), these subgenera are not used herein. A new species, P. tasmaniaensis AMÉZIANE & ROUX (2011) is intermediate in several characters between the subgenera Ptilocrinus and Chambersaecrinus.] Holocene: Southern Ocean, northern Pacific Ocean (lower bathyal to abyssal).-FIG. 87,2a. *P. pinnatus; proximal column and base of crown, MNHN EcPs237, ×3 (Roux, Messing, & Améziane, 2002; courtesy of the Bulletin of Marine Science).-FIG. 87,2b-d. P. brucei VANEY; b, basal circlet with topmost column, c, proximal part of arm, d, middle part of arm, Southern Ocean at 4970 m, holotype, RSM 1921.143.1743, ×3 (Mironov & Sorokina, 1998b).
- Thalassocrinus A. H. CLARK, 1911a, p. 474 [*T. pontifer; M]. Basals 3 or fused. The most frequent proximal arm pattern with second nonmuscular articulation between brachials 4 and 5, third synostosis between brachials 6 and 7, no series of 3 or more brachials united by synostoses before brachial 10. (In middle part of arm of T. pontifer, muscular articulations regularly follow pair of brachials joined by synostosis). First pinnule on brachial 5; each pinnular with 2 to 2.5 pairs of cover plates. Well-developed oral and anal cones. Number of tegminal plates greater than 10 in each interradius. Proximal columnals hexagonal or hexalobate, columnals of mesistele hexagonal. Symplexies with 6 or 7 crenular units of 1 to 3 crenulae each. [Median brachial formula, form of cover plates, and columnals of mesistele unknown in T. depauperatus. The genus was divided by MIRONOV and SOROKINA (1998b) into 2 subgenera, Thalassocrinus s. str., with T. pontifer as type species; and Conferocrinus MIRONOV & SOROKINA (1998b, p. 39) with T. depauperatus MIRONOV & SORO-KINA (1998b, p. 39), as type species. As discussed by ROUX (2002), Conferocrinus is probably a



FIG. 86. Hyocrinidae (p. 174-176).



FIG. 87. Hyocrinidae (p. 176–179).

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

CYRTOCRINIDA Hans Hess

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Order CYRTOCRINIDA Sieverts-Doreck, 1952

[Cyrtocrinida Sieverts-Doreck in Moore, Lalicker, & Fischer, 1952, p. 614]

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

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

others, 2007); and the Upper Jurassic sponge facies (Oxfordian) of France, Germany, and Switzerland (QUENSTEDT, 1876; DE LORIOL, 1882–1889; JAEKEL, 1892; HESS, 1975; HESS & SPICHIGER, 2001).] Lower Jurassic (Sinemurian)–Holocene.

Suborder CYRTOCRININA Sieverts-Doreck, 1952

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

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

Superfamily EUGENIACRINITOIDEA Roemer, 1855

[nom. correct. HESS, herein, pro Eugeniacrinitacea ARENDT, 1968, p. 156, nom. transl. ex ROEMER, 1855, in BRONN & ROEMER, 1851–1856, p. 227]

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

Family EUGENIACRINITIDAE Roemer, 1855

[nom. correct. RASMUSSEN, 1978, p. 832, ex Eugeniacrinidae ROEMER, 1855 in BRONN & ROEMER, 1851–1856, p. 227]

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

Eugeniacrinites MILLER, 1821, p. 111 [*E. quinquangularis; M; = Encrinites cariophilites VON SCHLOTHEIM, 1813, p. 68, ex Caryophyllitea WALCH, 1762, p. 80 and caryophylli WALCH, 1769 in 1768-1773, p. 114; = Encrinites cariophyllites VON SCHLOTHEIM, 1820, p. 332; =E. caryophyllatus GOLDFUSS, 1829 in 1826-1844, p. 163; =Pentacrinus? paradoxus GOLDFUSS, 1831 in 1826-1844, p. 200; = Eugeniacrinus angulatus D'ORBIGNY, 1850 in 1850-1852, p. 383; = Eugeniacrinus impressus D'ORBIGNY, 1850 in 1850-1852, p. 383] [=Eugeniacrinus AGASSIZ, 1836, p. 195, nom. van.; =Eugeniocrinites AGASSIZ, 1842-1846, p. 147, nom. null.; = Eugeniocrinus AGASSIZ, 1842-1846, p. 147, nom. nov. pro Eugeniacrinus AGASSIZ, 1836, p. 195, nom. null.]. Cup conical to funnel shaped, rarely nearly cylindrical. Radial articular facet steep, low, and wide, with small, aboral ligament fossa, deeply excavated

interarticular fossae and low adoral muscle fossae, separated by ridge parallel to fulcral ridge. Articular facets separated by small interradial projections. Radial cavity wide and rather shallow. Aboral side of cup entirely occupied by almost flat, articular facet for column. First primibrachials very low. Axillary second primibrachials large, with compact, spearhead-shaped, median prolongation above small, lateral, articular facets for secundibrachials, and joined aborally by symplectial facets as protective lid over adoral side of cup when retracted. Arms small, may be coiled between second primibrachials. Columnals cylindrical to slightly conical, commonly high. Uppermost columnal with diameter equal to base of cup, commonly closely attached to cup. Articular facet of columnals with marginal granulation. [WAGNER (1684) first recorded the type species under the name Caryophyllos aromaticos, as the petrified fruit of clove tree (Eugenia caryophyllata). LHWYD (1699) referred it to the crinoids, and it has since been recorded under pre-Linnean names such as Caryophyllitarum (ROSINUS, 1718) and Caryophyllis (SCHEUCHZER, 1752). The unavailable (unpublished, but distributed to a few people) name Symphytocrinus caryophyllum KOENIG (1825) is based on this species.] Middle Jurassic (Bathonian)-Lower Cretaceous (Valanginian): Albania, Czech Republic, France, Germany, Hungary, Italy, Portugal, Romania, Slovakia, Switzerland, Russia.-FIG. 88, 1a-g. *E. cariophilites (VON SCHLOTHEIM), Oxfordian; *a–b*, cup and column, *a*, lateral, *b*, lower facet, Germany, $\times 3$; *c*, distal view of cup, Germany, $\times 3$; d-e, primibrachial 2, d, aboral, e, lateral, Germany, \times 4; f, adoral view of primibrachial 2, Germany, \times 4 (Jaekel, 1891); g, reconstruction of closed crown, foremost primibrachials removed to show coiled arm, ×2.5 (Jaekel, 1907).

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



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

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

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

Family GUTTICRINIDAE Klikushin, 1987

[Gutticrinidae KLIKUSHIN, 1987a, p. 252]

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

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

Family HOYACRINIDAE Delogu & Nicosia, 1986

[Hoyacrinidae DELOGU & NICOSIA, 1986, p. 3]

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

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

Family PHYLLOCRINIDAE Jaekel, 1907

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

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

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



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

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

- Apsidocrinus JAEKEL, 1907, p. 304 [*A. remesi; M] [=Pyramidocrinus REMEŠ, 1912, p. 162 (type, Phyllocrinus cyclamen REMEŠ, 1902, p. 205, SD REMEŠ, 1912, p. 162)]. Cup large, with lobate basal part; interradial grooves prolonged into prominent interradial projections that are curved inward and bladelike at top, and may meet adorally. Brachials and columnals unknown. Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Valanginian): Czech Republic, Hungary, Italy, Turkey.-FIG. 89,3a-b. *A. remesi; cup, a, lateral, b, proximal, Valanginian, Czech Republic, GIP 171/9, ×2.5 (Žítt, 1978a).—FIG. 89,3c. A. moeschi (ZITTEL in DE LORIOL, 1879 in 1877-1879); reconstruction, Tithonian, Poland, ×2 (Ausich & others, 1999; redrawn from Pisera & Dzik, 1979).
- Nerocrinus MANNI & NICOSIA, 1999, p. 328 [*N. petri; M]. Small cup composed of 3 distinct basals and 5 radials with small facets sunken between interradial projections. Radial cavity deep. Brachials and columnals unknown. [HESS (2006) did not accept the family Nerocrinidae (order Dadocrinida, suborder Cyrtocrinina, superfamily Eugeniacrinitoidea), proposed by MANNI and NICOSIA (1999), on the basis of the presence of the distinct basals. Reduction and fusion or absorption of basals is a relatively simple process that does not justify the creation of an additional higher taxon.] Lower Jurassic (Pliensbachian): Italy, Switzerland.-—Fig. 89,4a-b. *N. petri, Switzerland; a, lateral view of cup, NMB M10017, ×10; b, proximal view of cup, NMB M10019, ×10 (Hess, 2006).
- Ticinocrinus HESS, 2006, p. 35 [*T. coronatus; M]. Cup small, composed of a circlet of 5 distinct, low basals and 5 bulging, weakly keeled, high radials. Basals with symplectial facet to column and a concave central area. Radials with moderately high, blunt interradial projections; radial articular facet very small, sunken. Radial cavity deep. Brachials and columnals unknown. Lower Jurassic (Pliensbachian): Switzerland.——FiG. 89,5a-e. *T. coronatus; a-c, cup, a, lateral, b, proximal, c, lateral-distal, holotype, NMB M10020, ×7.5; d-e, radial, d, aboral, e, adoral, paratype, NMB M10023, ×7.5 (Hess, 2006).

Family PROHOLOPODIDAE Žitt, 1974

[Proholopodidae ŽITT, 1974a, p. 28]

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

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

Family PSALIDOCRINIDAE Žitt, 1978

[Psalidocrinidae ŽITT, 1978a, p. 117]

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

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



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



FIG. 91. Sclerocrinidae (p. 188-189).

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

Family SCLEROCRINIDAE Jaekel, 1918

[Sclerocrinidae JAEKEL, 1918, p. 75] [=Hemicrinidae RASMUSSEN, 1961, p. 233; =Paragammarocrinitidae JAGER, 1982, p. 76]

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

- Sclerocrinus JAEKEL, 1891, p. 621 [*S. strambergensis; SD RASMUSSEN, 1961, p. 217]. Cup mostly round, extremely massive; radial articular facet rounded, sloping strongly outward, with very small muscle fossae; interradial processes low or lacking; radial cavity small. Facet to column large and deep, with differentiated inner part containing minute columnals. Upper Jurassic (Oxfordian)-Lower Cretaceous (Valanginian): Czech Republic, Hungary, Poland.-FIG. 90,3a-i. *S. strambergensis, Valanginian, Czech Republic; a, lateral view of cup, lectotype, $\times 3$; *b*, proximal view of cup, $\times 3$; c, distal view of cup, $\times 3$; d-f, distal columnal, d, lateral, e, lower, f, upper facet, $\times 2$; g-i, fused primibrachials 1 and 2, g, aboral, h, adoral, i, proximal, ×6 (Jaekel, 1891).
- Ascidicrinus HESS, SALAMON, & GORZELAK, 2011, p. 124 [*A. armatus; OD]. Cup rather low, bulging or lobed interradially, especially in proximal view, commonly ornamented; radial articular facets broad, not sunken; radial cavity relatively deep, variable in diameter; facet for the column deep. Upper Jurassic (Tithonian): Poland.——FIG. 91,1a-c. *A. armatus, cup; a, lateral, b, aboral, c, adoral, holotype, GIUS 8-3577AaH, ×10 (Hess, Salamon, & Gorzelak, 2011).
- Cyrtocrinus JAEKEL, 1891, p. 602; emend., JAEKEL, 1907, p. 278 [*Eugeniacrinites nutans GOLDFUSS, 1829 in 1826–1844, p. 164; SD JAEKEL 1907, p. 281]. Cup compact, low, more or less oblique, with wide and deep concave base obliquely attached to top of column and distinctly overhanging uppermost columnal, which may be triangular in side view or rudimentary. Radial cavity small to moderately large, shallow. Radial articular facet large, almost flat, sloping outward, muscle fossae distinct,

commonly small and deep. First primibrachial axillary, composed of completely or incompletely fused primibrachials 1 and 2. Secundibrachials stout, angular, ability to curl, rectangular or cuneate. Column short, with cylindrical columnals. Surface of cup, brachials, and columnals generally smooth but may be sculptured by granules. [Cups of C. nutans have great variation in height, sculpturing, radial cavity diameter, and inclination of radial facets to column axis (see also DE LORIOL, 1879 in 1877-1879, pl. 18,29-52, and DE LORIOL, 1882 in 1882-1889, p. 115). Specimens from a single locality are linked by intermediates, so that assignment to distinct species is not possible. For example, HESS and SPICHIGER (2001) reported a ratio of radial cavity diameter to cup diameter between 80 and 20 percent in specimens from the middle Oxfordian Birmenstorf Member of Holderbank, Switzerland; such variation corresponds to QUEN-STEDT's (1876) "subspecies" nutans apertus and nutans opertus. Granular specimens, designated by GOLDFUSS (1826-1833 in 1826-1844) as Eugeniacrinites compressus, were assigned by JAEKEL (1891, p. 626) to his genus Sclerocrinus and by RASMUSSEN (1978, p. 831) to Gammarocrinites. However, these may be merely variants or ecophenotypes of one species. The material from the Birmenstorf Member includes specimens with a radial articular facet at a right angle to the column axis caused by either a triangular or a bent top columnal; the radials and the cup also exhibit a tendency to fuse with the top columnal, suggesting that Cyrtocrinus is ancestral to Hemicrinus.] Middle Jurassic (Bathonian)-Lower Cretaceous (Valanginian): France, Bathonian; Albania, France, Germany, Switzerland, Oxfordian-Tithonian; Austria, Czech Republic, Valanginian. FIG. 91, 2a-g. *C. nutans (GOLD-FUSS), Oxfordian; a, coiled arm, Germany, ×4 (Jaekel, 1891); b-c, cup on triangular top columnal, b, oblique lateral, c, lower columnal facet, Switzerland, NMB M10578, ×5; d, cup obliquely attached to single columnal, Switzerland, NMB M10679, ×3; e, proximal view of granular cup, Switzerland, NMB M10576, ×4; *f*–g, top columnal, *f*, lateral, g, distal facet, Switzerland, NMB M10577, ×4 (Hess, new).

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

- Hemicrinus D'ORBIGNY, 1850 in 1850-1852, p. 90 [*H. astierianus; M; =Cyrtocrinus granulatus JAEKEL, 1891, p. 611]. Cup low and bowl shaped, more or less oblique or irregular, formed by 5 distinctly asymmetric radials, fused, generally at right angle to column part, with a slender, conical cylindrical or claviform proximal columnal; sutures commonly indistinct. Proximal columnal may be articulated directly to holdfast, which is similar to proximale, cylindrical to conical with irregularly expanded distal end attached to substrate. [In contrast to RASMUSSEN (1978, p. 831), ŽITT (1983) distinguished Torynocrinus from Hemicrinus (based on a crystallographic study) on the basis of a spoon-shaped part of fused elongate radials and no column versus fused radials connected to a column part that articulates symplectially with the holdfast. Both have similar holdfast parts. This argument is followed herein even though recognition of fused radials only (as opposed to radials fused with top columnal) may be difficult in practice.] Upper Jurassic (Kimmeridgian)-Lower Cretaceous (Albian): Crimea, Czech Republic, England, France, Hungary, Poland, Slovakia.-FIG. 91, 3a-d. *H. astierianus, Neocomian, France; a-c, cup, a, lateral, b, aboral, c, adoral, lectotype, MNHN B14793, ×2.5 (Rasmussen, 1961); d, reconstruction, ×3 (Ausich & others, 1999).
- Neogymnocrinus HESS, 2006, p. 77 [*Gymnocrinus richeri Bourseau, Améziane-Ĉominardi, & Roux, 1987, p. 595; OD]. Cup asymmetric, formed mostly by first primibrachials with closely fitting extensions that seal the adoral side of the cup. Radials rudimentary or fused with the proximal columnal. Crown strongly asymmetric, with some arms much shorter than others; branching and number of arms highly variable; primibrachial 1 or 2 axillary; further branching may occur to tetribrachial 13, and the first brachials of 3 consecutive brachitaxes may all be axillary. Primibrachial 1 and secundibrachial 1 united orally, enclosing radial furrow; arms may curl inward to form a compact fist. Brachials asymmetrical, more or less cuneate in aboral view, thicker part with pinnule socket and thinner part developed into winglike extension, coiled pinnules fitting into depression on the extension of the neighboring brachial; all brachial articulations muscular. Column composed of a granular or smooth proximal columnal of variable length, and a smooth, much shorter distal columnal attached to the substrate by a slightly expanded base. Holocene: southwestern tropical Pacific Ocean (bathyal).—FIG. 92, 1a-b. *N. richeri (BOURSEAU, AMÉZIANE-COMINARDI, & ROUX); a, intact specimen, New Caledonia at 470 m, holotype, MNHN Spec. No. 1 Chalcal 2, station DW 76, ×1.5 (D. Brabant, new); b, facet of proximal secundibrachial, MNHN spec. No. 12 Chalcal 2, station DW 76, ×6 (Bourseau & others, 1991).
- Paragammarocrinites JÅGER, 1982, p. 76 [*P. campanicus; M]. Cup compact, without interradial projections, composed of 5 distinct radials; radial articular facet large, nearly horizontal; radial cavity small;

underside of cup wide and deeply concave, with 5 small, hidden basals. [JÄGER (1982, p. 76) proposed the family Paragammarocrinitidae for this form, based on the presence of vestigial basals but agrees with its assignment herein to the Sclerocrinidae (M. JÄGER, personal communication, 2004).] *Upper Cretaceous (Campanian):* Germany.——FIG. 91,4a-c.*P: campanicus; cup, a, lateral, b, proximal, c, distal, holotype, NLfB kca 37, ×6 (Jäger, 1982).

- Pilocrinus JAEKEL, 1907, p. 290 [*Eugeniacrinus moussoni DESOR, 1845, p. 220; M] [=Gymnocrinus DE LORIOL, 1879 in 1877-1879, p. 249 (type, G. moeschi, M), nomen dubium, HESS, 2006, p. 77]. Cup wide, almost cylindrical, slightly restricted at midheight; radial articular facets wide, outward sloping, separated by interradial projections; proximal side of cup with wide, deep concavity with rather large articular facet for column. Primibrachials 1 and 2 united by synostosis. Primibrachial 2 axillary with thickened sides, mostly united adorally and enclosing radial furrow. Secundibrachials commonly prolonged on one side but may also be united adorally. [A Lower Cretaceous occurrence is doubtful (KLIKUSHIN, 1996, p. 108), but RASMUSSEN (1975; 1978, fig. 559-3) figured a cup from the Upper Cretaceous (Campanian) of Germany. Pilocrinus has interradial projections; but radial articular facet, arms, and articulation to column correspond to other Sclerocrinidae. The name Gymnocrinus DE LORIOL, 1879 in 1877-1879, is a nomen dubium. Its type species, G. moeschi DE LORIOL, 1879 in 1877-1879, recognized as belonging to a previously described species in a valid genus (=Pilocrinus moussoni [DESOR, 1845]), is invalid as a junior synonym (ICZN, 2009, Article 23) (HESS, 2006). KLIKUSHIN (1996) rejected the combination of the orally enclosed primibrachial 2 of "G. moeschi" with the cup of Pilocrinus moussoni. However, material from the middle Oxfordian of northern Switzerland includes a primibrachial 1 with a proximal muscular facet (Fig. 92,2e) matching the radial facet of the cup of Pilocrinus moussoni (Fig. 92,2a) and with a distal synostosial facet (Fig. 92,2f) matching the proximal facet of an orally open (Fig. 92,2i) or united (Fig. 92,2g) primibrachial 2.] Upper Jurassic (Oxfordian): Crimea, France, Germany, Hungary, Poland, Switzerland.-FIG. 92,2a-i. *P. moussoni (DESOR), Switzerland; a, cup, NMB M10580, ×5.5; b, proximal view of cup, NMB M10581, ×4; c, proximal view of cup with columnal, NMB M10582, ×4 (Hess, new); d, facet of columnal, NMB M9293, ×6 (Hess, 1975); e-f, primibrachial 1, e, proximal, f, distal, NMB M10528, \times 5; g-h, primibrachial 2, g, proximal, h, distal, NMB M10529, ×5; i, proximal view of primibrachial 2, NMB M10530, ×5 (Hess, new).
- Strambergocrinus ŽITT, 1979b, p. 238 [* Cyrtocrinus remesi SZÖRÉNYI, 1959, p. 240; OD]. Cup club shaped to very low, attached to encrusting holdfast of variable height by highly concave to flat facet with narrow band of marginal crenulae (symplexy) that may rarely become cryptosymplectial. Distal side of cup more or less slanting, 2 to 5 articular



FIG. 92. Sclerocrinidae (p. 189).



FIG. 93. Sclerocrinidae (p. 189–192).

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

lateral facet with adjacent depressions for reception of arms, SMO Z-2511/17, ×5.3, ×10 (Žítt, 1979b); *d*, reconstruction, ×2 (Žítt, 1979b).

Torynocrinus SEELEY, 1866, p. 174, nom. nov. pro Koninckocrinus SEELEY, 1864, p. 277, nom. nud. [*T. canon; M] [= Torynocrinus (Collarocrinus) SZÖRÉNYI, 1959, p. 250 (type, T. (C.) phialaeformis, OD); = Torynocrinus (Labiocrinus) SZÖRÉNYI, 1959, p. 250 (type, T. (L.) labiatus, OD)]. Cup composed of 5 more or less elongate asymmetric radials, forming a spoonlike element; sutures between radials partly visible, especially in adoral part. Radial articular facets more or less equal, forming right angle with column part of radials. Cup articulated directly to holdfast. [In spite of considerable individual variation in species of Torynocrinus, SZÖRÉNYI (1959) divided this genus into 3 subgenera, 2 of them new, proposing 9 new species. ŽITT (1983, p. 93, pl. 12,4-5) described a specimen of Torynocrinus canon, preserved in the Natural History Museum, London, as having a primibrachial with

thickened sides united adorally and enclosing the radial furrow, similar to *Neogymnocrinus richeri* and "*Gymnocrinus moeschi*" (=*Pilocrinus moussoni*). *Torynocrinus* is obviously closely related to *Hemicrinus*, from which it seems to have developed by paedomorphosis (arrested column growth, followed by elongation and partial fusion of the radials). Specimens from the Albian Shenley Limestone have a circlet of 5 basals within the cup (HESS & GALE, 2010).] *Lower Cretaceous (Valanginian–Albian):* Czech Republic, England, Hungary, Slovakia.— FIG. 93,2*a–b.* **T. canon*; cup, *a*, adoral, *b*, lateral, Albian, England, holotype, CAMSM B.18178, ×1.25 (Rasmussen, 1961).

Family UNCERTAIN

- Ancepsicrinus SALAMON & GORZELAK, 2010, p. 876 [*A. parvus; M]. Small, spoonlike crinoid with rosette-like, elongate cup, bilaterally symmetrical. Two radial articular facets on opposite axis of symmetry. Facet to column symplectial, with coarse crenulae. Upper Jurassic (Tithonian): Poland.— FIG. 94,1a-b. *A. parvus, cup; a, adoral, b, aboral, holotype, GIUS 8-2850And/ApvH, ×10 (Salamon & Gorzelak, 2010).
- Capsicocrinus DELOGU & NICOSIA, 1987, p. 158 [*C. souti; M]. Cup comparatively large and massive, conical to bell shaped, composed of 5 radials with flat upper side and only small interradial processes; radial articular facet large and wide, filling most of the oral surface, corresponding central cavity very small. Two high primibrachials united by synostosis; primibrachial 2 axillary, unspecialized. Aboral nervous system with a single commissure. Column unknown. [SIMMS and others (1993, p. 504) assigned the genus to Eugeniacrinitidae, but the primibrachials differ from those of Eugeniacrinites. According to DELOGU and NICOSIA (1987), the type locality is Pliensbachian, but according to NICOSIA (1991), it is Sinemurian.] Lower Jurassic (Sinemurian-Pliensbachian): Turkey.——FIG. 94,2a-e. *C. souti; a-c, cup, a, lateral, b, proximal, c, distal, holotype, UR NS 6/153 ×2.3 (Nicosia, 1991); d, 2 radial articular facets, UR NS 6/155b, ×2.5 (Delogu & Nicosia, 1987); e, adoral view of radial, UR NS 6/155b, ×2.5 (Delogu & Nicosia, 1987).
- Castaneacrinus HESS, 2006, p. 46 [*C. selliformis; M]. Cup unknown. Brachials small, saddle shaped, aboral surface wrinkled; first primibrachial high, with distal synostosis; secundibrachials with only muscular facets and large pinnule sockets. Column unknown. Lower Jurassic (Pliensbachian): Switzerland.——FIG. 94,3a-e. *C. selliformis; a-b, secundibrachial, a, oblique lateral, b, adoral, holotype, NMB M10147, ×10; c-d, primbrachial 1, c, aboral, d, adoral, paratype, NMB M10142, ×10; e, oblique distal view of secundibrachial, paratype, NMB M10144, ×20 (Hess, 2006).
- Crataegocrinus MANNI & NICOSIA, 1985a, p. 137 [**C. toniellii;* M]. Cup relatively flat, composed of 5 low radials; articular facets semilunate and

rather wide, interradial processes relatively low. Brachials and columnals unknown. [The low cup with outward bulging radial articular facet and moderate, rounded interradial processes is similar to *Lonchocrinus staszici*, Tithonian, Poland (PISERA & DZIK, 1979; see Fig. 88,2g).] *Middle Jurassic* (*Bajocian*): Italy.——Fig. 94,4*a*-*b*. **C. toniellii;* cup, *a*, lateral, *b*, proximal, holotype, UR NS 6/46, ×1.5 (Manni & Nicosia, 1985a).

- Fischericrinus Castellana, Manni, & Nicosia, 1989, p. 74 [*F. sandrae; M]. Radials with lateral median bulge increasing distally in thickness, with broad, outward sloping articular facet on top, leading to subtriangular cross section; interradial extensions moderately large; interradial sutures sunken. Primibrachial 2 axillary, high, with spinelike median process separating distal articular facets; crenulate lateral facets indicate that ossicles were joined laterally as enlargement of radial cavity. First primibrachials and columnals unknown. [Fischericrinus was assigned by the authors to Eugeniacrinitidae. It resembles some cups from the Lower Cretaceous described by ŽíTT (1974b) as Eugeniacrinites zitteli JAEKEL. Unfortunately, the distinctive radial articular facets are not well preserved in the Italian material. The well-developed primibrachial 2 that the authors combined with the cups differs from that of Eugeniacrinites cariophilites.] Middle Jurassic (Bajocian)-Upper Jurassic (Oxfordian): Italy, Bajocian; Poland, Callovian-Oxfordian.-FIG. 94,5a-c. *F. sandrae, Bajocian, Italy; a, lateral view of cup, paratype, UR NS 6/249, ×5 (Manni & Nicosia, 1994); b, proximal view of cup, UR NS 6/314, $\times 5$; *c*, adoral view of second primibrachial, paratype, UR NS 6/316, ×6.5 (Castellana, Manni, & Nicosia, 1989).
- Fusicrinus HESS, 2006, p. 45 [*F. simmsi; M]. Cup unknown. Brachials high, spindle to crescent shaped, with very small articular facets, facets muscular or synostosial; ambulacral groove narrow, mostly with scalloped or corrugate margin for accommodation of cover plates; pinnule sockets absent. Columnals unknown. Lower Jurassic (Pliensbachian): Switzerland.——FIG. 94,6a-d. *F. simmsi; a-b, primibrachial 1, a, adoral, b, proximal, holotype, NMB M10133, ×10; c, adoral view of primibrachial 2, paratype, NMB M10139, ×6; d, oblique lateral view of secundibrachial, paratype, NMB M10138, ×10 (Hess, 2006).
- Ninocrinus CASTELLANA, MANNI, & NICOSIA, 1990, p. 18 [*N. parvulus; M]. Cup small. Radial articular facet small, outward sloping; interradial projections high and thin, subtriangular in cross section. Radial cavity wide and deep. Brachials and columnals unknown. [This genus should be classified in family Uncertain, according to the authors. It resembles *Fischericrinus*, with which it may be congeneric, in bearing a radial facet on a median bulge, and it resembles *Phyllocrinus* in the high interradial projections.] *Middle Jurassic (Bajocian):* Italy.— FIG. 94,7. *N. parvulus; cup, holotype, UR NS 6/452, ×10 (Castellana, Manni, & Nicosia, 1990).



FIG. 94. Uncertain (p. 192).

Superfamily PLICATOCRINOIDEA Zittel, 1879

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

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

Family PLICATOCRINIDAE Zittel, 1879

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

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

Plicatocrinus MÜNSTER, 1839, p. 89 [*P. hexagonus; SD SIEVERTS-DORECK, 1964b, p. 135]. Cup conical, more or less stellate in section with rounded radial ridges and interradial embayments; composed of 4 to 8, generally 6, thinwalled radials attached to a bowl- or funnel-

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

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

Family TETRACRINIDAE Nicosia, 1991

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

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

Cyrtocrinida



FIG. 95. Plicatocrinidae (p. 194).

lated by synostosis, in *Praetetracrinus* also by muscular articulation. Secundibrachials with only muscular articulations. Columnals cylindrical or lenticular to barrel shaped, with radiating marginal crenulae that may be arranged in groups corresponding to the number of the radials. [The family Tetracrinidae was proposed by NICOSIA (1991) for *Tetracrinus* and the 2 Liassic genera *Shroshaecrinus* KLIKUSHIN and *Quenstedticrinus* KLIKUSHIN, and he assigned the family to the suborder Eudesicrinina MANNI & NICOSIA (1990b). Herein, *Quenstedticrinus* is considered to belong in a separate family of Cyrtocrinina (Quenstedticrinidae KLIKUSHIN), and *Shroshaecrinus* is considered to belong to Millericrinida.] *Lower Jurassic (Sinemurian)–Lower Cretaceous* (Valanginian).

- Tetracrinus MÜNSTER, 1839, p. 88 [*Eugeniacrinites moniliformis MÜNSTER in GOLDFUSS, 1829 in 1826-1844, p. 165; M]. Cup low, compact, with 3 to 6, commonly 4, radials, separated by a constriction and suture from compact basal element, which may be discoidal, lenticular, barrel shaped, or low subconical, resembling a columnal. Radial cavity moderate, continued in shallow central depression in basal element, generally less than half diameter of cup. Radial articular facet large and broad, occupying entire distal edge of cup and meeting along interradial sutures. Primibrachials 1 and 2 fused. Columnal articular facets with few crenulae or ridges, commonly in 4 groups. Middle Jurassic (?Aalenian), Upper Jurassic (Oxfordian)-Lower Cretaceous (Valanginian): Czech Republic, France, Germany, Poland, Switzerland.-FIG. 96,1a-h. *T. moniliformis (MÜNSTER), Oxfordian; a-b, top columnal with basal and radial circlets, a, lateral, b, distal, Germany, ×4 (Jaekel, 1892); c, proximal view of basal circlet, Switzerland, NMB M10775, ×8; d, distal view of basal circlet, Switzerland, NMB M10774, ×8; e, aboral view of radial, Switzerland, NMB M10743, ×8; f, adoral view of fused primibrachials 1 and 2, Switzerland, NMB M10740, ×8; g, distal view of secundibrachial with pinnule socket, Switzerland, NMB M10742, ×10; h, fused pinnule, Switzerland, NMB M10753, ×8 (Hess, 1975).
- Arzocrinus HESS, 2006, p. 44 [*A. lenticularis; M]. Cup composed of 4 or 5 radials. Radials with smooth, exposed surface, concave in side view; proximal facet small, triangular, symplectial; radial cavity narrow. Arms unknown. Column composed of nodals without cirri and internodals alternating in diameter and height. Columnals circular, lenticular, or cushionlike; proximal columnals weakly pentagonal. One columnal facet concave, the other convex; facets restricted to half or two-thirds of total diameter except in very low, proximal columnals. Lumen narrow, areola smooth; crenulae strong, straight or somewhat irregular, restricted to peripheral ring. [Arzocrinus was tentatively assigned by HESS (2006) to Tetracrinidae because the profile and the facets of the columnals resemble those of Tetracrinus moniliformis.] Lower Jurassic (Pliensbachian): Switzerland. FIG. 96,2a-c. *A. lenticularis; pluricolumnal of 2, a, lateral, b, distal, c, proximal, holotype, NMB M10132, ×5 (Hess, 2006).
- Bilecicrinus MANNI & NICOSIA, 1990a, p. 367 [*B. anatolicus; M]. Cup moderately high, generally oblique, with 4 or 5 unequal radials, in case of 4 radials, the largest mostly with 2 facets, no interradial projections. Radial cavity small, extending to at most half the radial height. Cup attached to wedge-shaped aboral or basal element or top columnal. Synostosis between primibrachials 1 and 2. Secundibrachials with only muscular articulations; large pinnule sockets at right angle to distal facet. Columnals barrel shaped to cylindrical; facets symplectial with uniform, marginal crenulae. Surface of all types of ossicles covered with uniform granules. [Bilecicrinus anatolicus was characterized by MANNI and NICOSIA (1990a) as the only known crinoid with 4 radials, one of which with 2 radial facets, presumably the result of 2 fused radials. Cups of the Turkish species typically have one radial with 2 facets, but NICOSIA (1991, p. 414) also mentioned a cup composed of 4 radials with only one facet each. Bilecicrinus was assigned by NICOSIA (1991) to Eudesicrinidae BATHER (emended by MANNI & NICOSIA, 1990b), a family of essentially stalkless forms with the cup attached to the substrate by an expanded base (so-called dorsal element). No columnals with a granular surface that could be assigned to Bilecicrinus anatolicus were recorded by MANNI and NICOSIA (1990a) and NICOSIA (1991); however, such columnals were assigned to the closely related species B. arenosus by HESS (2006), who also described distinctive secundibrachials assumed to belong to this species.] Lower Jurassic (Sinemurian-Pliensbachian): Switzerland, -FIG. 96,3a-b. *B. anatolicus; cup, a, Turkey.lateral, b, proximal, Turkey, UR NS 6/239, ×8 (Nicosia, 1991).—FIG. 96,3c-k. B. arenosus HESS, 2006, Pliensbachian, Switzerland; c-e, radial with 2 facets, c, aboral, d, oblique aboral-distal view of facets, e, adoral, paratype, NMB M10097, ×10; f-h, primibrachial 1, f, aboral, g, adoral, h, proximal, paratype, NMB M10013, ×8; i, aboral view of primibrachial 2, syntype, NMB M10107, ×10; *j*, proximal view of primibrachial 2, syntype, NMB M10106, $\times 10$; k, oblique distal view of secundibrachial with large pinnule socket, syntype, NMB M10113, ×10 (Hess, 2006).
- Praetetracrinus JÄGER, 1995, p. 12 [*P. doreckae; OD]. Cup composed of mostly 4 relatively thin, high radials and a low basal circlet; diameter comparable to column. First and second primibrachials thin, articulated by synostosis or muscular articulation. First pinnule on secundibrachial 2, pinnulars not fused. Column probably rather high, ratio of columnal diameter to height very variable; articular facets with few crenulae commonly in 4 groups. Lower Jurassic (Toarcian)–Middle Jurassic (Aalenian): Germany, England.—FIG. 96,4a-e. *P. doreckae, Toarcian, Germany; a-b, basal circlet, a, proximal, b, distal, syntype, SMNS 62568/39, ×13; c-d, pluricolumnal, c, lateral, d, facet, holotype, SMNS 62568/1, ×13; e, adoral view of radial, syntype, SMNS 62568/42, ×13 (Jäger, 1995).

Cyrtocrinida



FIG. 96. Tetracrinidae (p. 196).



FIG. 97. Quenstedticrinidae (p. 198).

Family QUENSTEDTICRINIDAE Klikushin, 1987

[Quenstedticrinidae KLIKUSHIN, 1987a, p. 245]

Cup wide, conical, composed of 5 large, distinct radials of similar size and cryptic basal circlet within the radial circlet; deep concave facet to column. Synostosis between primibrachials 1 and 2. Column slender, cylindrical, sharply separated from cup. Columnal facets with irregular, radiating crenulae. *Lower Jurassic (Pliensbachian–Toarcian).* Quenstedticrinus KLIKUSHIN, 1987a, p. 245 [*Q. quenstedti; OD]. Characters as for family. [KLIKUSHIN (1987a, p. 245) erected the family Quenstedticrinidae for this genus, but recognized it as clearly allied with Plicatocrinus, differing primarily in the cryptic nature of the basal circlet and the pentaradial symmetry of the cup. It may perhaps be a sister group to Plicatocrinus (SIMMS, 1989a, p. 92).] Lower Jurassic (Pliensbachian-Toarcian): Eurasia.-FIG. 97a-e. *Q. quenstedti, Pliensbachian, Caucasus, Russia; a-b, cup, a, proximal, b, distal, holotype, LGI JB-2-1, $\times 2$, *c*, section through basal circlet and 2 radials, $\times 2$; d, reconstruction of proximal column and cup with primibrachials, $\times 2$; e, columnal facet, LGI JB-2-1, ×6 (Klikushin, 1987a).-FIG. 97f-i. Q. deslongchampsi (DE LORIOL, 1882 in 1882-1889); f-g, cup, f, proximal, g, distal, Toarcian, France, ×2.5 (de Loriol, 1882 in 1882–1889); h-i, radial, h, adoral, i, distal, Pliensbachian, Switzerland, NMB M10078, ×5 (Hess, 2006).

Suborder HOLOPODINA Arendt, 1974

[Holopodina Arendt, 1974, p. 150]

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

Family HOLOPODIDAE Zittel, 1879

[nom. correct. BATHER, 1899, p. 923, ex Holopidae ZITTEL, 1879 in 1876–1880, p. 346; emend., AMEZIANE & others, 1999, p. 440] [incl. Cyathidiocrinidae and Holopocrinidae ROEMER, 1855, in BRONN & ROEMER, 1851–1856, p. 226]

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



FIG. 98. Holopodidae (p. 199-201).

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

Holopus D'ORBIGNY, 1837, p. 1 [**H. rangii*; M]. Cup tubular, more or less irregular, commonly with

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



FIG. 99. Holopodidae (p. 201).

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

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

Family COTYLEDERMATIDAE Wright, 1876

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

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

- Cotylederma QUENSTEDT, 1852, p. 631 [*C. lineati QUENSTEDT, 1858, p. 161; SD QUENSTEDT, 1858, p. 161] [=Cotyloderma DE LORIOL, 1879 in 1877-1879, p. 249, nom. null.; = Cotylecrinus DE LORIOL 1882 in 1882-1889, p. 188, nom. van.]. Cup flat, bowl shaped or shield shaped to cylindrical, only slightly oblique. Lower Jurassic (Pliensbachian-Toarcian): England, France, Germany, Italy, Switzerland, Bulgaria, Turkey.-FIG. 100,1a. *C. lineati QUENSTEDT; attachment elements on ammonite, Pliensbachian, Germany, SMNS 29674, ×5 (Sieverts, 1932b).-FIG. 100, 1b-e. C. docens DESLONGCHAMPS in DESLONGCHAMPS & DESLONG-CHAMPS, 1858, Toarcian, France; b-c, radial circlet on attachment element, b, lateral, c, distal, $\times 4$; d, adoral view of primibrachial 1, \times 4; e, adoral view of primibrachial 2, ×4 (de Loriol, 1882 in 1882-1889).----FIG. 100, 1f-j. C. inaequalis HESS, 2006, Pliensbachian, Switzerland; f-g, radial, f, oblique aboral-distal, g, proximal, syntype, NMB M10041, $\times 7$; *h*-*i*, primibrachial 1, *h*, aboral, *i*, proximal, paratype, NMB M10050, ×7; j, adoral view of primibrachial 2, paratype, NMB M10052, ×7 (Hess, 2006).
- Paracotylederma MANNI & NICOSIA, 1990b, p. 88 [*P. gracile; OD]. Cup conical, composed of thin radials with narrow facets and thin basals; radial cavity deep and wide, with opening to unknown basal element. Lower Jurassic (Toarcian): Italy.——FIG. 100,2a-c. *P. gracile; reconstructed cup, a, lateral, b, proximal, c, distal, ×4 (Manni & Nicosia, 1987).



FIG. 100. Cotyledermatidae (p. 201).

Family EUDESICRINIDAE Bather, 1899

[Eudesicrinidae BATHER, 1899, p. 923, emend., HESS, herein, to exclude Cotylederma and to include Dolichocrinus] [=Cotyledermidae WRIGHT, 1876, p. 94, recte Cotyledermatidae, partim]

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

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

Cyrtocrinida



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

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

- Dinardocrinus MANNI & NICOSIA, 1990b, p. 83 [*D. tiburtinus; OD]. Cup strongly elongate, composed of radials of extremely different length, proximal end (facet to column) concave. Radial cavity narrow, rather shallow. Brachials and attachment unknown. Lower Jurassic (Pliensbachian-Toarcian): Italy, Switzerland. FIG. 101,2a-c. *D. tiburtinus, Pliensbachian, Switzerland, NMB M10029; cup with 2 occluded radials R1 and R2, a, lateral, R1-R4, individual radials; b, facet to column, ×5, c, oblique distal, ×7.5 (Hess, 2006).
- Dolichocrinus DE LORIOL, 1891, p. 130 [*Eugeniacrinus aberrans DE LORIOL, 1882 in 1882-1889, p. 148; M] [= Tetanocrinus JAEKEL, 1891, p. 628, obj.]. Cup elongate columnlike, composed of mostly high radials that may preserve joint facets toward a basal circlet; radials rarely low and connected to high basals leading to twisted sutures. Radial articular facets large, outward sloping, of equal size. Radial cavity narrow, prolonged into columnlike part of radial and basal circlets. Brachials and attachment unknown. [RASMUSSEN (1978, p. 926) considered Dolichocrinus a nomen dubium of uncertain order and family. It was transferred from Cyrtocrinida to Millericrinida by JAEKEL (1907, p. 291), where indication of a basal circlet was found. A topotype specimen from the Bathonian, La Clapouze, Ardèche, France (Fig. 101,3c), has one low radial connected to a high basal by synostosis, whereas the other radials are high. Therefore, the columnlike cup may be composed of fused radials and basals. Elongate cups also occur in other cyrtocrinids such as Dinardocrinus and Hemicrinus.] Middle Jurassic (Bathonian)-Upper Jurassic (Tithonian): Crimea, France, ?Poland, Portugal.—FIG. 101,3a-c. *D. aberrans (DE LORIOL); a-b, cup, a, lateral, b, proximal, Portugal, ×5 (de Loriol, 1891); c, cup with occluded radial, Bathonian, France, topotype, NMB M10584, ×7 (Hess, new).
- Proeudesicrinus AMÉZIANE-COMINARDI & BOURSEAU in AMÉZIANE-COMINARDI & others, 1990, p. 119 [**P. lifouensis*; M]. Cup compact, with deep radial cavity, lower portion a fused cylinder (perhaps basals, or basals plus uppermost columnal); radials

wide and high, with lateral sutures visible but no clear basal sutures. Four narrow and one wider radial articular facet. Lower facet of cup with lateral crenulae for attachment to unknown columnal or basal element. Brachials unknown. *Holocene:* New Caledonia at 960 m.—FIG. 101,4*a*-*c*. **P. lifouensis; a,* oblique distal view of cup, holotype, MNHN EcPs39, ×7; b, facet of cup to column, syntype, MNHN EcPs39, ×15; *c,* distal view of cup, syntype, MNHN EcPs39, ×15 (Améziane-Cominardi & others, 1990).

Family HEMIBRACHIOCRINIDAE Arendt, 1968

[Hemibrachiocrinidae ARENDT, 1968, p. 156]

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

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



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

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

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

Family PSEUDOSACCOCOMIDAE Patrulius, 1956

[Pseudosaccocomidae PATRULIUS, 1956, p. 187]

Cup bowl shaped, composed of 5 thickwalled, rugose radials; cup cryptodicyclic

with 5 basals that may be irregularly developed or fused into centrale; rarely, tiny infrabasals are present, but these are mostly fused into small centrale. Radial cavity wide, radials with wide articular facets. Cup fused with massive basal element of variable shape and size, surface sculpture of cup only visible after separation from basal element. [Cup and base (Hüllkörper of BACH-MAYER, 1958; ballast ossicle of SEILACHER & MACCLINTOCK, 2005) invariably are embedded in a hard calcareous matrix. They may be separated to show the distinctive rugose surface, but the lower side of the base is never exposed. BACHMAYER (1958, p. 43) proposed the subfamily Pseudosaccocominae of the family Saccocomidae for Pseudosaccocoma, and this was followed by RASMUSSEN (1961, p. 392; 1978, p. 926) with PATRULIUS (1956) as the author of the subfamily. KÄSTLE (1982) rejected a relationship of Pseudosaccocoma with Saccocoma and, thus, assignment to the Roveacrinida; and he considered the form to be related to Isocrinus. Based on the dendritic surface of the cup impressed onto the base, SEILACHER and MACCLINTOCK (2005, p. 235) discussed a possible homology of the base to a comatulid centrodorsal, but they also considered a sessile form such as Cotylederma as a stepping-stone stage to a secondary, soft-bottom dweller, with the expanded proximal columnal anchoring the animal. The irregular base, fused with the cup, and the wide radial cavity suggest placement in Holopodina.] *Upper Jurassic* (*Tithonian*)–Lower Cretaceous (Aptian).

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

ROVEACRINIDA Hans Hess

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Order ROVEACRINIDA Sieverts-Doreck, 1953

Family ROVEACRINIDAE Peck, 1943 [Roveacrinidae Peck, 1943, p. 461; emend., RASMUSSEN, 1961, p. 360]

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

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

Cup with double body cavity in most forms, composed of radials that have overgrown, small, discrete basals, forming an upper (oral) cavity above the basals and a secondary, mostly closed, and globose lower (aboral) cavity below the basals. Cup sculptured by spines, ridges, wings, and flanges; similar sculpturing on brachials. [RASMUSSEN (1978, p. 921) subdivided the Roveacrinidae into the subfamilies Roveacrininae PECK, 1943, and Somphocrininae PECK, 1978. Following SIMMS and others (1993), they are treated, herein, as separate families. SCHNEIDER (1989, 1995) suggested that development of the lower, aboral cavity during growth increased the capacity of gases and lower density fluids and, thus, compensated for the increased weight of the animal. He speculated that gas and/or fluid exchange between the 2 cavities may have enabled vertical movement without muscle activity; see also JAGT (2005).] Lower Cretaceous (Hauterivian)-Lower Paleogene (Danian).

Roveacrinus DOUGLAS, 1908, p. 358 [*R. alatus; OD] [=Drepanocrinus JAEKEL, 1918, p. 72 (type, D. sessilis, OD)]. Cup with small semicircular arm facets and 5 undivided radial ridges extending from proximal portion of arm facets to aboral apex and sometimes beyond as an aboral spine; distal part of radial ridges may also bear spines, wings, or flanges. Basals absent in some species or distinct in others, and some species with additional circlet of tiny ossicles (cryptodicyclic cup); if present, basal circlet in radial cavity connected to the upper rim of the proximal part of the cup and separating the 2 cavities (see Fig. 5,6). [As discussed by SCHNEIDER (1987, 1989), development of basals is highly variable in Roveacrinus; cups are cryptodicyclic, monocyclic, or lack basals altogether.] Lower Cretaceous (Hauterivian)-Lower Paleogene (Danian): Spain, Algeria, Angola, Brazil, Hauterivian, Albian; Tunisia, Albian-Cenomanian; Germany, USA (Texas), Morocco, Turkey, Cenomanian; England, Cenomanian-Coniacian; Turkey, Syria, Cenomanian-Turonian; Crimea, Spain, Africa, Brazil, Turonian; Poland, Danian.-FIG. 103, 1a-b. *R. alatus; cup, a, lateral, b, distal, Coniacian, England, holotype, BMNH E45704,



FIG. 103. Roveacrinidae (p. 207-211).

×15 (Rasmussen, 1961).——FIG. 103, *Ic. R. communis* DOUGLAS; cup, Cenomanian, Germany, IPB (specimen missing), ×15 (Sieverts-Doreck, 1933b, as *Drepanocrinus sessilis* JAEKEL, 1918).— FIG. 103, *Id. R. occultus* SCHNEIDER, 1987; adoral view of radial cavity with 2 circlets of platelets, Cenomanian, Germany, holotype, Schneider Coll. Düsseldorf, ×50 (Schneider, 1987).

- Birgenelocrinus JAGT, 1999a, p. 148 [*B. degraafi; M]. Cup high, conical, strongly sculptured. Radials large, elongate with prominent interradial extensions and well-developed, nearly flat and almost vertical articular facets. Basals small, compact, forming aboral end and enclosing an aboral cavity. Secundibrachials with keeled aboral surfaces, deep ambulacral grooves, and paired, prominent flanges near both ends. Upper Cretaceous (Maastrichtian): Netherlands.——FIG. 103,2a-d. *B. degraafi; a, lateral view of cup, paratype, NHMM MB 506-15j, ×30; b, aboral view of cup, paratype, NHMM JJ 9543a, ×30; c, distal view of cup, paratype, NHMM MB 506-15h, ×30; d, lateral view of brachial, NHMM MB 506-15c, ×35 (Jagt, 1999a).
- Discocrinus PECK, 1943, p. 474 [*D. catastomus; OD]. Cup low, without prominent wings or spines, large facets for arms located on outer sides of radials and almost parallel to aboral-adoral axis. [According to RASMUSSEN (1961, p. 387; 1978, p. 922), growth of radials below basals was incomplete, leading to the aboral cavity being open at the base. However, Discocrinus integer HESS (in HESS & GALE, 2010) from the Albian of England has an intact cup closed at the base, indicating that an open lower cavity is due to breakage or preservation, rather than to incomplete growth.] Lower Cretaceous (Albian)-Upper Cretaceous (Cenomanian): USA (Texas), England, Albian; England, Cenomanian.-—Fig. 104,1a-b. *D. catastomus, Albian, Texas; a, cup, paratype, UM E-13-5; b, distal view of cup, holotype, UM E-13-4, ×20 (Peck, 1943).
- Hyalocrinus DESTOMBES, 1985, p. 10 [*H. bulliensis; M]. Radials and brachials consisting largely of vitreous, transparent expansions, those on brachials in form of lateral wings. Lower Cretaceous (Albian): France.—__FIG. 103,3a-c. *H. bulliensis; a, aboral view of radial, holotype, MHNH; b, aboral view of primibrachial 1, paratype, MHNH; c, adoral view of primibrachial 2, paratype, MHNH, ×20 (Destombes, 1985).
- Orthogonocrinus PECK, 1943, p. 464 [*O. apertus; OD]. Cup more or less conical with undivided vertical radial ridges. Facets for arms well developed, occupying most of distal surface and parts of sides of radials, making almost right angle turn at transverse ridge. Arms unknown. Lower Cretaceous (Albian)–Upper Cretaceous (Coniacian): USA (Texas), Albian–Cenomanian; Czech Republic, Turonian; England, France, Germany, Cenomanian– Coniacian.——FIG. 103,4a–c. *O. apertus, Albian, Texas; a, cup, paratype, UM E-21-4, ×20; b–c, cup, b, aboral, c, radial articular facet, holotype, UM E-21-5, ×20 (Peck, 1943).

- Platelicrinus DESTOMBES & BRETON, 2001, p. 38 [**P. campaniensis*; M]. Cup with 5 unequal interradial processes, one considerably larger than the others. *Upper Cretaceous (Campanian):* France.——FIG. 103,5*a*–*c.* **P. campaniensis*; cup, *a*, lateral, *b*, aboral, *c*, distal, holotype, MHNH 9019, ×15 (Destombes & Breton, 2001).
- Plotocrinus PECK, 1943, p. 469 [*P. hemisphericus; OD]. Cup hemispherical with large arm facets; radial sculpturing consisting of either simple vertical ridges or simple ridges flanked along their distal half by additional ridges. Spines, wings, or horizontal flanges not developed. Lower Cretaceous (Albian): USA (Texas).——FIG. 104,2a-d. *P. hemisphericus; a-b, cup, a, lateral, b, distal, holotype, UM E-10-2; c, adoral view of primibrachial 1, UM E-10-5; d, aboral view of primibrachial 1, UM HTL 35, ×15 (Peck, 1943).
- Poecilocrinus PECK, 1943, p. 471 [*P. dispandus; OD]. Cup with a prominent horizontal wing on each radial, sometimes fused around the cup, or each radial with curved, bowl-shaped wing with the opening of the concavity outward or downward. Radial ridge from wing to aboral apex. Radial articular facet outward sloping and connected with the wings by short lateral ridges. Interradial processes rather short and stout. Lower Cretaceous (Albian)–Upper Cretaceous (Cenomanian): USA (Texas).-FIG. 104, 3a-d. *P. dispandus, Albian; a, lateral view of cup, holotype, UM E-19-5; b, distal view of cup, paratype, UM E-19-4, ×15 (Peck, 1943); c, aboral-distal view of primibrachial 1, USNM 220404, ×20; d, reconstruction, ×4 (Scott & others, 1977).
- Roveacrinoides RASMUSSEN, 1971, p. 287 [**R. nudus*; OD]. Similar to *Roveacrinus* but with small aboral cavity containing enclosed basal circlet, leaving only small opening to adoral cavity; adoral part of cup bowl shaped, similar to *Saccocoma*, without pronounced radial wings. [Genus established by RASMUSSEN (1971) based on basal circlet not being overgrown by radials and thus forming the aboral cavity. As demonstrated by SCHNEIDER (1987, p. 201), the basals are within the aboral cavity, which is formed by the radials.] *Upper Cretaceous* (*Turonian*): England, Germany.——FIG. 104,4*a*–*b*. **R. nudus*, England, cup; *a*, oblique aboral, *b*, distal, holotype, CAMSM B.97380, ×20 (Rasmussen, 1971).
- Styracocrinus PECK, 1955, p. 1022 [*Drepanocrinus peracutus PECK, 1943, p. 463; OD]. Cup small, elongate conical; radial articular facet triangular or semicircular in shape, sloping outward and downward at an angle from horizontal, slightly greater outside traverse ridge than inside; aboral ligament fossa steeply inclined, high, and very narrow. Axillary primibrachial 2 high and slender with narrow median ridge and thin lateral flanges. Lower Cretaceous (Albian)–Upper Cretaceous (Cenomanian): USA (Texas), Poland, Albian–Cenomanian; England, Cenomanian.—FIG. 103,6a-c. *S. peracutus (PECK); a, cup, Albian, Texas, holotype, UM E-23-3, ×20; b, distal view of cup, Albian,



FIG. 104. Roveacrinidae (p. 209-211).

Texas, UM E-22-4, ×20 (Peck, 1943); *c*, cup with brachials, Cenomanian, England, BMNH E45862, ×15 (Rasmussen, 1961).

Veugelersia JAGT, 1999a, p. 150 [*V. diana; M]. Cup broadly conical. Radials with prominent interradial flanges united into stellate base, and high, distally rounded and perforate interradial extensions; articular facets oblique with distal, flangelike continuation; bottom of body cavity formed by stellate basal ring. Upper Cretaceous (Campanian-Maastrichtian): Netherlands, -FIG. 104,5a-d. *V. diana, Maastrich-France.tian, Netherlands; a, lateral view of cup, holotype, NHMM MB 517-1a; b, aboral view of cup, paratype, NHMM MB 517-1b; c, aboral view of upper part of cup with basal ring, paratype, NHMM MB 865-17a; d, distal view of cup, paratype, NHMM MB 865-17b, ×30 (Jagt, 1999a).

Family AXICRINIDAE Hess, new family

[Axicrinidae Hess, herein] [type genus, *Axicrinus* Kristan-Tollmann, 1977, p. 195]

Cup smooth, with high, contiguous basals. Radials and primibrachials compact, without flanges or spines. Muscle fossae of radials, second primibrachial and secundibrachials large, prolonged in high processes. Arms with side branches or pinnules. [The sloping cryptosynarthries between primibrachials 1 and 2 and secundibrachials 1 and 2 as well as the nature of the muscle fossae indicate that this form belongs to the Roveacrinida, but the presence of well-developed basals is unique in this order. In addition, the ossicles are rather compact. KRISTAN-TOLLMANN (1977) thought that Axicrinus probably represented a new family but did not name it.] Upper Triassic (Carnian).

Axicrinus KRISTAN-TOLLMANN, 1977, p. 195 [*A. alexandri; M]. Characters as for family. Upper Triassic (Carnian): Italy.——FIG. 105a-e. *A. alexandri; a, oblique aboral-distal view of radial, holotype, Kr-To V 79; b, oblique adoral-proximal view of radial, Kr-To collection; c, aboral view of primibrachial 1, Kr-To collection; d, aboral view of primibrachial 2, Kr-To collection, ×15; e, lateral view of 2 secundibrachials with socket for pinnule or side branch, Kr-To collection, ×20 (Kristan-Tollmann, 1977).

Family SACCOCOMIDAE d'Orbigny, 1852

[Saccocomidae D'ORBIGNY, 1852 in 1850-1852, p. 137]

Cup bowl shaped, composed of radials that may be thick walled in early forms. Basals small or vestigial; minute central piece



FIG. 105. Axicrinidae (p. 211).

may be present but mostly fused with basals. Upper Jurassic–Upper Cretaceous.

Subfamily SACCOCOMINAE d'Orbigny, 1852

[nom. transl. BACHMAYER, 1958, p. 43, ex Saccocomidae D'ORBIGNY, 1852 in 1850–1852, p. 137]

Cup open on adoral side, composed of spherical radials that may be thick walled in early forms; minute central piece may be present. Arms well developed. Radials and brachials in advanced forms with lightened skeleton, flanges, and wings; some forms with spines on the cup. *Middle Jurassic* (*Callovian*)–Lower Cretaceous (Albian).

Saccocoma AGASSIZ, 1836, p. 193 [**Comatula tenella* GOLDFUSS, 1831 in 1826–1844, p. 204, pl. 62,*1;*



Saccocoma

FIG. 106. Saccocomidae (p. 211-213).

SD HESS, 1999c, p. 218; = Comatula pectinata GOLDFUSS, 1831 in 1826-1844, p. 205; = Comatula filiformis GOLDFUSS, 1831 in 1826-1844, p. 205] [=Saccosoma D'ORBIGNY, 1850 in 1850-1852, p. 381, error pro Saccocoma AGASSIZ, 1836; = Eothrix LOMBARD, 1945, p. 163 (type, E. alpina, partim, OD); =Lombardia BRONNIMANN, 1955, p. 44, (type, L. arachnoidea, OD)]. Cup a hemisphere or open bowl with deep radial cavity, very thin walled, surface covered with network of anastomosing ribs that reinforce area beneath articular facets where antlerlike processes may be present. Knob of fused basals and centrale mostly indistinct. Radial articular facet with small aboral part and elongate muscle fossae articulating with V-shaped muscle fossae on first primibrachial. Primibrachial 1 with low exposed aboral side, no lateral wings. Axillary primibrachial 2 and some of the secundibrachials with dishlike lateral wings, the more distal brachials with paired vertical adoral processes in the type species. Arms may branch distally. [JAEKEL, 1918, p. 92, assigned Comatula filiformis GOLDFUSS,

1831 in 1826-1844, to Saccocoma AGASSIZ, and he proposed Saccoma JAEKEL, a new genus, for Comatula tenella GOLDFUSS, 1831 in 1826-1844. Eothrix alpina was described by LOMBARD, 1945, from thin sections, thought to belong to algae. BRONNIMANN (1955) described similar thin sections from the Tithonian of Cuba and renamed the remains Lombardia, establishing three species (L. arachnoidea, L. perplexa, and L. angulata). VERNIORY (1954, 1956) recognized that the fossils in the thin sections are brachials of Saccocoma, and BRONNIMANN's three species corresponded to sections made under different angles.] Middle Jurassic (Callovian)-Lower Cretaceous (Albian): Austria, Germany, France, Italy, Poland, western Atlantic Ocean sediments, Cuba, Japan, Callovian-Tithonian; Germany, Albian.-FIG. 106. *S. tenella (GOLDFUSS); cup and proximal arms, Tithonian, Germany, lectotype, IPB Goldfuss 423, ×10 (Hess, 2002).—FIG. 107a-e. *S. tenella (GOLDFUSS); a, middle part of arm with adoral processes; b, distal part of arm with three side



FIG. 107. Saccocomidae (p. 211-213).

branches, Tithonian, Germany, ×15 (Jaekel, 1892); *c*, facet of brachial with adoral processes, Tithonian, Germany, ×20 (Jaekel, 1892); *d*, aboral projection, ×1.6 (Hess, 1999c, adapted from Jaekel, 1918); *e*, reconstruction in life position, sculpturing omitted; *R*, radial, *IBr*, primibrachial, *IIBr*, secundibrachial, ×10 (Hess & Etter, 2011, adapted from Brodacki, 2006).——FIG. 107*f–g. S. longipinna* HESS, 2002, Kimmeridgian–Tithonian, France; *f*, aboral view of upper part of radial with articular socket, MHNG 73691; *g*, adoral view of proximal brachial, holotype, MHNG 73690, ×20 (Hess, 2002). Crassicoma SIEVERTS DORECK & HESS in HESS, 2002, p. 11 [*C. schattenbergi; OD]. Cup low, composed of thick-walled to thinner radials with interradial processes and basals that may be fused with a centrale. Radial cavity shallow. Aboral apex sunken or with protruding knob. Radials articulated to each other by flat synostoses; aboral surface of radials coarsely reticulate or pitted to finely rugose, without median ribs; lower edge truncated. Muscle fossae of radials strongly developed, attached to daggerlike interradial processes, in some forms encroaching from base of processes on inner wall of the radial. Primibrachial 1 high and flat with narrow profile, winglike lateral processes apparently forming a protective wall around adoral side of cup, proximal facet with ligamentary part forming an angle of 60 to 80 degrees with the commonly scalloped muscle fossae situated on inner side, distal facet a flat cryptosynarthry visible on approximately half the outer surface and nearly parallel (angle approximately 20 degrees) to the inner side. Brachials mostly dumbbell shaped. Pinnules or ramules present but few. Upper Jurassic (Oxfordian-Kimmeridgian): Germany, western Atlantic Ocean sediments.-FIG. 108, 1a-f. *C. schattenbergi, Kimmeridgian, Germany; a, proximal view of cup, holotype, SMNS 64734, $\times 8$; b, aboral-distal view of radial, paratype, SMNS 64726, ×11; c, aboral view of primibrachial 1, SMNS 64728, ×15; d, adoral view of primibrachial 1, SMNS 64715, ×15; e-f, radial, primibrachial 1, and primibrachial 2 combined, R, radial, IBr1, first primibrachial, IBr2, second (axillary) primibrachial, e, aboral, f, lateral, paratypes, SMNS 64697-64699, ×2.3 (Hess, 2002).

Subfamily APPLINOCRININAE Hess, new subfamily

[Applinocrininae HESS, herein] [type genus, *Applinocrinus* PECK, 1973, p. 95]

Cup highly variable in profile and sculpturing. Basals small, may be elongated aborally. Radials lacking articular facet for attachment of arms. Radial cavity covered by oral plates nearly radial in position and meeting at center of adoral side with clockwise twist. [PECK (1973) found no articular facets for the attachment of arms on cups of Applinocrinus cretaceus but detected 2 small openings to the oral cavity on the aboral surface of the covering plates (PECK 1973, pl. 1,1–2). DONOVAN, MILSOM, and VELTKAMP (1996) thought it unlikely that Applinocrinus was armless, although they could not identify a distinct articular facet on the cups. A second species, Applinocrinus texanus PECK, 1973, with a high-domed oral cover and an elongate basal circlet open at the proximal end, was considered by JAGT (1999a) to represent an extreme morphology, with material from the lower Maastrichtian of Rügen linking the 2 species. Among several hundreds of cups in JAGT's (1999a) material, only a few had the oral covering plates preserved, suggesting that these plates were only weakly articulated to the margin of the radials. FERRÉ (written communication, 2005) collected brachial

plates similar to those of *Saccocoma* in strata with cups of *Applinocrinus cretaceus*.] *Upper Cretaceous (Campanian–Maastrichtian)*.

Applinocrinus PECK, 1973, p. 95 [*Saccocoma cretacea BATHER, 1924, p. 113; OD]. Characters as for subfamily. Upper Cretaceous (Campanian-Maastrichtian): USA, Mexico, Jamaica, England, Belgium, Germany, Netherlands, Sweden, India.——FIG. 108,2a-e. *A. cretaceus (BATHER), Campanian; a-b, cup with cover plates, a, lateral, b, distal, England, holotype, BMNH E24767, ×10 (Rasmussen, 1961); c, oblique distal view of cup, USNM 179144, ×30 (Peck, 1973); d, distal view of cup without cover plates, USNM 179141, ×40; e, lateral view of cup with aboral and distal projections, USNM 179140, ×40 (Peck, 1973, as A. texanus PECK).

Family SOMPHOCRINIDAE Peck in Rasmussen, 1978

[nom. transl. HESS, herein, ex Somphocrininae PECK in RASMUSSEN, 1978, p. 923]

Cup composed of 5 radials resting aborally on a hollow central piece, probably representing fused basals, commonly prolonged into a spinelike projection (so-called dorsal spine; has also been called the centrodorsal); only one radial cavity. [SIMMS (1990a) considered the status of many of the somphocrinid taxa described from Upper Triassic strata as uncertain; specimens were commonly isolated by treatment of limestones with acid, leading to corrosion.] *Middle Triassic (Ladinian)–Upper Triassic (Carnian).*

Somphocrinus PECK, 1948, p. 82 [*S. mexicanus; OD] [=Vasculicrinus DONOFRIO & MOSTLER, 1975, p. 18 (type, V. inflatus, OD)]. Upper part of aboral projection embayed, articulated to radial circlet along central rim. Radials thin, in contact with each other. Primibrachials wide, adoral processes of axillary primibrachial 2 high and serrated. First secundibrachials low. [Vasculicrinus differs from Somphocrinus by its inflated aboral projection, and it was considered by SIMMS (1990a) to be probably congeneric with Somphocrinus.] Upper Triassic (Carnian): Mexico, Austria, Italy, Timor.-FIG. 109, 1a-i. *S. mexicanus; a, aboral projection, centrodorsal, Mexico, holotype, USNM 104235 (Peck, 1948, pl. 20-15); b, aboral view of radial, Mexico, paratype, USNM 104237e (Peck, 1948, pl. 20-34); c, adoral view of radial, Mexico, paratype, USNM 104237f (Peck, 1948, pl. 20-35); d, aboral view of primibrachial 1, Mexico, paratype, USNM 104237c (Peck, 1948, pl. 20-32); e, adoral view of primibrachial 1, Mexico, paratype, USNM 104237b, ×10 (Peck, 1948, pl. 20-31); f, facet of



FIG. 108. Saccocomidae (p. 213-214).

centrodorsal to radial circlet, Austria, Kr-To collection, ×35 (Kristan-Tollmann, 1977); g, aboral view of radial, Austria, Kr-To collection, ×20 (Kristan-Tollmann & Tollmann, 1983); h, aboral view of primibrachial 2, Austria, Kr-To collection, ×35; i, lateral view of secundibrachial, Austria, Kr-To collection, ×35 (Kristan-Tollmann, 1977).

- Ossicrinus KRISTAN-TOLLMANN, 1970, p. 788 [*O. reticulatus; OD]. Radials joined to aboral projection along notched ring. Radial articular facet lacking adoral ridge and groove; muscle fossae small and on distal end of radials. Brachials unknown. *Middle Triassic (Ladinian):* Italy, southern Alps.——FIG. 109,2*a*–*b.* *O. reticulatus; cup with aboral projection, tip broken, *a*, lateral, *b*, distal, Italy, holotype, Kr-To collection, ×40 (Kristan-Tollmann, 1970).
- Osteocrinus KRISTAN-TOLLMANN, 1970, p. 784 [**Rhabdotites rectus* FRIZZELL & EXLINE, 1956, p. 66; OD] [=*Poculicrinus* MOSTLER, 1972, p. 720 (type,

P. glaber, OD)]. Aboral projection of variable length, articulated to radial circlet along broad ring. Radials compact; articular facets strongly bent at transverse ridge, with large aboral ligament fossa directed outward and muscle fossae encroaching adorally (on inner side). Interarticular ligament fossae and muscle fossae divided centrally by narrow ridge sloping toward interior of cup and carrying a fairly deep furrow. Brachials elongate and thin, with swollen ends; terminal brachials (so-called palmalia) palmate. [According to KRISTAN-TOLLMANN (1977), Poculicrinus may be a junior synonym of either Osteocrinus or Ossicrinus.] Middle Triassic (Ladinian)-Upper Triassic (Carnian): Austria, Italy, Romania, Turkey, Afghanistan, China, Nepal, Timor.—FIG. 109, 3a-f. *O. rectus (FRIZZELL & EXLINE); a, reconstruction of cup with aboral projection, Ladinian, ×20 (Kristan-Tollmann, 1977); b, adoral view of primibrachial



FIG. 109. Somphocrinidae (p. 214-216).

1, partly broken, Ladinian, Italy, Kr-To collection, \times 40; *c*–*d*, primibrachial 2, broken proximally, *c*, lateral, *d*, adoral, Ladinian, Italy, Kr-To collection, \times 50; *e*, adoral view of secundibrachial, Ladinian, Italy, Kr-To collection, \times 50 (KristanTollmann, 1970); *f*, terminal brachial (so-called palmal), Anisian, China, ×60 (Kristan-Tollmann & Tollmann, 1983).—FIG. 109,*3g. O. rimosus* KRISTAN-TOLLMANN; reconstruction of cup with centrodorsal, ×20 (Kristan-Tollmann, 1977).

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Order UNCERTAIN Family CYCLOCRINIDAE Sieverts-Doreck, 1953

[Cyclocrinidae SIEVERTS-DORECK in UBAGHS, 1953, p. 764]

Crown unknown. Pluricolumnals exceptional. Columnals cylindrical, mostly large and low, latera may be weakly convex; presence of axillary columnals or columnals with additional facets indicate branching, lateral sockets for small side branch also occur. Lumen very narrow. Facets with numerous tubercles that may be uniformly distributed or arranged in groups, rarely ringlets, vermiculi, or a smooth surface. There may be a fine marginal crenulation. Small columnals may have a few, mostly paired, radial crenulae. Loose stereom near articular facets and around lumen. Attachment by disk with one to multiple concave column facets. [Cyclocrinus has been classified in the Millericrinida, family Apiocrinidae by BIESE (1935–1937), or as a separate family, Cyclocrinidae, in the Cyrtocrinida by SIEVERTS-DORECK (in UBAGHS, 1953) and HESS (1975). RADWAŃSKA and RADWAŃSKI (2003) interpreted the columnals as elements of radicles or radicular cirrals and, thus, placed the form in the order Bourgueticrinida. HESS (2008, p. 475) saw affinities with Amaltheocrinus but left assignment to the order Millericrinida open, pending discovery of cup plates.] Middle Jurassic (Bajocian)-Lower Cretaceous (Albian).

Cyclocrinus D'ORBIGNY, 1850 in 1850–1852, p. 291 [*Bourgueticrinus rugosus D'ORBIGNY, 1841 in 1840–1841, p. 96; SD DE LORIOL, 1886 in 1882– 1889, p. 2] [=Acrochordocrinus TRAUTSCHOLD, 1859, p. 112 (type, A. insignis, M)]. Characters as for family. Middle Jurassic (Bajocian)–Lower Cretaceous (Albian): France, Germany, Poland, Russia, Switzerland, Bajocian–Oxfordian; England, Albian.— FIG. 110, 1a–k. *C. rugosus (D'ORBIGNY); a, attachment disk with three column facets, Callovian, Switzerland, NMB M10482, ×3; b–c, small high columnal, b, lateral, c, facet, Callovian, Switzerland, NMB M10483, ×6 (Hess, 2008); d–f, columnal, *d*, lateral, *e*, facet, *f*, part of facet enlarged, Bajocian, France, syntype, $\times 1$; *g*–*h*, columnal with lateral socket, *g*, lateral, *h*, facet, Bajocian, France, syntype, $\times 1$; *i*–*k*, axillary columnal, *i*, *k*, lateral, *j*, 2 facets, Callovian, France, $\times 1$ (de Loriol, 1886 in 1882–1889).

Family LANTERNOCRINIDAE Kristan-Tollmann, 1990

[Lanternocrinidae KRISTAN-TOLLMANN, 1990, p. 87]

Microcrinoids with reduced arms or armless. Cup with small basals and narrow, high, keeled radials. Radial articular facet small, deeply sunken between interradial processes. First primibrachials may be tightly joined by corrugated margins. Upper Triassic (Norian-Rhaetian).

- Lanternocrinus KRISTAN-TOLLMANN, 1988b, p. 135 [*L. lanterna lanterna; OD; a holotype for the species was designated only in KRISTAN-TOLLMANN, 1990, p. 56]. Microcrinoids with cup of minute basals and triangular keeled radials with short interradial processes, arms reduced to shovel-shaped, keeled primibrachials with corrugated margins, all elements tightly fitting when closed. Total height of cup 3 to 6 mm. Column unknown but probably short and thin; attachment unknown. Upper Triassic (Norian-Rhaetian): Tethys realm (Austria, Timor).—FIG. 110,2a-d. *L. lanterna, Austria; a-b, juvenile crown of cup and primibrachials, a, lateral, b, proximal, Rhaetian, holotype, Kr-To sample R330, ×20; c, aboral view of radial, Norian, Kr-To sample R26, ×15; d, adoral view of primibrachial, Rhaetian, Kr-To sample R330, ×20 (Kristan-Tollmann, 1990).
- Nasutocrinus KRISTAN-TOLLMANN, 1990, p. 60 [*N. dentatus; OD]. Microcrinoids with reduced arms. Cup composed of basals and radials. Radial articular facet in deep notch, high interradial extensions with grooves and ridges for articulation of primibrachial 1; primibrachial 2 axillary, trapezoidal, laterally closely fitting; arms short, with only few secundibrachials. Secundibrachials thin, with wide ambulacral furrow, articulated by flat synostosis; no pinnules. Upper Triassic (Norian): Tethys realm (Turkey, Timor, Germany).----FIG. 110,3a-h. *N. dentatus; a, reconstructed cup and base of crown, ×10; b-d, radial, b, adoral, c, lateral, d, distal, Turkey, holotype, Kr-To sample V 154, ×15; e, aboral view of radial, Turkey, Kr-To collection, ×20; f, adoral view of radial, Turkey, Kr-To collection, ×20; g, proximal view of primibrachial 1, Turkey, Kr-To collection, $\times 25$; *h*, adoral view of



FIG. 110. Cyclocrinidae, Lanternocrinidae, and Leocrinidae (p. 217–219).

primibrachial 2, Timor, Kr-To sample A16, ×10 (Kristan-Tollmann, 1990).

Family LEOCRINIDAE Kristan-Tollmann, 1990

[Leocrinidae KRISTAN-TOLLMANN, 1990, p. 87]

Microcrinoids with cup of 5 basals, possibly infrabasals, and radials. Radials robust, trapezoidal, aborally curved, outer side flat, broad orally, large articular facet not visible from outside. Arms short, branched at axillary primibrachial 2; primibrachials and the 4 to 6 secundibrachials high, rectangular; brachials of the different rays united laterally symplectially (by grooves and ridges); secundibrachials articulated by synostosis, no pinnules. Column probably short and compact. Upper Triassic (Norian–Rhaetian).

Leocrinus KRISTAN-TOLLMANN, 1990, p. 64 [*L. krystyni; OD]. Characters as for family. Upper Triassic (Norian-Rhaetian): Tethys realm (Austria, Turkey, Timor).——FIG. 110,4a-h. *L. krystyni, Norian; a, reconstruction, ×4; b-d, radial, b, lateral, c, adoral, d, distal, Timor, holotype, Kr-To V 156, ×10; e-g, primibrachial 1, e, adoral, f, aboral, g, proximal, Turkey, Kr-To Su/2b, ×8; h, aboral view of primibrachial 2, Turkey, Kr-To Su/2b, ×8 (Kristan-Tollmann, 1990).—FIG. 110,4i-j. L. armatus KRISTAN-TOLLMANN; 2 columnals, i, lateral, j, upper facet, Norian, Austria, Kr-To sample S359, ×8 (Kristan-Tollmann, 1990).

Family QINGYANOCRINIDAE Stiller, 2000

[Qingyanocrinidae STILLER, 2000, p. 34]

Crown unknown. Column long, cylindrical, with numerous cirri; nodals of all parts of column with 1 to 5 circular cirrus sockets; larger cirrus sockets crenulated around lumen. Nodals very numerous, commonly several successive cirrinodals. Columnal articular facets symplectial with radial crenulae; bifurcation of culmina and insertion of additional culmina possible. Lumen circular or lobed; mostly with perilumen, sometimes with areola. Distal holdfast rootlike (radix). *Middle Triassic* (Anisian). 10,20–25, which is *Bangtoupocrinus kokeni* STILLER, 2000, p. 42)]. Characters as for family. *Middle Triassic (Anisian)*: China (Qingyan, Guizhou Province).——FIG. 111,1*a–f.* *Q. *kueichounensis* (DUBA-TOLOVA & SHAO); *a–b*, distal pluricirrinodal, *a*, lateral, *b*, facet, NIGPAS B3B-1.Cr2.F37-1; *c–d*, nodal from mesistele, *c*, lateral, *d*, facet, NIGPAS B3B-1.Cr2.F43-3; *e*, pluricirrinodal, NIGPAS B3B-1.Cr2.Fbt-6; *f*, dististele, NIGPAS B3B-1. Cr2.Fbt-21, ×3 (Stiller, 2000).

Family TULIPACRINIDAE Kristan-Tollmann, 1980

[Tulipacrinidae KRISTAN-TOLLMANN, 1980, p. 224]

Microcrinoids with compact, biconical cup composed of 5 fused radials and thin ring of fused basals; distally narrowing to blunt cone with narrowing axial canal, no radial cavity. Radial articular facet concave, divided by strong fulcral ridge into somewhat larger proximal part with broad and deep ligament fossa and distal part with single elliptical to triangular muscle fossa. Facet to column synostosial and deeply concave with relatively wide axial canal. Arms reduced to 5 single, high, triangular brachials with adorally encroaching muscle fossa; lateral synostoses indicate formation of a pyramid-like roof over the cup. [Cup shape of this form is unique among articulate crinoids, with its distally narrowing part leaving no room for a radial cavity proper. KRISTAN-TOLLMANN (1980, 1990) assigned low internodals and high nodals with large cirrus sockets to this form; if paired, they are barrel shaped. Such a column with alternating nodals and noncirriferous internodals would support assignment to the Isocrinida (SIMMS, 1990a, p. 73), a classification that is considered doubtful. No articulate order is known where the cup narrows distally with a narrow axial canal in place of a radial cavity, and a single triangular muscle fossa is also quite unique among articulates. The family Tulipacrinidae was proposed for this form by Kristan-Tollmann (1980, p. 224), who in 1990 established a second species, Tulipacrinus latus, from the same lower Carnian Cassian Beds. However, T. latus may be conspecific with T. tulipa. KLIKUSHIN (1992, p. 64) proposed an order for Tulipacrinus,

Qingyanocrinus STILLER, 2000, p. 34 [*Cyclocyclicus kueichounensis DUBATOLOVA & SHAO, 1959, p. 47; M; =Entrochus rotiformis KOKEN, 1900, p. 188, 212–214, pl. 10,16–19, partim (non pl.



FIG. 111. Qingyanocrinidae and Tulipacrinidae (p. 219-220).

Tulipacrinida, with the following diagnosis (*fide* MIRONOV, personal communication, 2002): "Dwarfish forms with short column composed of cirri-bearing nodals alternating with internodals; cup composed of fused radials and basals; brachial series transformed into long plates with muscular articulations." The small size is suggestive of a paedomorphic form, and establishment of a separate order does not seem justified without further knowledge.] *Upper Triassic (Carnian–Norian).*

Tulipacrinus KRISTAN-TOLLMANN, 1980, p. 225 [*T. tulipa; M]. Characters as for family. Upper Triassic (Carnian–Norian): Italy, Austria.——FIG. 111,2a-h. *T. tulipa, Carnian, Italy, holotype, Kr-To x 21; *a*, distal view of cup; *b*, proximal view of cup, \times 20; *c*, lateral view of juvenile cup, \times 40; *d*–*e*, brachial, *d*, aboral, *e*, adoral, \times 15; *f*, lateral view of nodal; *g*, proximal facet of nodal; *h*, facet of internodal, \times 20 (Kristan-Tollmann, 1980).

Order and Family UNCERTAIN

Bihaticrinus KRISTAN-TOLLMANN, 1990, p. 85 [*B. manipulus; M]. Microcrinoids with column composed of very long, thin columnals. Columnals round, dumbbell shaped, articular facets elliptical to circular-elongate with strong radial crenulae. Nodals with 5 very small, circular cirrus sockets. [The circular cirrus sockets and multiradiate articular facets exclude assignment to the holocrinids or isocrinids, and assignment to any taxonomic group is not possible without additional material.] Upper Triassic (Norian): Austria, Timor.— FIG. 112, 1a-b. *B. manipulus; nodal, a, lateral, b,



FIG. 112. Uncertain and nomina dubia (p. 220-223).

facet, Timor, holotype, Kr-To sample V 161, ×25 (Kristan-Tollmann, 1980).

- Cratecrinus MIRONOV, herein, p. 225, nom. nov. pro Craterocrinus MIRONOV & SOROKINA, 1998b, p. 63, non GOLDRING, 1923, p. 185 (type, C. ruedemanni GOLDRING, 1923, p. 186) [*Craterocrinus geminatus MIRONOV & SOROKINA, 1998b, p. 63; OD]. Columnals circular, nontuberculate with concave articular facet or with concave areola and flat crenularium. Crenulae 24 to 36, not grouped or with tendency to grouping into crenular units; crenulae long, straight, simple or bifurcated. [The genus was proposed for columnals collected from bottom sediments of seamounts of unknown age and for 2 Lower Cretaceous forms. Its assignment to Hyocrinida is doubtful.] Lower Cretaceous-Paleogene (Danian), ?Holocene.
 - C. (Cratecrinus). Characters as for genus, with concave articular facet. Areola absent. Crenulae

24 to 26, reaching lumen, simple or bifurcated. Fossil component of sediment from seamount in the northern Atlantic. Subgenus also contains *Cratecrinus (C.) crimicus* (MIRONOV & SOROKINA), 1998b, p. 64, *Lower Cretaceous:* Crimea.——FIG. 112,2. **C. (C.) geminatus* (MIRONOV & SOROKINA); part of columnal facet, subfossil, northern Atlantic, holotype, ZMM C-22, ×5 (Mironov & Sorokina, 1998b).

C. (Excavocrinus) MIRONOV & SOROKINA, 1998b, p. 65 [*E. actinodromus; M]. Characters as for genus, with concave areola and flat crenularium. Crenulae 28 to 36, undivided. C. (Excavocrinus) actinodromus, fossil component of sediment from seamount, northern Atlantic. Subgenus also contains C. (E.) ilimanangei (RASMUSSEN), 1972a, p. 28 (as Calamocrinus). Paleogene (Danian): Greenland.—Fig. 112,3a. **C. (E.) actinodromus*; part of columnal facet, subfossil, northern Atlantic, holotype, ZMM C-23, ×10 (Mironov & Sorokina, 1998b).— FIG. 112,*3b. C. (E.) ilimanangei* (RASMUSSEN); pluricolumnal, Danian, Greenland, MGUH 12757, ×8 (Rasmussen, 1972a).

Taurocrinus KLIKUSHIN, 1984, p. 81 [* T. tauricus; M]. A genus possibly related to Hyocrinida with flat columnal articular facets. Basal circlet low, fused, with gradual transition to upper part of column. Columnals as much as 5.7 mm in diameter, elliptical or subcircular; sides nontuberculate or 5 or 6 tubercles in small columnals. Lumen circular, proximally wide, distally narrow. Numerous (17 to 22) crenulae with tendency for grouping into crenular units. Crenulae thick, curved or straight, simple or bifurcated, extending from margin almost to lumen. Some crenulae with narrow, longitudinal fissure. Column with attachment disk. Lower Cretaceous (Albian): Crimea.-FIG. 112,4. *T. tauricus; facet of columnal, syntype, LGI KK-42-4, ×10 (Klikushin, 1984).

NOMINA DUBIA

- Acariaeocrinus BIESE, 1935 in 1935–1937, p. 109, nom. nov. pro Microcrinus TERQUEM & PIETTE, 1865, p. 122, 158, non EMMONS, 1858, p. 311 [*Microcrinus liasinus TERQUEM & PIETTE, 1865, p. 122, 158; M]. Genus and only species based on 2 specimens of an extremely small crinoid attached to shell of a Pecten with a 3 mm high, cylindrical column consisting of 40 to 50 columnals unequal in height. Crown 2 mm high, with 5 atomous arms. Lower Jurassic (Sinemurian): France.— FIG. 112,5. *A. liasinus (TERQUEM & PIETTE); 2 specimens on shell of Pecten, ×9 (Terquem & Piette, 1865).
- Carpenterocrinus A. H. CLARK, 1908c, p. 319 [*Pentacrinus mollis CARPENTER, 1884a, p. 338; M]. Dubious genus, based on a very irregular and small single crown with a few columnals attached, probably a strongly regenerated specimen of Endoxocrinus alternicirrus. The specimen was collected by the Challenger off southern Japan, where many specimens of Endoxocrinus alternicirrus are known (OII, 1989, p. 32).
- Flabellocrinites KLIPSTEIN, 1845 in 1843–1845, p. 277 [*F. cassianus; M]. [Based on a badly preserved pluricolumnal of an encrinid, nomen dubium according to HAGDORN, 2004a, p. 247.] Middle Triassic (Ladinian): Italy.—FIG. 112,6. *F. cassianus; columnal facet, ×1 (Klipstein, 1845 in 1843–1845).
- **Polycerus** FISCHER VON WALDHEIM, 1811, p. 28. Proposed to replace name *Pentacrinites* for Isocrinida, including *Polycerus stoloniferus* FISCHER (a synonym of *Pentacrinus basaltiformis*, according to BRONN, 1848 in 1848–1849) and the living so-called palmier marin (*=Isis asteria*, type of *Cenocrinus*).

Tauriniocrinus ROVERETO, 1939, p. 616 [*Pentacrinus gastaldi MICHELOTTI, 1847, p. 59; OD]. Genus of Isocrinidae, insufficiently characterized. Crown unknown. Column pentalobate or rounded subpentagonal, rarely circular in section. Columnals commonly alternating in height, proximal columnals with radial pores in the suture. Length of internodes unknown, but as many as 14 internodals or more. Articular facet of columnals similar to Isocrinus, crenulae not very long, generally leaving a smooth, radial, marginal area. Nodals higher than internodals, with 5 rather large, elliptical cirrus sockets occupying entire height of nodal and facing outward. Very rarely less than 5 sockets. Paleogene (Oligocene)-Neogene (Miocene): Austria, Czech Republic, France, Italy.

Subclass UNCERTAIN

Archaeoisocrinus WEBSTER & JELL, 1999, p. 334 [*A. occiduaustralis; M]. Cup cryptodicyclic; supposed infrabasals and basals in deep basal cavity, covered by proximal columnals. Radials forming base and cup wall; no anal or anal notch in cup. Radial articular facet wide, gap between radial and primibrachial 1 indicates well-developed aboral ligament fossa. Arms 10, primibrachial 2 axillary. Brachials cuneate uniserial, with small, dual, internal, entoneural canals. Brachial articulations alternating between oblique muscular and cryptosyzygial. First pinnule on secundibrachial 1. Proximal column pentalobate with thin columnals. More distal parts of column and articulation facets unknown. [This form is known only from one small, insufficiently preserved specimen. It was assigned by WEBSTER and JELL (1999) to the Isocrinidae, thus extending the range of the isocrinids back approximately 30 myr. According to these authors, Archaeoisocrinus differs from all other isocrinids in that the basals lie within the basal cavity and are not visible in aboral or lateral views. However, basals and infrabasals are not readily visible in the type specimen, the column is unknown, and brachials facets are not displayed, so the presence of cryptosyzygial and syzygial articulations cannot be ascertained. The first Articulata after the end-Permian extinction event were the holocrinids, and these have distinct infrabasals, very high basals, and a column of cirrinodals and internodals. In the isocrinids, which evolved from holocrinids, basals are distinct, although they are much lower than the radials. Thus, Archaeoisocrinus cannot be assigned to either holocrinids or isocrinids. Some characters invite comparison with encrinids. Very flat cups with low radials and hidden basals and infrabasals are characteristic of adult encrinids or subadult specimens that were partly compressed (HAGDORN & SCHULZ, 1996). Pentalobate, isocrinid-like proximal columns are known from encrinids such as Chelocrinus (HAGDORN, 1982), a form with uniserial arms in early ontogeny. Paired or unpaired axial canals occur in the same taxa of small Triassic crinoids (HAGDORN, personal communication, 2004). Pending further discoveries, the systematic position of *Archaeoisocrinus* remains doubtful.] *Lower Permian (Artinskian):* western Australia.——FIG. 112,7. **A. occiduaustralis*, aboral view of crown, holotype, QMF 38879, ×3 (Webster & Jell, 1999).

NOMINA NUDA

- Lotocrinus KRISTAN-TOLLMANN in TOLLMANN, 1976, p. 280, fig. 165 [*L. reticulatus; M]. Cup perhaps belonging to cyrtocrinids. [This genus was figured without description and designation of type.] Upper Triassic (upper Norian-Rhaetian): Austria.——FIG. 112,8a-b. *L. reticulatus, Rhaetian; a, aboral view of radial; b, proximal view of basal circlet with infrabasal, ×40 (Tollmann, 1976).
- Picteticrinus Étallon, 1857, p. 282 [*P. parasiticus; M]. A nomen nudum, non Picteticrinus DE LORIOL in DE LORIOL & PELLAT, 1875, p. 298, which is a junior homonym.
- Waikaripites EAGLE, 2005, p. 35 [*W. tekumi; M]. Two articular facets for arms on each radial. [Genus and species based on single radials, holotype not designated in the only figured radial. Figures and description are insufficient for proper recognition.] Paleogene (Paleocene): New Zealand.——FIG. 112,9. *W. tekumi; oblique view of radial, enlarged (Eagle, 2005).

REJECTED NAMES

- Alecto LEACH, 1815, p. 61 [*A. horrida; SD A. H. CLARK, 1908d, p. 449]. According to CLARK (1908d), genus name, previously used for several extant and fossil comatulids, was based on A. horrida, which he considered unidentifiable. This view was accepted by RASMUSSEN (1978, p. 927). Name was subsequently introduced as a junior homonym by LAMOUROUX, 1821, for a bryozoan.
- Asteriatites VON SCHLOTHEIM, 1813, p. 68, 99, 109. Name unavailable (Code, 1999, Art. 20), introduced by VON SCHLOTHEIM in the combination A. pennatus (=Pterocoma pennata), A. filiformis (=Saccocoma filiformis), A. rosaceus (=Saccocoma filiformis), A. eremita (nom. nud., =Asteriacites ophiurus von SCHLOTHEIM, 1820, p. 325, an indeterminable ophiuroid), A. spinosus (nom. nud.), A. pentagonatus (nom. nud.), and probably as a misprint Osteratites siderolites (pro MONTFORT, 1808, p. 150, =Siderolites calcitrapoides). LOEBLICH and TAPPAN (1964, in Treatise, Part C, p. 796) incorrectly claimed Asteriacites ophiurus VON SCHLOTHEIM, 1820, to be the type species by subsequent monotypy. SPENCER and WRIGHT (1966 in Treatise, Part U, p. 103) considered Asteriatites (=Asteriacites) to be a dubious synonym of Saccocoma.
- Astropodium LHWYD, 1699, p. 19 [=*Astropoda* DE BLAINVILLE, 1830, p. 239, *nom. null.*]. Pre-Linnean

name used by LHWYD for various crinoid columnals, also recorded in BERTRAND, 1763 (publication rejected by ICZN, 1999, for nomenclatorial purposes), in WALCH, 1769 in 1768–1773, and in URE, 1793, but not as a proper genus name. DEFRANCE (1819, p. 467–468), adopted this name from German authors (presumably WALCH, 1769 in 1768–1773, p. 72) and used it in the combination "astropode elegante" or "astropodium elegans" for a species of Apiocrinites. He was considered by RASMUSSEN (1978, p. 927) to have established a new species, A. elegans, in combination with a genus name not available (ICZN, 1999, Art. 17).

- Leiocrinus D'ORBIGNY, 1850 in 1850–1852, p. 180, non SPRINGER, 1902, p. 95 [*Eugeniacrinites essensis F. A. ROEMER, 1840 in 1840–1841, p. 26; M]. Based on strongly corroded, cylindrical columnals, commonly with radiating marginal crenulae or a marginal furrow. According to RASMUSSEN (1961, p. 155), genus indeterminable, although probably belongs to the Millericrinida or Cyrtocrinida. Found in Cenomanian conglomerate, but may well be of Jurassic origin from Germany.
- Symphytocrinus. Name unavailable, attached by KOENIG to 4 figured but undescribed species in his unpublished second part of *leanes Fossilium Sectiles* (KOENIG, 1825, p. 195). Quoted by AGASSIZ, 1836, as a synonym of *Apiocrinus* and of *Eugeniacrinus*. DE LORIOL (1878 in 1877–1879, p. 62) identified S. caryophyllum as a copy of VON SCHLOTHEIM's (1820) figure of *Eugeniacrinites cariophilites*, and BATHER (1900) recorded the name as a synonym of *Eugeniacrinus*.

NAMES NOT BASED ON CRINOIDS

- Gasterometra GISLÉN, 1925a, p. 1, 30 [*G. polycirra; M]. Originally referred to Palaeantedonidae but demonstrated by NIELSEN (1943, p. 61) to be dorsal plate of asteroid Stauranderaster.
- Nodolanx KRISTAN-TOLLMANN in TOLLMANN, 1976, p. 145, fig. 65 [*N. multinodosa; M] [Nomen nudum, figured without description and designation of type]. According to BIZZARINI (1993, p. 160), a central and a radial shield from the dorsal side of an asteroid. In a later paper, BIZZARINI (2001, p. 189) assigned the remains to the Ophiuroidea and established a second species, N. gambillarai. Upper Triassic (Carnian): Austria, Italy.
- **Pogocrinus** GAGNEBIN, 1930, p. 219 [**P. raafensis*; M]. Unidentified fossil from Middle Triassic of Switzerland, interpreted as arms of a crinoid. Rejected by RASMUSSEN (1978, p. 927) from echinoderms.
- Rhabdocrinus. Misprint by Etheridge, 1882, p. 179, for the echinoid *Rhabdocidaris*.
- Trigonocrinus BATHER, 1889a, p. 161 [* T. liratus; M]. A fossil described as the cup of a crinoid referred to Eugeniacrinitidae from the Upper Jurassic (Oxfordian) of Germany. Interpreted by RASMUSSEN (1978, p. 927) as the tube of a serpulid.

NOMENCLATORIAL NOTE

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ANTHOMETRINA, NEW NAME FOR THE GENUS ANTHOMETRA A. H. CLARK, 1915 (CRINOIDEA, COMATULIDINA), PREOCCUPIED BY ANTHOMETRA BOISDUVAL, 1840 (ARTHROPODA, LEPIDOPTERA)

During preparation of the manuscript for volume 3 of the revised crinoid *Treatise on Invertebrate Paleontology.* it was realized that the comatulid crinoid genus *Anthometra* A. H. CLARK, 1915, p. 135, is preoccupied by a lepidopteran genus published by BOISDUVAL, 1840, p. 231 (see p. 135 herein). According to Article 60 of ICZN rules (1999), we here propose the name *Anthometrina* as replacement name for *Anthometra* A. H. Clark, 1915. The type species for *Anthometrina* is *Antedon adriani* Bell, 1908, p. 4.

ACKNOWLEDGMENTS

We would like to thank Jill Hardesty for her advice on this matter.

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NOMENCLATORIAL NOTE

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CRATECRINUS, NEW NAME FOR THE GENUS *CRATEROCRINUS* MIRONOV & SOROKINA, 1998 (CRINOIDEA, ORDER UNCERTAIN), PREOCCUPIED BY *CRATEROCRINUS* GOLDRING, 1923 (CRINOIDEA, MONOBATHRIDA)

During preparation of the manuscript for volume 3 of the revised crinoid *Treatise on Invertebrate Paleontology*, it was realized that the articulate crinoid genus *Craterocrinus* MIRONOV & SOROKINA (1998, p. 63) is preoccupied by a crinoid genus published by GOLDRING, 1923, p. 185 (see p. 221 herein). According to Article 60 of ICZN rules (1999), the name *Cratecrinus* as replacement name for *Craterocrinus* GOLDRING, 1923, is here proposed (A. MIRONOV, personal communication, 2002). The type species for *Cratecrinus* is *Craterocrinus geminatus* MIRONOV & SOROKINA, 1998, p. 63.

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I would like to thank Jill Hardesty for her advice on this matter.

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