

N690

FIG. E152. Cooperellidae (1); Glauconomidae (2); Rzehakiidae (3) (p. N690).

valve with two thin cardinals, 1 and bifid 3b; left valve with three cardinals, 2b bifid; ligament depressed, seated on laminar nymph; pallial sinus wide. *Mio.-Rec.*

Cooperella CARPENTER, 1864, p. 639 [*Oedalia (C.) scintillaeformis, p. 639 (=*O. subdiaphana, p. 639); M (synonymy of generic and specific names established by first reviser, DALL, 1900] [=Oedalia CARPENTER, 1864 (non Oedalea MEIGEN, 1820); Oedalina CARPENTER, 1865 (pro Oedalia)]. Mio.-Rec.

- C. (Cooperella). Hinge with 2b deeply divided; pallial sinus deep, its apex rounded. Mio.-Rec., E.N.Am.-W.N.Am.-S.Am.—FIG. E152,1. *C. (C.) subdiaphana (CARPENTER), Rec., USA (Calif.); 1a, RV int., ×1.3; 1b,c, LV and RV hinges, ×2 (515; Arnold, 1903).
- C. (Cooperellopsis) WOODRING, 1925 [*C. (C.) thaumasta; OD]. More quadrate and inflated than C. (Cooperella); 2b not deeply bifid; pallial sinus obscure (695). Mio., Carib.

Family GLAUCONOMIDAE Gray, 1853

[=Glauconomyidae CHENU, 1862; Glaucomyidae, Glauconomeidae (spelling errors)]

Elongate shells, smooth, with conspicuous periostracum; hinge with three cardinal teeth in either valve, lateral teeth wanting. *Rec.*

Glauconome GRAY, 1828 [*G. chinensis; M] [=Glauconomya BRONN, 1838 (obj.); Glaucomya WOODWARD, 1854 (nom. van.); Glauconoma CHENU, 1862 (nom. null.); Glauconometta IRE-DALE, 1936 (type, G. plankta; OD); Glauconomella ALLAN, 1950 (nom. null.)]. Periostracum light to dark green, smooth or wrinkled. [Habitat, marine to brackish water.] Rec., IndoPac.-Australia. —FIG. E152,2. *G. chinensis, E.Indies; 2a,b, LV ext., int., X1 (Habe, 1954); 2c, RV int., X1 (305).

Family RZEHAKIIDAE Korobkov, 1954 [=Onchophoridae Davidaschvilli, 1934]

Ovate, moderately small, strongly inequilateral, nearly smooth, beaks low; hinge lacking lateral teeth, with two cardinals in right valve (1 and 3b), and three in left (2a, 2b, and 4b); anterior adductor muscle scar deeply sunken, bordered by ridge posteriorly; pallial sinus shallow (716). [Apparently aberrant brackish-water descendants of marine Tapetinae.] M.Mio.-U.Mio.

Rzehakia KOROBKOV, 1954 [pro Oncophora RZEHAK, 1882 (non DIESING, 1851)] [*Oncophora socialis RZEHAK, 1882; OD]. Cardinal teeth slightly bifid. M.Mio.-U.Mio., E.Eu.—FIG. E152,3. *R. socialis (RZEHAK), Mio., CZech.; 3a-c, RV int., ext., LV int., $\times 1$ (RZehak).

Order MYOIDA Stoliczka, 1870

[nom. correct. NEWELL, 1965 (ex order Myacea Stoliczka, 1870)] [Adapedonta Auctr., in part] [Diagnosis by N. D. NEWELL]

Thin-shelled, burrowing forms with welldeveloped siphons; strongly inequilateral, equivalve or inequivalve; isomyarian or anisomyarian; one cardinal tooth in each valve, or edentulous; lunule and escutcheon absent, or poorly developed; shell not nacreous. *Carb.-Rec.*

Suborder MYINA Stoliczka, 1870

[nom. transl. et correct. Newell, 1965 (ex order Myacea STOLICZKA, 1870)] [Diagnosis by N. D. Newell]

Hinge edentulous or with one cardinal tooth on each valve; ligament external, borne on well-marked nymphs, in some forms with internal resilium; sinupalliate. *Perm.-Rec.*

Superfamily MYACEA Lamarck, 1809

[nom. transl. Gill, 1871 (ex family Myacea Goldfuss, 1820) (=myaires Lamarck, 1809)] [Materials for this superfamily prepared by MYRA KEEN] Myoida—Myina—Myacea



FIG. E153. Myidae (p. N691-N692).

Valves elongate or ovate, subequal, porcelaneous to chalky, with thin periostracum; hinge margin mostly without teeth; ligament mainly internal; valve margins smooth; pallial sinus, with some exceptions, well developed. U.Jur.-Rec.

Family MYIDAE Lamarck, 1809

[nom. correct. BRODERIP, 1839 (pro family Myacea Goldfuss, 1820) (=myaires Lamarck, 1809)] [=Myacidae d'Orbiony, 1845]

Elongate, chalky, mostly burrowing forms with wide posterior gape; chondrophore present in LV. *Paleoc.-Rec.*

Mya Linné, 1758 [*M. truncata; SD Children, 1822 (ICZN Op. 94, Dir. 72)] [=Hiatula Modeer, 1793; SD Winckworth, 1935 (obj.); Myarius DUMÉRIL, 1806 (nom. van.); Myes, AUCTT. (nom. van.)]. Of medium size, chondrophore in LV large; sculpture of concentric growth lines. Oligo.-Rec., Eu.-N.Am.-Japan.

N691

- M. (Mya). Chondrophore with triangular anterior portion in front of anterior ridge. *Oligo.-Rec.*, Eu.-N.Am.-Japan.—Fig. E153,10. *M. (M.) *truncata* LINNÉ, Rec., Eng.; 10a-c, LV ext., LV and RV hinges, ×1 (Jeffreys).
- M. (Arenomya) WINCKWORTH, 1930 [*M. arenaria LINNÉ, 1758; OD]. Chondrophore bounded anteriorly by ridge; posterior end of shell elongateovate. Mio.-Rec., Eu.-N.Am.-Japan.——FIG. E153, 9. *M. (A.) arenaria LINNÉ, Rec., N.Atl.; 9a-c, LV ext., int., RV hinge, $\times 0.5$ (H. Adams & A. Adams).
- Cryptomya CONRAD, 1848 [*Sphaenia californica CONRAD, 1837; M]. Hinge as in Mya, shell narrowly gaping, somewhat compressed; chondro-

phore in RV appressed under beaks; shell thin and nearly smooth. *Mio.-Rec.*, N.Am.-S.Am.-Asia-Pac.

- C. (Cryptomya). Chondrophore smooth in front; pallial line entire. *Mio.-Rec.*, W.N.Am.-S.Am.-E. Asia.——FIG. E153,4. *C. (C.) californica (CON-RAD), Rec., USA(Calif.); 4a,b, RV ext., LV int., $\times 0.7$ (after Olsson, 1961).
- C. (Venatomya) IREDALE, 1930 [*Sphaenia elliptica A. ADAMS, 1851; OD]. Hinge with small 2a in front of chondrophore; pallial sinus of varying size. Rec., Pac.—FIG. E153,2. *C. (V.) elliptica (A. ADAMS), Australia; 2a-c, RV ext., RV int., LV int., ×1 (Hedley, 1913).
- Paramya CONRAD, 1861 [pro Myalina CONRAD, 1845 (non de KONINCK, 1842)] [*Myalina subovata CONRAD, 1845; M]. Small, smooth, quadrate, with chondrophore in either valve. Mio.-Rec., SE.N.Am. —FIG. E153,3. *P. subovata (CONRAD), Mio., USA(Va.); 3a,b, RV ext., LV int., ×5 (Glenn, 1904).
- Platyodon CONRAD, 1837 [*Mya (P.) cancellata; M] [=Cryptodonta CARPENTER, 1864 (obj.) (in synonymy)]. Resembling Mya but with chondrophore smaller and with concentric sculpture formed by raised growth striae; pallial sinus large and deep. Mio.-Rec., Afr.-N.Am.-S.Am.
- P. (Platyodon). Shell 30 mm. or more in length. Mio.-Rec., W.Afr.-W.N.Am.—Fig. E153,6. *P. (P.) cancellatus (CONRAD), Rec., USA(Calif.); 6a,b, LV int. (oblique), ext., $\times 0.5$ (Grant & Gale).
- P. (Austroplatyodon) OLSSON, 1961 [*P. (A.) australis; OD]. Shell less than 6 mm. in length. Rec., W.S.Am.—-Fig. E153,7. *P. (A.) australis, Ecuador; LV int., $\times 5$ (688).
- Sphenia TURTON, 1822 [*S. binghami; SD GRAY, 1847] [=Sphaena, Sphaenia, spelling errors; Tyleria H. ADAMS & A. ADAMS, 1854 (type, T. fragilis; M)]. Small to minute, shell quadrate but apt to be distorted by nestling habit; pallial sinus small to large. Paleoc.-Rec., Eu.-N.Am.-E.Asia.— Fto. E153,1. *S. binghami, Rec.; Eng; 1a, LV and RV hinge; ×1 (Woodward); 1b,c, RV and LV hinges, ×4, ×6 (Lamy).
- Tugonia Récluz, 1846 [*Mya anatina GMELIN, 1791 (ex "Le Tugon" Adanson, 1757); SD GRAY, 1847] [=Tagonia, spelling error]. Globose, gaping posteriorly; posterior area set off by constriction; chondrophores subequal; pallial sinus shallow. Eoc.-Rec., Eu.-N.Am.-IndoPac.-Asia-Australia.
- T. (Tugonia). Sculpture reticulate; shell of moderate size. Oligo.-Rec., Eu.-IndoPac.—Fig. E153,8. *T. (T.) anatina (GMELIN), Rec., W. Afr.; 8a-c, LV int., ext., RV hinge, $\times 1$ (H. Adams & A. Adams).
- T. (Antiguamya) EFFINGER, 1938 [*Saxicava arnoldi DICKERSON, 1917; OD]. Umbonal grooves marked, posterior area sharply set off, larger than in T. (Tugonia). Eoc.-L.Oligo., W.N.Am.— FIG. E153,5. *T. (A.) arnoldi (DICKERSON), Oligo., USA(Ore.); LV int., ×1.5 (Effinger).

- T. (Distugonia) IREDALE, 1936 [*D. inopinata; OD]. Sculpture weak, of concentric growth lines; posterior area small, attenuated. Rec., Australia-E.Asia.
- T. (Tugonella) JOUSSEAUME, 1891 [*Tugonia divaricata REEVE, 1863; M]. Inflated, small, sculpture faint; chondrophore in RV smaller than in T. (Tugonia); pallial sinus small. Rec., Indo-Pac.
- T. (Tugoniopsis) DALL, 1898 [*T. (T.) compacta; OD]. Small to minute, short, chondrophore in front of dentiform projection; posterior adductor scar large and deep; pallial sinus moderate. Mio., SE.N.Am.—Fig. E153,11. *T. (T.) compacta, USA(Fla.); LV int., X3 (Dall, 1898).

Family CORBULIDAE Lamarck, 1818

[nom. correct. BRODERIP, 1839 (ex Corbulidées LAMARCK, 1818, vernac.)] [=Corbularia GRAY, 1823; Corbuladae FLEMING, 1828]

Small to moderate-sized sturdy shells, normally with resilifer in one valve; valves inequilateral, LV tending to be smaller than RV; pallial sinus small to wanting. U.Jur.-Rec.

Subfamily CORBULINAE Gray, 1823

[nom. transl. STOLICZKA, 1870 (ex family Corbularia GRAY, 1823)]

LV only slightly smaller than RV, mostly with projecting chondrophore; posterior end somewhat rostrate. *U.Jur.-Rec*.

- Corbula BRUGUIÈRE, 1797 [*C. sulcata LAMARCK, 1801; SD SCHMIDT, 1818] [=Aloidis MEGERLE VON MÜHLFELD, 1811 (obj.)]. Moderately inflated, smooth to concentrically ribbed. Cret.- Rec., Afr.-Eu.-Asia-IndoPac.-C.Am.-N.Am.-S.Am.
- C. (Corbula). Solid, strongly ribbed, rostrate, LV without projecting chondrophore but with posterior cardinal tooth and ligamental pit, RV with posterior lateral. *Rec.*, W.Afr.—Fig. E154,5. *C. (C.) sulcata LAMARCK, Senegal; 5a, RV ext., X1; 5b, LV ext., X1; 5c,d, RV int., LV int., X1 (944).
- C. (Anisocorbula) IREDALE, 1930 [*Corbula macgillivrayi SMITH, 1885; OD]. Elongate-quadrate, with sharp umbonal keel, ventral margin sinuous; pallial sinus obsolete. *Rec.*, IndoPac.——FiG. E154,8. *C. (A.) macgillivrayi SMITH, New Guinea; 8a,b, RV int., ext., ×1 (944).
- C. (Bicorbula) FISCHER, 1887 [*C. gallica LA-MARCK, 1801; M]. Large, inequivalved, keel obsolescent; sculpture weak; pallial sinus broad and shallow. Paleoc.-Rec., Eu.-Afr.-Asia.—-FIG. E154,10. *C. (B.) gallica LAMARCK, Eoc., France; 10a-e, RV ext., int., dorsal, LV ext., int., ×1 (944).
- C. (Bothrocorbula) GABB, 1873 [*C. viminea GUPPY, 1866; M]. Moderately large, thick, sculpture of concentric waves and sparse radial threads;

ligamental pit broad in RV, one small dentiform projection and deep lunular pit in LV. *Mio.*, E.C. Am.-W.Indies.——FIG. E154,7. **C.* (*B.*) viminea GUPPY, Jamaica; 7*a-c*, LV ext., int., RV int., X1.5 (944). C. (Caryocorbula) GARDNER, 1926 [*Corbula alabamiensis LEA, 1833; OD]. Subquadrate, both valves acutely keeled posteriorly, concentrically rugose; pallial sinus short. Eoc.-Rec., N.Am.-S. Am.-E.Asia.——FIG. E154,2. *C. (C.) alabami-



FIG. E154. Corbulidae (Corbulinae) (p. N692-N694).



FIG. E155. Corbulidae (Corbulinae) (p. N694).

ensis LEA, EOC., USA(Ala.); 2a,b, LV dorsal, RV ext., $\times 1.5$ (944); 2c,d, RV int., LV int., $\times 1$ (944; Stenzel et al., 1957).

- C. (Cuneocorbula) CossMANN, 1886 [*Corbula biangulata DESHAYES, 1857; SD DALL, 1898]. Small, thin, birostrate, concentric sculpture weak, valves subequal; pallial sinus small. Eoc., Eu.-N.Am.—Fig. E154,3. *C. (C.) biangulata DESHAYES, France; 3a,b, RV ext., int., ×2.5 (944).
- C. (Cuspicorbula) OLSSON, 1928 [*Corbula busera; OD]. Solid, inflated, coarsely sculptured, posterior end contracted and set off by deep sinus. Eoc., S.Am.—FIG. E154,6. *C. (C.) busera OLSSON, Peru; RV ext., ×1.5 (944).
- **?C.** (Eoursivivas) OTA, 1964 [*C. matsumotoi HABE, 1960; OD]. Hinge lacking dorsolateral

ridge on chondrophore. Cret.(L.Neocom.), Japan. ——FIG. E155,3. *C. (E.) matsumotoi HABE, Kumamoto Pref.; 3a-d, LV ext., RV int., LV int., hinge, $\times 1.5$ (Ota, 1964).

- C. (Flexicorbula) CHAVAN, 1947 [*Varicorbula (F.) vokesi; OD]. Resembling C. (Varicorbula) but beaks prosogyrate. Cret.(Campan.), W.Asia. ——FIG. E154,1. *C. (F.) vokesi (CHAVAN), Palestine; 1a-d, RV int., LV int., both valves (LV view), RV ext., ×1.5 (105).
- C. (Hexacorbula) OLSSON, 1932 [*C. hexacyma BROWN & PILSBRY, 1913; OD]. Resembling C. (Bothrocorbula) but lacking lunular pit. Mio. Rec., E.C.Am.-W.C.Am.——FIG. E154,4. *C. (H.) hexacyma BROWN & PILSBRY, Mio., E.Panama; LV ext., ×3 (944).
- C. (Juliacorbula) OLSSON & HARBISON, 1953 [*C. cubaniana D'ORBIGNY, 1853 (=C. knoxiana C. B. ADAMS, 1852); OD]. Valves solid, similar in size and shape, rectangular, rostrum bordered by keel. Mio. - Rec., E. C. Am.-W. C. Am.-S. Am.—FIG. E154,9. *C. (J.) knoxiana ADAMS, Rec., W.Indies; 9a-c, LV ext., post., ant., ×2.5 (Dall, 1889).
- ?C. (Nipponicorbula) OTA, 1964 [*N. mifunensis; OD]. Sculpture discrepant, cancellate in RV, concentric in LV. U.Cret., Japan.—FIG. E155,1.
 *C. (N.) mifunensis (OTA), Kumamoto Pref.; 1a-d, RV ext., LV ext., RV int., LV int., ×2.5 (Ota, 1964).
- C. (Notocorbula) IREDALE, 1930 [*N. vicaria; OD]. Large, chondrophore bipartite; adductor scars large. Rec., Pac.——FIG. E156,1. *C. (N.) vicaria (IREDALE), Australia; 1a-c, RV ext., LV ext., RV int., $\times 1$ (944).
- ?C. (Pulsidis) OTA, 1964 [*P. nagatoensis; OD]. Resembling Caryocorbula but chondrophore without median ridge. L.Cret., Japan.——Fig. E155, 2. *C. (P.) nagatoensis (OTA), Yamaguchi Pref.; 2a-d, RV ext., LV ext., RV int., LV int., ×2.5 (Ota, 1964).
- C. (Serracorbula) OLSSON, 1961 [*S. tumaca; OD]. Solid, heavy, subequivalve, convex, ventral margin evenly serrate; adductor scars large. Rec., W.C.Am.-S.Am.—Fig. E156,4. *C. (S.) tumaca (OLSSON), W.Colombia; LV int., $\times 2.2$ (688).
- C. (Solidicorbula) HABE, 1949 [*C. erythrodon LAMARCK, 1818; OD]. Heavy, convex, solid; LV with knob at posterior end; chondrophore in LV and resilifer in RV divided by ridge; muscle scars deep, pallial sinus wanting. Rec., W.Pac. ——FIG. E157,1. *C. (S.) erythrodon LAMARCK, Japan; 1a-c, LV ext., RV int., LV int., ×1 (Habe, 1949).
- C. (Tenuicorbula) OLSSON, 1932 [*C. tenuis SOWERBY, 1833; OD]. Thin, subequilateral, posterior end set off by keel; sculpture strong, of concentric threads. *Mio.-Rec.*, E.C.Am.-W.C.Am.-W.S.Am.---FIG. E156,3. *C. (T.) tenuis SOWERBY, Rec., W.Colom.; 3a,b, LV ext., RV dorsal, ×1 (688).

C. (Varicorbula) GRANT & GALE, 1931 [*Tellina gibba OLIVI, 1792; OD] [=Corbula AUCTT. (non BRUGUIÈRE)]. Small, sculpture discrepant, RV with concentric ribbing, LV with faint radials and concentric growth striae; pallial sinus small or wanting. L.Eoc.-Rec., E.N.Am.-Eu.-E.Pac.-W. Pac.——FIG. E156,8. *C. (V.) gibba (OLIVI), Rec., Eng.; 8a-d, RV ext., int., LV int., both valves (LV view), $\times 2$ (944).

C. (Vokesula) STENZEL & TWINING in STENZEL,



FIG. E156. Corbulidae (Corbulinae) (p. N694-N696).

KRAUSE & TWINING, 1957 [*C. aldrichi MEYER, 1885, var. smithvillensis HARRIS, 1895; OD]. Inflated, valves discrepant, RV larger, concentrically ribbed, LV nearly smooth; pallial sinus small, nearly vertical. L.Eoc.-L.Oligo., E.N.Am.—FIG. E156,7. *C. (V.) smithvillensis HARRIS, M.Eoc., USA(Tex.); 7a-c, both valves (LV view), LV int., RV ext., ×2.5 (Stenzel & Twining, 1957).

- Anapteris VAN WINKLE [PALMER], 1919 [*A. regalis; M]. LV with winglike flare anteriorly; both valves with posterior area set off by keel. Eoc., E.N.Am.—FIG. E156,9. *A. regalis, USA (Va.); 9a,b, LV ext., LV int., $\times 3$; 9c, RV ext., $\times 2.8$ (944).
- Corbulomima VOKES, 1945 [*C. nuciformis; OD]. Without special structures in either valve for reception of resilifer, otherwise resembling C. (Corbula). U.Jur.-L.Cret.(Apt.), Eu.-W.Asia.——FIG. E156,2. *C. nuciformis, Lebanon; 2a-c, LV int., RV int., both valves (LV view), $\times 2$ (944).
- Panamicorbula PILSBRY, 1932 [*Potamomya inflata C. B. ADAMS, 1852; OD]. Thin, inflated, not rostrate posteriorly; hinge with toothlike lateral buttresses to dorsal grooves of RV. *Rec.*, C.Am.— FIG. E156,6. *P. inflata (C. B. ADAMS), W.Panama; 6a, ext. RV, X1; 6b,c, LV and RV hinges, X2 (688).
- Physoida PALLARY, 1900 [*Corbula physoides DE-SHAYES, 1845-48; OD]. Small, smooth, fragile, with low umbonal ridge. Rec., N.Afr.——FIG. E156,11. *P. physoides (DESHAYES), Algeria; 11a-c, RV ext., LV hinge, RV int., ×3 (944).
- Potamocorbula HABE, 1955 [*Corbula amurensis SCHRENCK, 1867; OD]. Hinge of RV with strongly projecting tooth in front of deep pit; LV with longitudinal keel on chondrophore; periostracum present, thick. Rec., NE.Asia.——FIG. E156,5. *P. amurensis (SCHRENCK), Korea; 5a,b, RV ext., LV int., $\times 1$ (Habe, 1955).
- Ursirivus Vokes, 1945 [nom. subst. pro Anisorhynchus Conrad in MEEK & HAYDEN, 1871 (non Schoenherr, 1842)] [*Corbula pyriformis MEEK, 1871; OD]. Large, pyriform, with deep lunule and small but definite pallial sinus. U.Cret., N.Am. —Fig. E156,10. *U. pyriformis (MEEK), USA (Wyo.); 10a-c, RV ext., int., LV int., ×1 (944).

Subfamily CAESTOCORBULINAE Vokes, 1945

Valves discrepant in shape, LV more equilateral and less rostrate than RV; accessory siphonal plate posterior to LV fitting into rostrum of RV; projecting chondrophore of hinge of LV. *Cret.-Eoc.*

Caestocorbula VINCENT, 1910 [*Corbula henckeliusiana NYST, 1836 (as C. henckeliusi, spelling error); OD] [=Ficusocorbula KOROBKOV, 1954 (type, Corbula ficus SOLANDER, 1766); OD]. L.Cret.-Eoc., Eu.-N.Am.-Asia-Afr.



FIG. E157. Corbulidae (Corbulinae) (p. N694, N696).

C. (Caestocorbula). Siphonal plate obliquely trapezoidal, with distinct median ridge; pallial sinus well developed, broad and rounded. L.Cret. (Apt.)-Eoc., E.N.Am.-Eu.-Asia.——FIG. E158,6.
*C. (C.) henckeliusiana (NYST), Eoc., Belg.; both valves (LV view), ×1 (Vincent, 1910; 944).
C. (Parmicorbula) Vokes, 1944 [*Corbula near-

C. (Parmicorbula) VOKES, 1944 [*Corbula neaeroides BLANCKENHORN, 1890; OD]. Siphonal plate small, rectangular, with faint median groove; otherwise resembling C. (Caestocorbula). U.Cret. Eoc., Eu.-Asia-E.N.Am.-Afr.—FIG. E158,3. *C. (P.) neaeroides (BLANCKENHORN), U.Cret., Lebanon; 3a-d, RV int., ext., both valves (LV views), ×1.5 (944).

Subfamily CORBULAMELLINAE Vokes, 1945

Small, valves subtrigonal lacking both posterior rostrum and umbonal ridge. Posterior adductor on raised, spoon-shaped lamella. *Cret.*

Corbulamella MEEK & HAYDEN, 1857 [*Corbula? gregaria; OD]. Umbones inflated, slightly prosogyrate; sculpture of fine concentric lines; pallial sinus shallow. Cret., N.Am.—FIG. E158,1. *C. gregaria (MEEK & HAYDEN), U.Cret., USA(S. Dak.); 1a-d, RV int., ext., both valves (LV view), ant. view, $\times 5$ (944).

Subfamily LENTIDIINAE Vokes, 1945

Small, essentially tellinid in external shape, RV lacking hinge plate; cardinal tooth on subumbonal thickening that projects from interior of valve. *Paleoc.-Rec.*

Lentidium CRISTOFORI & JAN, 1832 [genus without named species] [*L. maculatum (=*Tellina mediterranea Costa, 1829); SM] [=Corbulomya NYST, 1844 (type, Corbula complanata SowERBY, 1822; SD HERRMANNSEN, 1847)]. Shell thin, chondrophore projecting; muscle scars small and impressed, pallial sinus broad and shallow. Paleoc.-Rec., Eu.-Asia-Atl.-Medit.

L. (Lentidium). Beaks central or posterior to midline. Paleoc.-Rec., Eu.-E.Atl.-Medit.——Fig. E158,



FIG. E158. Corbulidae (Caestocorbulinae) (3,6), (Corbulamellinae) (1), (Lentidiinae) (4-5), Pachydontinae (2,7), Subfamily Uncertain (8) (p. N696-N698).

5. *L. (L.) mediterraneum (Costa), Rec., Italy; 5a,b, RV ext., int., $\times 4$ (944).

L. (Janschinella) MERKLIN, 1961 [*L. (J.) garetzkii; OD]. Anterior end short, beaks well forward of mid-line. M.Oligo-L.Mio., C.Asia-W.Eu. ——FIG. E158,4. *L. (J.) garetzkii, Oligo., USSR; 4a-c, RV ext., int., LV hinge, ×2 (Merklin).

Subfamily PACHYDONTINAE Vokes, 1945

Valves tending to be twisted and distorted, ligamental area attaching resilium to lateral rather than dorsal face of resilifer. *Oligo.-Plio.*

- Pachydon GABB, 1868 [*P. obliqua; SD VOKES, 1944] [=Anisothyris CONRAD, 1871 (obj.); Pachyodon, nom. van., MEEK, 1878 (non von MEYER, 1838)]. Sculpture of weak concentric ridges; outline cordate, umbonal ridge narrow; pallial_sinus broad, shallow. Plio., S.Am.—FIG. E158,7. *P. obliquus, Peru, 7a-e, RV int., LV int., RV ext., both valves ant., LV view, ×2 (944).
- Tiza DE GREGORIO, 1890 [*Corbula? amara (=*C. aliformis CONRAD, 1885); M]. More quadrate than Pachydon, somewhat donaciform; pallial line angular at junction with posterior adductor scar. Oligo., E.N.Am.—FIG. E158,2. *T. aliformis (CONRAD), USA(Miss.); 2a-d, RV ext., int., RV ext., LV int., $\times 1$ (944).

N697

Subfamily UNCERTAIN

?Coquandia SEGUENZA, 1882 [*C. italica; SD KEEN,



FIG. E159. Erodonidae (2); Pleurodesmatidae (4), Raetomyidae (5-6); Spheniopsidae (1,3) (p. N698-N699).

herein]. Relatively large, hinge with a Mya-like chondrophore, known only from internal molds; pallial line with a small sinus; shell not gaping. U.Cret.(Cenoman.), Eu.—Fig. E158,8. *C. italica, Italy; 8a,b, RV int. mold, both valves int. molds dorsal, $\times 0.7$ (Seguenza, 1882).

Harlea, Raleta, Tomala GRAY, 1842 (nomina nuda). Described as Corbulidae but without citation of species names. Unrecognizable from descriptions. Semicorbula CossMANN & PEYROT, 1909 [*S. nadali; OD]. Oligo.(Aquitan.), Eu. Based on single RV, indeterminate from figure.

Family ERODONIDAE Winckworth, 1932

Resembling Corbulidae but with chondrophore of LV broad, projecting, as in *Mya*. *U.Eoc.-Rec*.

Erodona Bosc (ex DAUDIN, MS), 1801 [*E. mactroides; SD DALL, 1898] [==Potamomya J. SOWER-BY, 1835 (type, Mya plana SOWERBY, 1814; SD KEEN, herein); Azara D'ORBIGNY, 1842 (obj.); Phaenomya WEAVER & PALMER, 1922 (type, P. vaderensis; OD)]. Ovate-trapezoidal in outline; umbo of LV higher than RV; inequivalve, RV larger; hinge of RV with 2 thin cardinals bordering triangular resilial pit; pallial sinus small. [Habiat mainly brackish-water.] U.Eoc.-Rec., N.Am.-C. Am.-N.Eu.-SE.S.Am.—FIG. E159,2. *E. mactroides, Rec., Arg.; 2a,b, LV int., RV int., ×0.6 (Woodward).

Family PLEURODESMATIDAE Cossmann & Peyrot, 1909

Small, porcelaneous, quadrate to trapezoidal, mostly smooth or with laminar growth striae; hinge with one cardinal tooth in either valve and long excavated cavity on posterior dorsal hinge margin for resilium; pallial line entire. U.Oligo.-Mio.

Pleurodesma Hörnes, 1859 [*P. mayeri; M]. Beaks prosogyrate; resilifer bordered by low lamina below; muscle scars and pallial line inconspicuous. U. Oligo.(Aquitan.)-Mio.(Burdigal.), Eu.—Fic. E159,4. *P. mayeri, Mio., Austria; 4a-c, LV int., RV int., LV ext., ×1; 4d, RV hinge, ×5 (after Hörnes, 1859).

Family RAETOMYIDAE Newton, 1919 [=Amotapidae Olsson, 1928]

Ovate, thin, sculptured with undulating concentric ribs, posteriorly compressed and gaping; hinge with large projecting chondrophore in LV, smaller sunken chondrophore in RV entering umbonal cavity vertically. Resembling mactrid group *Raeta* exteriorly but with myacean hinge. *Eoc.*

- Raetomya NEWTON, 1919 [*Lovellia schweinfurthi MAYER-EYMAR, 1887; OD]. Ovate-quadrate, chondrophore in LV 3-lobed. Eoc., NE.Afr.-W.C.Afr. — FIG. E159,5. *R. schweinfurthi (MAYER-EYMAR), U.Eoc., Nigeria; 5a, RV ext., ×0.5; 5b,c, LV hinge, ×1; 5d, RV hinge, ×1 (Newton, 1919).
- Amotapus OLSSON, 1928 [*Perna arbolensis Woods, 1922; OD]. Elongate-ovate, posterior end short; chondrophore in LV rounded, not conspicuously lobed. *Eoc.*, W.S.Am.——Fig. E159,6. *A. arbolensis (Woods), M.Eoc., Peru; 6a,b, LV hinge, RV ext., 0.5 (6a, Stanford specimen; 6b, Olsson).

Family SPHENIOPSIDAE Gardner, 1928

Small, ovate-triangular, RV with 2 hinge teeth, LV edentulous, with resilial socket; pallial sinus rounded. *M.Eoc.-Rec.*

- Spheniopsis SANDBERGER, 1863 [*Corbula scalaris BRAUN in WALCHNER, 1851; OD]. Trigonal, posteriorly rostrate; smooth to concentrically undulate; anterior hinge tooth in RV triangular, posterior lamellar. *M.Eoc.-Mio.*, Eu.-E.N.Am.—FIG. E159, 1. *S. scalaris (BRAUN), Oligo., Aus.; 1a-c, LV int., ext., RV int., ×5 (Sandberger).
- Grippina DALL, 1912 [*G. californica; OD]. Ovatetrigonal, finely concentrically sculptured, with radial ridges bounding lunule and escutcheon. Rec., W.N.Am.-W.C.Am.—FIG. E159,3. *G. californica, USA(Calif.); 3a-c, RV ext., int., LV int., X8 (Oldroyd, 1925, and specimen, Stanford Univ.).

Superfamily GASTROCHAENACEA Gray, 1840

[nom. trans. THIELE, 1934 (ex Gastrochaenidae GRAY, 1840)] [Materials for this superfamily prepared by MYRA KEEN]

Burrowing shells, lying free within linear cavity; hinge edentate, valves broadly gaping, porcelaneous (517). U.Jur.-Rec.

Family GASTROCHAENIDAE Gray, 1840

[nom. correct. Adams & Adams, 1856 (pro Gastrochaenadae GRAY, 1840)]

Characters of superfamily. U.Jur.-Rec.

Gastrochaena SPENGLER, 1783 [*G. cuneiformis; SD CHILDREN, 1822] [=Chaena PHILIPSSON, 1788 (ex RETZIUS, MS) (nom. van.); Rocellaria DE BLAINVILLE, 1829 (type, Gastrochaena modiolina LAMARCK, 1818, =Mya dubia PENNANT, 1777, M); Gastrochaenolites LEYMERIE, 1842 (nom. van.); Gastrochaenoecium, Gastrochaenites BRONN, 1848 (nom. van.); Cucurbitula GOULD, 1861 (type, Fistulana lagenula LAMARCK, 1801, =Gastrochaena



FIG. E160. Gastrochaenidae (p. N699-N700).

cymbium SPENGLER, 1783; M); Dufoichaena LAMY, 1925 (ex JOUSSEAUME, MS) (type, Gastrochaena dentifera DUFO, 1840; M)]. Cavity flaskshaped, in rock or shell; shell triangular to quadrate in outline. ?U.Jur., U.Cret.-Rec., N.Am.-W. Indies-Eu.-E.Indies.

- G. (Gastrochaena). Shell smooth or nearly so, oval, tube short, formed of successive increments. ?U.Jur., U.Cret.-Rec., N.Am.-Eu.-circumtrop.— FIG. E160,5. *G. (G.) cuneiformis SPENGLER, Rec., IndoPac.; 5a,b, LV ext., ventral, ×1 (Reeve).
- G. (Spengleria) TRYON, 1862 [*G. mytiloides LAMARCK, 1818; SD STOLICZKA, 1871]. Valves divided by oblique furrow, posterior area with vertical striae. Rec., E.Indies-W.Indies.——FIG. E160,4. *G. (S.) mytiloides LAMARCK, E.Indies; 4a,b, LV ext., ventral, $\times 1$ (Reeve).
- Eufistulana EAMES, 1951 [*Gastrochaena mumia SPENGLER, 1783; OD] [=Fistulana BRUGUIÈRE,

1789 (non MÜLLER, 1776); SD FLEMING, 1818]. Elongate valves enclosed in adventitious tubular structure; widely gaping. *Eoc.-Rec.*, Eu.-N.Afr.-IndoPac.——FIG. E160,1. *E. mumia (SPENGLER), Rec., E.Indies; both valves, LV view, $\times 0.5$ (Fischer).

- Gastrochaenopsis CHAVAN, 1952 [*Gastrochaena unicostata DESLONGCHAMPS, 1838; OD]. Posterior cardinal margin patulous, accentuated by 2 dorsal carinae. U.Jur., Eu.—FIG. E160,2. *G. unicostata (DESLONGCHAMPS), France; RV ext., ×1 (Chavan).
- Kummelia STEPHENSON, 1937 [*Gastrochaena americana GABB, 1860; OD]. Shell resembling Gastrochaena but ventral margin broadly rounded, not truncate; tube cylindrical, not tapering, annular, rough, somewhat sinuous. Eoc., E.N.Am. —FIG. E160,3. *K. americana (GABB), USA (N.J.); 3a,b, tube, RV ext., ×0.5 (Stephenson).

Superfamily HIATELLACEA Gray, 1824

[nom. transl. NEWELL, 1965 (er Hiatellidae GRAY, 1824] [Materials for this superfamily prepared by MYRA KEEN except as otherwise recorded]

Quadrate to trapezoidal, valves slightly to widely gaping; habit nestling or burrowing; hinge with one or two weak teeth, ligament on nymph; pallial sinus mostly well developed (516). Perm.-Rec.

Family HIATELLIDAE Gray, 1824

[nom. correct. WINCKWORTH, 1932 (pro Hyatelladae GRAY, 1824)] [=Saxicavidae Swannson, 1835; Glycimeridae Deshayes, 1839 (nom. correct. PETIT DE LA SAUSSAYE, 1869, pro Glycimeridées)]

Characters of superfamily. Perm.-Rec.

Hiatella Bosc (ex DAUDIN, MS), 1801 [*H. monoperta (=Mya arctica LINNÉ, 1767); SD WINCK-WORTH, 1932] [=Saxicava Fleuriau de Belle-VUE, 1802 (obj.), Laxicava CONRAD, 1855 (nom. null.); Haicana SACCO, 1901 (nom. null.); Clotho FAUJAS DE SAINT FOND, 1808 (nom. dub.); Didonta SCHUMACHER, 1817 (obj.) (type, Solen minutus LINNÉ, 1767, =Mya arctica; M); Byssonia de Blain-VILLE, 1817 (ex CUVIER, vernac.) (type, Mytilus pholadis LINNÉ, 1771), Bissomya, Bissomyia, Byssomia, Byssomya, spelling errors; Biapholius LA-MARCK (ex LEACH, MS), 1818 (in synonymy of Mytilus rugosus Linné, 1767); Biapholus, Biopholeus LEACH, 1847 (nom. null.); Pholeobia LEACH, 1819 (type, Mytilus rugosus Linné, 1767; M); Agina TURTON, 1822 (obj.; M); Rhomboides DE BLAINVILLE, 1824 (non GOLDFUSS, 1820); Coramya BROWN, 1844 (obj., in synonymy); Spongyophylla BRUSINA (ex NARDO, MS), 1866 (obj.; M). Small, trapezoidal, with thin periostracum; hinge teeth best developed in juvenile stages. U.Jur.-Rec., Asia-Eu.-N.Am.

- H. (Hiatella). Outline rendered irregular by nestling habit, in general with posterior end wider than anterior, gape small. Oligo.-Rec., E.Asia-N. Am.-Eu.——FIG. E161,1. *H. (H.) arctica (LINNÉ), Rec., France, 1a-d, LV ext., int., RV int., ext., ×1 (89a).
- H. (Pseudosaxicava) CHAVAN, 1952 [*P. bernardi; OD]. Hinge teeth weak, muscle scars elliptical. U.Jur., Eu.——Fig. E161,2. *H. (P.) bernardi (CHAVAN), France; 2a-c, RV ext., int., LV int., ×2 (Chavan).
- Capistrocardia TATE, 1887 [*C. fragilis; OD]. Rounded quadrate to elliptical, with internal radial ridge; not gaping; hinge with 2 teeth in LV, none in RV; pallial sinus small or wanting. Tert., Australia.—Fig. E161,3. *C. fragilis; 3a,b, LV ext., int., $\times 2$ (Tate).
- Cyrtodaria REUSS, 1801 (ex DAUDIN, VERNAC.) [*Mya siliqua SPENGLER, 1793; SD VOKES & COX, 1961] [=Cyrtodera DE BLAINVILLE, 1825 (nom. null.); Glycimeris LAMARCK, 1801 (non LAMARCK, 1799)]. Elongate, with thick, dark periostracum; hinge with 2 teeth, nearly central; pallial sinus small, irregular. Paleoc.-Rec., Eu.-Arctic.—Fig. E161,10. *C. siliqua (SPENGLER), Rec., N.Atl.; 10a,b, RV int. with LV hinge, RV ext., ×1 (H. Adams & A. Adams).
- Panopea MENARD, 1807 (ICZN, pend.) [*P. faujasi (=Mya glycimeris BORN, 1778); SD FLEMING, 1818] [=Glycimeris LAMARCK, 1799 (non DA COSTA, 1778); Panope MENARD, 1807 (nom. null.); Panodea OKEN, 1817 (nom. null.); Panopaea LAMARCK, 1818 (nom. null.); Myopsis AGASSIZ, 1840 (type, Mya mandibula J. SOWERBY, 1813; SD Cox, 1964); Heteromya MAYER, 1884 (type, P. (H.) lessepsi; M)]. Medium-sized to large, elongate, gaping, beaks subcentral; ligamental nymph large, high; pallial sinus wide. ?Trias., L.Cret.-Rec., Eu.-N.Am.-S.Pac.
- P. (Panopea). Hinge with 1 small cardinal tooth in either valve. ?Trias., L.Cret.-Rec., Eu.-S.Pac.-N.Am.——Fig. E161,7. *P. (P.) glycimeris (BORN), Rec., Medit.; 7a,b, LV ext., RV hinge, $\times 0.5$ (124b).
- P. (Degrangia) COSSMANN & PEYROT, 1909 [*Panopaea fischerina MAYER, 1861; OD]. Resembling P. (Panopea) in outline and shape of ligamental nymph and pallial sinus but hinge with 2 strong cardinal teeth in either valve. ?Eoc., Mio., Eu. ——FIG. E161,8. *P. (D.) fischerina (MAYER), Mio., France; 8a,b, LV and RV hinges, $\times 3$; 8c, RV ext., LV int., $\times 1$ (Mayer; Cossmann & Peyrot).
- P. (Panomya) GRAY, 1857 [*Mya norvegica SPENGLER, 1793 (not preoccupied by M. norwegica GMELIN, 1791); M] [=Chaenopaea MAYER, 1885 (obj.; OD)]. Smaller than P.

(Panopea), with median depressed area bordered by broadly rounded ridges; pallial line interrupted, forming series of oval scars. ?L.Cret. (Neocom.), Tert.-Rec., Eu.-N.Am.-Arctic.— FIG. E161,9. *P. (P.) norvegica (SPENGLER), Rec., N.Atl.; 9a,b, LV int. with RV hinge, LV ext., $\times 1$ (H. Adams & A. Adams).

Roxoa MENDES, 1952, p. 103 [*Anoplophora intrigans MENDES, 1944; OD]. Elongate, subelliptical, equivalve, compressed, with or without weak posterior umbonal fold; beaks prosogyre, small, situated well forward; lunule and escutcheon lacking; surface smooth with well-defined lateral sulcus and ventral sinus; edentulous; pallial line with deep sinus. [In view of CHAVAN, this genus is allied to *Cowperesia* MENDES and at least doubtfully assignable to the Tellinidae.]. *Perm.*(*Corumbatae F.*), S.Am.(S.Brazil).——FIG. E161,5. **R. intrigans* (MENDES); 5*a,b*, RV ext., RV int. mold, $\times 1$ (Mendes, 1952), [NEWELL]

Saxicavella FISCHER, 1878 [*"Mytilus plicatus GMELIN" of MONTAGU, 1808 (non GMELIN, 1791)



FIG. E161. Hiatellidae (p. N700-N702).

(=*S. jeffreysi WINCKWORTH, 1930); M] [=Arcinella PHILIPPI, 1844 (non SCHUMACHER, 1817); Arcinellina, spelling error]. Thin, small, inequilateral, gaping, subtrapezoidal; hinge edentulous or with small conical cardinal in RV and socket in LV; ligament short, external; pallial line slightly sinuous, pallial sinus large but not deep. U.Oligo.-Rec., Eu.-W.N.Am.—Fig. E161,4. *S. jeffreysi WINCKWORTH, Rec., N.Atl.; 4a-c, LV int., RV int., LV ext., ×3 (Jeffreys, 1865).

Suborder PHOLADINA H. Adams & A. Adams, 1858

[nom. transl. et correct. Newell, 1965 (ex order Pholadacea H. Adams & A. Adams, 1858)] [=Adesmacea auctr.] [Diagnosis by N. D. Newell]

Characters of superfamily Pholadacea. ?Carb., Jur.-Rec.

Superfamily PHOLADACEA Lamarck, 1809

[nom. transl. et correct. VOKES, 1967, p. 326 (ex Pholadaires LAMARCK, 1809)] [=family Pholadaria RAFINESQUE, 1815; Adesmacea DE BLAINVILLE, 1825, p. 577; Cladopoda GRAY, 1847, p. 187] [Materials for this superfamily prepared by RUTH D. TURNER, Museum of Comparative Zoology, Harvard University]

Bivalves characterized by closed mantle and truncate, more or less circular foot developed as suction disc. Shells inequilateral, dorsal margin reflected anterior to beak, forming attachment area for anterior adductor muscle which works counter to posterior adductor when animal is boring. Hinge teeth lacking, but small chondrophore and internal ligament usually present. Ventral adductor muscle or at least thickening of muscles of ventral margin of mantle located at union of anterior slope and disc, forming pivotal point opposite umbones on which valves rock when boring. Gills usually elongate, with two demibranchs except in the Xylophagainae and Teredinidae. Apophyses found in all Pholadacea except in some Pholadidae (Jouannetiinae, Xylophagininae). [The Pholadidae are characterized by the presence of one or more accessory plates and the Teredinidae by the presence of pallets. In the Pholadidae the intestine traverses the heart, whereas in all Teredinidae, except Kuphinae, it does not.] ?Carb., Jur.-Rec.

The Pholadacea is a highly specialized assemblage of bivalves adapted for boring into relatively hard substrata such as peat, wood, nuts, woody plant stems, stiff clays, soft or friable rocks, corals, and shells. Though most are marine, some species occur in brackish and even fresh water.

Semidiagrammatic sketches of the anatomy of the Pholadidae and Teredinidae given in Figure E162 show the relationship of the two families and will be referred to when defining some genera. As a result of close approximation of the anterior and posterior adductor muscles in the Teredinidae. it can be seen that the visceral mass has been extended posteriorly in a long loop, with the mouth and anus remaining in normal position, that the ventricle is anterior to the auricles, and that the kidney is dorsal to the heart. Recent work by TURNER on anatomy of the Teredinidae has shown some striking differences within the group which have necessitated the redefining of some genera and the reassignment of several species. It has also resulted in firm establishment of the subfamily Kuphinae.

Among living forms, the Teredinidae, Xylophagainae, and the genus *Martesia* of the Martesiinae are found normally only in wood or other plant materials.

The classification of living species in this superfamily is not difficult if complete specimens are available, but when dealing with fossil forms it is often impossible to assign them to a subfamily. The reason for this is that the shells may be deformed, either as a result of the material in which they were boring or as a result of processes of fossilization. Many fossil species and genera are based only on internal casts; in others the accessory plates are lacking, the siphonoplax is broken off, and the apophyses are usually imbedded so as not to be seen at all. Using only the outer surface of the valve, one finds it impossible definitely to distinguish some young Jouannetia from young Xylophaga or even some Teredinidae. The variation in size and shape of individuals of any one species of pholad or teredinid is extremely great, depending upon conditions under which the animal was living and on its age. Therefore, it is usually necessary to have large series in order to understand a species adequately. Such series are seldom available in fossil forms, and it is indeed seldom that a growth series, together with

complete adults showing characters of both the inner and outer surface of the valves, is found. It is little wonder, then, that the assignment of fossil genera to the welldefined subfamilies based on living species has been done either provisionally or not at all. In assigning fossil genera to subfamilies, the substrata in which they were found and the depth of the burrows are of prime importance. In the fossilized state, valves of the young of some species of *Martesia*, *Xylophaga*, and the Teredinidae—all woodborers—could be indistinguishable, but a



FIG. E162. Morphological features of Pholadidae (1) illustrated by semidiagrammatic drawing of soft parts of Zirfaea crispata LINNÉ with mantle partially cut away, ca. $\times 2$, and of Teredinidae (2) by similar drawing of Psiloteredo healdi BARTSCH, ca. $\times 2.5$ (Turner, 1965).



FIG. E163. Side views of LV (1, exterior, 2, interior) of diagrammatic composite shell showing morphological features of Pholadidae (921a).

Martesia burrow is only slightly longer than the shell, whereas Xylophaga may make burrows five to ten times the length of the shells, and the burrows of Teredinidae are long and wormlike (see footnote, p. N721).

The presence of an umbonal-ventral sulcus on the outer surface of the valve or the corresponding ridge on the inner surface immediately eliminates all Pholadinae except Zirfaea, which is a transition genus between this subfamily and the Martesiinae.

The presence of a callum immediately places a genus in the Martesiinae or Jouannetiinae. This is not always easy to determine, for after the animal dies the valves remain in place, though the accessory plates may move or disintegrate and the burrow is completely filled with silt. This filling protrudes beyond the valves and fills the anterior end of the burrow. When the entire mass is removed from the substratum, and particularly if it is an internal cast, the resulting specimen appears to have a callum. If a true callum is present, a central division should be evident, for the two halves of the callum do not fuse but are joined by a band of periostracum (in the case of the Martesiinae) or the line of overlap of the callum should be evident (e.g., Jouannetia). On the basis of such considerations the fossil genera have been placed in what seems to be the appropriate subfamily and the Recent genus to which they appear to be related is indicated.



FIG. E164. Morphological features of Teredinidae.—1, Bankia, entire animal, ca. $\times 2$.—2, Enlarged views of valves; 2a, outer view of right valve; 2b, inner view of right valve; 2c, anterior view of opposed valves showing the condyles on which the valves rock and the pedal gape.—3. Composite diagrammatic sketch of a Bankia pallet showing all characters (923; Clench & Turner, 1946).

In view of the large number of specialized terms used in describing the Pholadacea, a glossary is included, along with diagrammatic sketches indicating the specialized characteristics (Fig. E163, E164).

Special Morphological Terms Used For Pholadacea

- apophyses. Calcareous, styloid projections, one in each valve, extending from beneath umbo and serving for attachment of pedal muscles.
- callum. Closure of pedal gape in the Martesiinae and Jouannetiinae. It may be partial or complete, entirely calcareous or composed partly of periostracum. Generally halves of callum do not quite meet and are joined by a periostracal fold with only a minute pore remaining open.
- cephalic hood. Thickened fleshy fold of mantle covering umbonal area.

- chimney. Tube of agglutinized particles produced as result of boring activities. It fits over posterior end of shell and in some species extends anteriorly nearly to umbos. [Occurs in *Parapholas* and *Xylophaga*.]
- chondrophore. Projection of hinge area for support of internal ligament. Chondrophore of RV a small swelling with central depression, that of LV a small shelflike projection.
- hypoplax. Long, narrow, ventral plate covering space between valves and joined to ventral margin of valves by periostracal fold.
- mesoplax. Transverse plate, usually wider than long, which straddles valves at the umbos and protects posterior portion of anterior adductor muscle. It usually originates ventral to the muscle, is calcareous, and may be in one or two pieces.
- metaplax. Long, narrow plate covering gap between valves on dorsal margin behind mesoplax and joined to valves by periostracal fold.



FIG. E165. Accessory plates of genera in Pholadinae (921a).

- pallets. Pair of paddle-shaped, calcareous and periostracal organs located at base of siphons in Teredinidae and functioning to close entrance of burrow. They may be in one piece or composed of numerous elements.
- protoplax. Simple, nearly flat, elongate dorsal plate which rests on top of anterior adductor muscle but does not enclose it. It may be calcareous or periostracal, in one piece, or divided longitudinally.
- siphonal tube. Tube fused to siphonoplax and composed of secretions of mantle and agglutinized particles produced as result of boring. [Occurs in *Pholadidea*.]
- siphonoplax. Accessory structure secreted by mantle and added to posterior end of valves in adult stage. It may be calcareous, periostracal, or combination of both, and may be variously formed.

Family PHOLADIDAE Lamarck, 1809

[nom. correct. Vokes, 1967, p. 326 (pro family Pholadaires LAMARCK, 1809, p. 319)] [=Pholadaria RAFINESQUE, 1815, p. 146; Pholadariae LATREILLE, 1825, p. 223; Pholadae Flemino, 1828, p. 410, 456; Pholadiae GRAY, 1847, p. 20; Pholadoide AGASSIZ, 1847, p. 286; Pholidae Swainson, 1835, p. 30; Pholadeae Menke, 1828, p. 73]

Shells elongate to globular, with slitlike to nearly circular pedal gape which may or may not be closed by callum in adult; anterior portion of valves with imbricate or denticulate concentric ridges and commonly ribbed radially; umbonal-ventral sulcus may separate anterior slope from disc; posterior slope not generally demarked, but clearly defined in Parapholas; accessory plates present in all forms but varying in number. Dorsal and ventral condyles and internal umbonal-ventral rib (reflection of umbonal-ventral sulcus of outer surface of valve) present or absent; pallial sinus usually Siphons variable, usually united, deep. capable of considerable extension, smooth or papillose, and commonly enclosed in periostracal sheath, may or may not be completely retracted within valves when animal contracts; foot well developed, usually truncate and adapted for suction, atrophying in adults of callum-producing forms. [Members of this family bore into stiff clays or muds, shales, friable or soft rock, shells, poor grade cement, wood, nuts, or other plant products.] ?Carb., Jur.-Rec.



FIG. E166. Pholadidae (Pholadinae) (p. N707-N708).

Subfamily PHOLADINAE Lamarck, 1809

[nom. transl. et correct. Vokes, 1967, p. 326 (ex family Pholadaires LAMARCK, 1809, p. 319)] [=Pholadina GRAY, 1847, p. 187]

Shell elongate, rounded or beaked anteriorly and not closed by callum in adult; number of accessory plates variable, but hypoplax always lacking and siphonoplax lacking except in *Talona*, where a periostracal siphonoplax occurs, making this genus a transition form with the Martesiinae; apophyses present; condyles and umbonal-ventral rib and sulcus absent except in *Zirfaea*, which has weak rib, ventral condyles, and sulcus barely visible in adult, thus also seeming to be transitional with the Martesiinae. Foot well developed, not atrophying in adult. Animal not capable of retraction within shell. Gill with two demibranchs. Accessory plates in Pholadinae shown in Figure E165. *Cret.-Rec.*

Pholas LINNÉ, 1758, p. 669 [*P. dactylus; SD CHIL-DREN, 1822, p. 82] [=Pholadites DAVILA, 1767, p. 169 (refers to D'ARGENVILLE, 1757, pl. 26, fig. H, =*P. dactylus LINNÉ) (obj.); Polas GRONO-VIUS, 1781, p. 259 (nom. null.); Hypogaea Poli, 1791, p. 29 (obj.); Hypogaeoderma Poli, 1795, p. 251, 257 (obj.); Pholas LAMARCK, 1799, p. 90 (non LAMARCK, 1801, p. 127) (obj.); Phloas TUR-TON, 1802, p. 172 (nom. null.); Pholadites VON SCHLOTHEIM, 1813, p. 105 (nom. van.); Pholalites SCHLAEPFER, 1821, p. 278 (nom. null.); Xylotrya MENKE, 1830, p. 121 (obj.); Dactylina GRAY, 1847, p. 187 (non ZBORZEWSKI, 1843) (obj.); Pholadarius HERRMANNSEN, 1852, Suppl., p. 105 (nom. null.); Pholalithes PAETEL, 1875, p. 160 (nom. null.); Pragmopholas FISCHER, 1887, p. 1133 (obj.)]. Rock borers occurring in temperate and tropical seas. Shell elliptical, rounded or beaked anteriorly with septate umbonal reflections and 3 dorsal accessory plates; protoplax thin, calcareous, and divided longitudinally; mesoplax transverse, calcareous, and solid; metaplax calcareous, long and narrow. Cret.-Rec., E.Atl.-W. Atl.-E.Pac.-IndoPac.

P. (Pholas). Shell beaked anteriorly, nuclei of divided protoplax near posterior outer margin. *Mio.-Rec.*, Eu.-N.Afr.—Fig. E165,5; E166,1.



FIG. E167. Pholadidae (Pholadinae) (p. N708).



FIG. E168. Pholadidae (Pholadinae) (p. N708).

*P. (P.) dactylus LINNÉ, Rec., Malta; E165,5*a*, entire specimen (dorsal) showing protoplax, mesoplax, and metaplax in place; E165,5*b*, long, divided protoplax (dorsal); E165,5*c*,*d*, mesoplax (dorsal) showing variations; E165,5*e*, metaplax (dorsal); E166,1*a*,*b*, RV int. and LV ext. showing septate umbonal reflection, $\times 0.5$ (921*a*).

- P. (Monothyra) TRYON, 1862, p. 205 [*Pholas orientalis GMELIN, 1790, p. 3216; OD]. Shell beaked anteriorly; protoplax in one piece, with central nucleus. [The protoplax of this species has twice been described as a Scutum.] Cret.-Rec., IndoPac.——Fig. E167,1. *P. (M.) orientalis GMELIN, Rec., Singapore; 1a,b, RV ext., int., $\times 1.2$; 1c,d, inner and outer sides of protoplax, $\times 1.3$ (Turner, n).
- P. (Thovana) GRAY, 1847, p. 187 [*Pholas oblongatus SAY, 1822, p. 320 (=*P. campechiensis GMELIN, 1790, p. 3216); OD] [=Gitocentrum TRYON, 1862, p. 203 (obj.); Gitoventrum PAETEL, 1875, p. 86 (nom. null.)]. Shell rounded anteriorly, nuclei of divided protoplax anterior and more or less centrally located. Mio.-Rec., W.Atl.-E.Pac.—FIG. E165,6; E168,1. *P. (T.) campechiensis GMELIN, Rec., Trinidad; E165,6c,d, long, divided protoplax (dorsal, lat.); E165,6c, metaplax (dorsal); E168,1a,b, LV ext., int., ×0.75 (921a).
- Barnea LEACH in RISSO, 1826, p. 376 [*B. spinosa RISSO, 1826, p. 376 (=*Pholas candida LINNÉ, 1758, p. 669); OD] [=Barnia GRAY, 1840, p. 150; 1842, p. 76 (nom. null.); Barnia LEACH, 1852, p. 254 (obj.); Holopholas FISCHER, 1887, p. 1133 (obj.)]. Shell broadly oval to elliptical, beaked or rounded anteriorly; accessory plate a simple, calcareous, lanceolate protoplax; umbonal reflection simple; pedal gape ranging from narrow slit to broad oval. Sculpture consisting of concentric ridges and radial ribs. [Rock and peat borers.] Mio.-Rec., cosmop.
- **B.** (Barnea). Shells elliptical, rounded at both ends with slitlike pedal gape and slight posterior gape.

Mio.-Rec., E.Atl.-IndoPac.——Fig. E165,1; E169, 1. *B. (B.) candida (LINNÉ), Rec., France; E165,1a-c, protoplax (dorsal, ventral, lat.); E169, 1a-c, LV ext., RV int., opposed valves (dorsal) with protoplax in place, ×1 (921a).

- B. (Anchomasa) LEACH, 1852, p. 253 [*Anchomasa pennatiana LEACH, p. 253 (=*Pholas parva PENNANT, 1777, p. 77); OD] [=Anchomosa LAMY, 1925, p. 79 (nom. null.); Barnea (Umitakea) HABE, 1952, p. 241 (type, Pholadomya japonica Yokoyama, 1920, p. 106, =Barnea dilatata Souleyer; OD)]. Shell broadly to narrowly elliptical, beaked anteriorly with large oval pedal gape, rounded to truncate posteriorly with moderate to large posterior gape. Plio.-Rec., cosmop.——Fig. E165,2; E170,2. B. (A.) truncata (SAY), Rec., USA(Mass.); E165,2a-c, protoplax (dorsal, ventral, lat.); E170,2a,b, LV ext., int., $\times 1$; E170,2c,d, entire animal, dorsal view showing siphons and protoplax in place and ventral view showing foot, $\times 1$ (921a).—Fig. E170,1. *B. (A.) parva (PENNANT), Rec., Eng.; 1a,b, LV ext., RV int., X1 (921a).
- Clavipholas CONRAD, 1868, p. 728 [*Pholas pectorosa CONRAD, 1852, p. 200; OD]. Shell elongate, subtrigonal in outline, gaping slightly anteriorly, gape apparently closed by callum in adult; umbonal-ventral ridge and sulcus present, narrow and extending in sinuous curve from umbo to ventral margin. Sculpture on anterior slope consisting of strong radial ribs and rather weak concentric ridges. Accessory plates, apophyses, etc., unknown. U.Cret., N.Am.—Fig. E171,1. *C. pectorosa (CONRAD), USA(N.J.); 1a,b, dorsal and lat. views of holotype, $\times 1.5$ (889).



FIG. E169. Pholadidae (Pholadinae) (p. N708).



FIG. E170. Pholadidae (Pholadinae) (p. N708).

Cyrtopleura TRYON, 1862, p. 201 [*Pholas crucifera SOWERBY, 1849, p. 489 (=*Pholas cruciger SOWER-BY, 1834, p. 69); SD STOLICZKA, 1871, p. 22]. Shell rounded or beaked anteriorly; accessory plates consisting of thin, largely chitinous, triangular to T-shaped protoplax and heavy transverse, calcareous mesoplax which may be in one or two pieces; umbonal reflection well separated from umbos and supported at posterior end where sockets are formed for reception of anterior projections of mesoplax; apophyses broad and flattened, or more or less spoon-shaped. [Clay, peat, and soft rock borers.] *Mio.-Rec.*, E.Pac.-E.N.Am.-C.Am.-E.S. Am.

C. (Cyrtopleura). Shell beaked anteriorly, with broad oval pedal gape. Rec., E.Pac. ——Fig. E165, 3; E171,2. *C. (C.) cruciger (SowERBY), W. Panama; E165,3a, protoplax (dorsal); E165,3b, mesoplax (dorsal); E171,2a,b, LV ext., RV int., $\times 1$; E171,2c,d, dorsal and ventral views of opposed valves showing large chondrophore and small apophysis, $\times 1$ (921a).

C. (Scobinopholas) GRANT & GALE, 1931, p. 431 [nom. subst. pro Scobina BAYLE, 1880 (non LEPELETIER, 1825; nec WADE, 1917) (nom. van. pro Pholas LAMARCK, 1801, p. 127)] [*Pholas costata LINNÉ, 1758, p. 669; OD] [=Pholas LAMARCK, 1801, p. 127 (non LINNÉ, 1758; nec LAMARCK, 1799) (type, Pholas costata LINNÉ, 1758) (obj.); Pholadigenus RENIER, 1807, pl. vii (type, P. costata LINNÉ; OD, work rejected, ICZN Opinion 427); Pholas Adams & Adams, 1856, p. 325 (non LINNÉ, 1758) (type, Pholas costata LINNÉ, 1758; SD BAYLE, 1880) (obj.); Leuconyx ADAMS & ADAMS, 1863, p. 18; 1865, p. 755 (type, L. tayleriana ADAMS & ADAMS, = P. costata LINNÉ) (based on apophysis only) (nom. oblit.); Leuconix CROSSE, 1868, p. 298 (nom. null.)]. Shell rounded anteriorly with slitlike pedal gape. [The isolated apophysis of this species has been described as a Capulus and as noted above, the genus Leuconyx was created for them.] Mio.-Rec., E.N.Am.-E.S.Am.-Fig. E165,4; E172,1. *C. (S.) costata (LINNÉ), Rec., USA

(Fla.); 165,4*a,b*, protoplax and mesoplax (dorsal); E172,1*a,b*, LV ext., RV int., $\times 0.7$; E172, *1c,d*, mesoplax (dorsal, ventral), $\times 1.7$; E172, *1e-g*, RV apophysis showing cavity and curvature, $\times 1.7$ (921*a*).



FIG. E171. Pholadidae (Pholadinae) (p. N708-N709).

Talona GRAY, 1842, p. 76, 91 [*Pholas clausa HAN-LEY, 1842, p. 6, 336 (=Pholas explanata Speng-LER, 1792, p. 91); OD] [=Talona GRAY, 1840. p. 154 (nom. nud.); = Talena Sowerby, 1849. p. 498 (nom. null.)]. Shells elongate, rounded and closed anteriorly, rounded and gaping posteriorly; reflection of dorsal margin anterior to umbos narrow and nearly erect; umbonal-ventral sulcus lacking. Sculpture consisting of concentric ridges over entire surface and radial ribs on anterior slope and disc, ribs imbricate where they cross ridges; apophyses small, short, and thin. Mesoplax small, transverse, and composed of 2 triangular pieces. Posterior end of valves with reflected lobes which are composed largely of periostracum (seldom present in dried specimens) and form incipient siphonoplax. [Probably a transition genus between Cyrtopleura, which has a similar mesoplax and very thin protoplax composed almost entirely of periostracum and the Martesiinae. which have a siphonoplax.] Rec., W.Afr.-Fig. E173,1. *T. explanata (SPENGLER), Senegal; 1a,b, RV ext., LV int.; 1c,d, ventral and dorsal views of opposed valves showing incurving of valves, remains of siphonoplax, and left half of divided mesoplax remaining in position; all $\times 1$ (Turner, n).

Zirfaea LEACH in GRAY, 1842, p. 76 [*Pholas crispata LINNÉ, 1776, p. 111; SD GRAY, 1847, p. 188] [=Zirfaea GRAY, 1840, p. 154 (nom. nud.); Thurlosia CATLOW & REEVE, 1845, p. 3 (obj.); Zirphaea LEACH, 1852, p. 252 (obj.); Zyrphaea CLESSIN, 1891, p. 7 (nom. null.)]. Shells elongateoval in outline, beaked anteriorly, rounded to truncate posteriorly, widely gaping at both ends and with weak umbonal-ventral sulcus and internal ridge which may not be evident in older specimens; apophyses solid, commonly broad and spoon-shaped; single accessory plate (mesoplax), small and more or less triangular in outline. [Soft clay, mud and peat borers.] Mio.-Rec., N.Atl.-N. Pac.—FIG. E165,7; E174,1. *Z. crispata (LINNÉ), Rec.; E165,7a-c, mesoplax (dorsal, ventral, lat.) (921a); E174,1, USA(Mass.) (1a-c), USA(N.H.) (1d-f); E174,1a, RV int. showing umbonal-ventral ridge and apophysis, X1.5; E174,1b, LV ext. showing umbonal-ventral sulcus, X1.5; E174,1c, LV int. showing muscle scars, X1; E174,1d, dorsal view of entire specimen showing anterior adductor muscle covered only by periostracum with small mesoplax at posterior end, $\times 1$; E174,1e, side view of entire specimen showing foot and extent of periostracal covering on siphons, X1; E174,1f, ventral view of entire specimen showing foot, anterior muscular collar of mantle, and extent to which siphons can be contracted, $\times 1$ (921a).

Zirlona FINLAY, 1930, p. 257 [*Pholadidea increnata MARWICK, 1929, p. 914; OD]. Shell rounded anteriorly and only slightly gaping. Umbonalventral ridge and sulcus present. Anterior slope



FIG. E172. Pholadidae (Pholadinae) (p. N709).

sculptured with strong regularly spaced concentric lamellae which are slightly crenulate; disc and posterior slope sculpture with concentric ridges; radial sculpture lacking. Accessory plates unknown. *Tert.*(*Chatton F.*), N.Z.—FIG. E175,1. *Z. *increnata* (MARWICK); LV ext. (holotype), $\times 3$ (594).

Subfamily MARTESIINAE Grant & Gale, 1931

Shell elongate to globular, beaked and gaping anteriorly in young stage, completely closed by calcareous callum in adult in all genera except *Chaceia*, which produces only a partial callum; number of accessory plates variable but always lacking protoplax, apophyses, condyles, umbonal-ventral rib and sulcus present; siphonal tube, chimney, and periostracal laminae on posterior slope present in some forms. Foot well developed in young working stage but atrophied in adult. Siphons capable of complete retraction within shell except in *Chaceia*, which is transitional with Pholadinae. [Species of Martesiinae have been reported from Carboniferous strata, but, since the accessory plates are unknown, these are unassignable to subgenera. Plates typical of the subfamily are illustrated in Figure E176.] ?Carb., Jur.-Rec.

Martesia Sowerby, 1824, p. 2 [*Pholas clavata LAMARCK, 1818, p. 446 (=*P. striata LINNÉ, 1758, p. 669); OD] [=Mactresia GRAY, 1840, p. 154; Mactesia PAETEL, 1875, p. 119 (nom. null.); Martesiella VERRILL & BUSH, 1898, p. 777 (type, M. (M.) fragilis; OD); Hiata ZETEK & MCLEAN, 1936, p. 110 (type, H. infelix, =young M. striata (LINNÉ); OD) (obj.); Mesopholas TAKI & HABE, 1943, p. 109 (type, M. intusgranosa, =M. striata (LINNÉ); OD) (obj.); Diploplax BARTSCH & REH-DER, 1945, p. 10 (type, M. (D.) americana, =young M. striata (LINNÉ); OD) (obj.)]. Shells beaked and widely gaping anteriorly in young; adult with callum; beaks sinuously to sharply truncated, giving young Teredo-like appearance. Protoplax lacking, mesoplax variable, circular to cuneiform in outline; metaplax and hypoplax long and narrow, pointed anteriorly, pointed truncate or divided posteriorly. [Small wood-borers.] ?Carb. (subgenus unknown), Jur.-Rec., world-wide, temp.-



FIG. E173. Pholadidae (Pholadinae) (p. N710).

trop. [*Martesia* de Blainville, 1825, p. 578, 632 (obj.).]

M. (Martesia). Mesoplax of adult broadly oval to circular, cushion-like in adult; flat, semicircular, and located posteriorly beneath anterior adductor muscle in young; metaplax and hypoplax pointed or truncate posteriorly. ?Carb., Jur.-Rec., temp. and trop. seas of world.——Fig. E176,2; E177,1. *M. (M.) striata (LINNÉ), Rec.; E176,2, diagram.; E177,1, Trinidad (1a-c), USA(Fla.) (1d-g); E176,2a-c, mesoplax of adult (dorsal, ventral, lat.); E176,2d,e, mesoplax of young (dorsal, ventral) (921b); E177,1a, dorsal view of adult with mesoplax and metaplax in place, ant. to right, X1.2; E177,1b, ventral view of adult showing callum and hypoplax, ant. to left, $\times 1.2$; E177,1c, side view of adult, ant. to left, X1.2; E177,1d,e, LV ext., RV int. of young specimens; E177,1f, dorsal view of opposed valves with small, flat mesoplax of young in place; E177,1g, ventral view of opposed valves showing large pedal gape; all $\times 1.5$ (921b).

- M. (Particoma) BARTSCH & REHDER, 1945, p. 5 [*Pholas cuneiformis SAY, 1822, p. 322; OD]. Mesoplax cuneiform, similar in shape in young and adult; metaplax and hypoplax long, narrow, forked posteriorly and extending over posterior end of valve where they meet and fuse. ?Carb... Jur.-Rec., W.Atl.-E.Pac.-Fig. E176,3; E178,1. *M. (P.) cuneiformis (SAY), Rec., USA(N.Y.); E176, 3a-c, mesoplax (dorsal, ventral, lat.) (921b); E178,1a, dorsal view of adult with mesoplax and forked metaplax in place; E178,1b, dorsal view of young specimen showing similarity of mesoplax to that of adult; E178,1c, ventral view of adult showing forked hypoplax; E178,1d, side view of adult showing fused metaplax and hypoplax; E178,1e, ventral view of opposed valves of young specimen showing pedal gape, apophyses, and chondrophore; E178,1f, RV ext. of young specimen; E178,1g, LV int. of young specimen; all ×2.5 (921b).
- Aspidopholas FISCHER, 1887, p. 1137 [*Pholas scutata Deshayes, 1824, p. 252; OD] [=Scutigera COSSMANN, 1886, p. 25 (non LATREILLE, 1803); Calyptopholas LAMY, 1927, p. 180 (type, Pholadidea (Calyptopholas) cheveyi LAMY, 1927, p. 180, =Pholas obtecta Sowerby, 1849; OD)]. Shells similar to Pholadidea, beaked and gaping anteriorly in young stage; partially closed by callum in adult; umbonal-ventral sulcus and ridge narrow and rather weak; anterior slope sculptured by closely set, finely imbricate concentric ridges and weak radial ribs. Apophyses short, solid, and broad at free end; mesoplax greatly produced, forming cap which may cover anterior end of adult; siphonoplax small, calcareous extension of valves which may be covered with periostracum. Siphons may be retracted completely. [Coralborers.] Eoc., Eu.; Rec., IndoPac.-Fig. E179,1a. *A. scutata (Deshayes), Eoc., France(Paris Basin); specimen showing large mesoplax and lining of tube covering posterior end of shell, $\times 3$ (259, pl. 6, fig. 5).——Fig. E179,1b,c. A. cheveyi (LAMY), Rec., Annam; 1b, adult with dorsal plate removed; 1c, specimen with greatly enlarged mesoplax in place: both $\times 1.5$ (520).
- Chaceia TURNER, 1955, p. 66 [*Pholas ovoidea GOULD, 1851, p. 87; OD]. Shell beaked anteriorly, gaping widely in young stage, with pronounced umbonal ventral sulcus and partial callum in adult. Mesoplax small, transverse in one piece and Zirfaealike. No other accessory plates present. [Rock borers.] Rec., E.Pac.—FIG. E176,1; E179,2; E180,1. *C. ovoidea (GOULD), USA(Calif.); E176, 1a-c, mesoplax (dorsal, ventral, lat. with ant. at left) (921b); E179,2a,b, LV ext., RV int. of young specimens, ×1; E179,2c, ventral view of opposed valves of young specimen, ×1 (921b); E180,1a,



FIG. E174. Pholadidae (Pholadinae) (p. N710).

side view of entire adult showing partial callum and siphons, $\times 0.6$; E180,1*b*, ventral view of young specimen showing foot, large anterior gape, and meeting of valves at ventral condyle, $\times 0.6$; E180, 1*c*,*d*, LV ext., RV int. of adult specimens, $\times 0.6$ (921*b*).

Diplothyra TRYON, 1862, p. 449 [*D. smithii; OD] [=Schroteria TRYON, 1862, p. 221 (nom. oblit.) (type, Pholas cordata TRYON, 1862, p. 221, =Pholas cordata GMELIN, 1790) (refers to SCHRO-TER, 1786, v. 3, p. 554, pl. 9, fig. 22-24)]. Shell Martesia-like but with beaks obliquely truncated; mesoplax subquadrate to subtriangular in adult, extending anteriorly between dorsal extension of callum; metaplax and hypoplax pointed anteriorly and forked posteriorly, forked portions extending over posterior margins of valves and fusing with one another. [Small shell- and rock-borers, usually found in oysters and Haliotis]. Rec., W.Atl.-E.Pac. ---FIG. E176,5; E181,1-4. *D. smithii, USA (N.Y.); E176,5a-c, mesoplax of adult (dorsal, ventral, lat.); E176,5d,e, mesoplax of young (lat., dorsal) (921b); E181,1a,b, split shell of Crasso-



FIG. E175. Pholadidae (Pholadinae) (p. N710-N711).



FIG. E176. Accessory plates of genera in Martesiinae (921b).

straea virginica (LINNÉ) showing attack of D. smithii, $\times 1$; E181,2*a-c*, ventral and 2 dorsal views showing extension of callum around mesoplax and differences in shape of mesoplax; $\times 3.5$; E181, 3a,b, RV ext., RV int. of adult, $\times 3.5$; 4a,b, RV ext., LV int. of young specimen, $\times 4.5$ (921b).

Eutylus VINCENT, 1891, p. 164, pl. 4, fig. 1-4 [*Pholadomya cuneata SOWERBY, 1844, p. 40; OD] [=:Phenacomya DALL, 1898, p. 823 (obj.)]. Probably close to Pholadidea. Anterior slope sculptured with rather weak concentric ridges and only a few rather widely spaced radial ribs; umbonal-ventral sulcus weak; anterior margin sinuous; pedal gape small; callum ribbed, showing extension of radial ribs of anterior slope. Dorsal plates unknown. Apophyses probably present. [Mud-dweller.] Eoc., Eu.——FIG. E182,1. *E. cuneata (SowERBY), Belg.; 1a, RV ext.; 1b, ant. view of opposed valves; 1c, int. cast showing pallial sinus; 1d, dorsal view of opposed valves; all $\times 1$ (941).

Formosulus ZHIZHCHENKO, 1934, p. 44 [*F. lucidus; OD] [= Formesulus ZHIZHCHENKO, 1939 (errore NEAVE, p. 736)]. Shell small, more or less rectangular in outline, beaked anteriorly and divided into 3 distinct areas by 2 furrows extending from umbos in ventral margin. [Description and figure poor. Described as a hiatellid bivalve (Hiatellacea) but now regarded by Russian paleontologists as probably nonmolluscan, a cirriped plate, fide VOKES, 1967, p. 346.] *Mio.*, USSR(Ciscaucasia).——FIG. E161,6. **F. lucidus;* LV ext., ×10 (Zhizhchenko).

- Goniochasma MEEK, 1864, p. 34 [*Xylophaga stimpsoni MEEK & HAYDEN, 1857, p. 141; OD]. Shell Martesia-like, ovate-oblong with beak truncated at sharp angle; umbonal-ventral sulcus and ridge oblique, internal ridge faintly crenulate; posterior ridges very oblique, broad, rounded and not extending to margin. Mesoplax present (889, p. 249). [Is probably a young Martesia. From fossilized wood.] U.Cret., N.Am.-India.——Fro. E182,2. *G. stimpsoni (MEEK & HAYDEN), USA (Idaho); 2a, LV ext., X2; 2b, cast of holotype, X1 (609, pl. 30, fig. 9a-b).
- Heteropholas FISCHER, 1887, p. 1136 [*Pholas xylophagina DESHAYES, 1860, p. 142; OD]. Shell Martesia-like but with beaks obliquely to sinuously truncated; umbonal-ventral sulcus very oblique and with 2 additional grooves on outer surface, one anterior, other median. Accessory plates and apophyses unknown. Eoc., Eu.—FIG. E183,1. *H. xylophagina (DESHAYES), France(Paris Basin); 1a,b, LV ext., int., ×2 (259).
- Lignopholas TURNER, 1955, p. 98 [*L. clappi; SD TURNER, 1956, p. 188]. Shell Martesia-like, posterior slope elongated and having series of fringed, overlapping, thin, periostracal lamellae; mesoplax divided longitudinally; other accessory plates lacking; apophyses long and thin, chondrophore prominent. [Small wood borers, in brackish and fresh water.] Rec., W.Atl.-IndoPac.-Fig. E184.1-3. *L. clappi, Nicaragua; 1a, adult, lat. view, ant. to left; 1b, dorsal view of adult, ant. to right, showing divided mesoplax (holotype), ×4; 2a, young LV ext., ant. to left; 2b, young RV int., ant. to left (paratype), $\times 6$; *3a-c*, dorsal, ventral, lat. views of mesoplax of adult, $\times 6$; 3d, dorsal view of mesoplax of young, anterior for all to left, $\times 6$ (921b).
- **Opertochasma** STEPHENSON, 1952, p. 139 [*0. venustum; OD]. Shell Martesia-like but with 2 radial grooves extending from beak to ventral margin in area of umbonal-ventral ridge; posterior slope sculptured. Mesoplax long and narrow, divided longitudinally and extending anteriorly in adult in 2 lobes over umbos; hypoplax lacking. [Probably close to Parapholas.] U.Cret., N.Am.—Fig. E183,2. *0. venustum, Woodbine F., USA(Tex.); 2a, LV ext., 2b-d, dorsal, ant., and ventral views of opposed valves; 2a-c, \times 3; 2d, \times 2 (890).
- Parapholas CONRAD, 1848, p. 121 [*Pholas californica CONRAD, 1837, p. 226; OD] [=Paraphola PAETEL, 1875, p. 152 (nom. null.)]. Shell divided into 3 distinct areas, anterior slope, disc, and posterior slope being clearly marked; posterior slope having series of overlapping periostracal plates; accessory plates consisting of oval mesoplax, elongate metaplax, and hypoplax, which may

10 1Ь Martesia lc 1f 1d le lg

FIG. E177. Pholadidae (Martesiinae) (p. N712).

or may not be forked posteriorly; siphonoplax lacking; chimney not attached to valves but fitting over end of valves and composed of fine particles which have been ejected from siphons and cemented together. [Moderate-sized to rather large rock-borers.] Cret.-Rec., E. Pac.-Indo Pac.-W. Afr. -FIG. E176,6; E185,1. *P. californica (Con-RAD), Rec., USA(Calif.); E176,6a-c, metaplax (dorsal, ventral, lat.); E176,6d,e, hypoplax (dorsal, ventral); E176,6f-h, mesoplax of adult (dorsal, ventral, lat.); E176,6i,j, mesoplax of young (dorsal, ventral); E185,1a, side view of adult, $\times 1$; E185,1b, ventral view of young specimen showing foot, X1; E185,1c, adult RV int., X1; E185,1d, ventral view of adult showing hypoplax in place, $\times 0.7$; E185,1e, dorsal view of adult showing mesoplax and metaplax in place, $\times 0.7$; E185,1*f*, chimney of specimen in fig. 1*d*, $\times 0.7$. [Figures show variation in size of adults] (921b).



FIG. E178. Pholadidae (Martesiinae) (p. N712).

- Penitella VALENCIENNES in ABEL DU PETIT-THOUARS, 1846, pl. 24 [*P. conradi; SD HABE, 1952, p. 243] [=Penicilla CONRAD, 1854, p. 335 (nom. null.); Navea GRAY, 1851, p. 385 (type, N. subglobosa GRAY, 1851, p. 385; SD TURNER, herein)]. Shell oval in outline, beaked anteriorly in young stage with pronounced umbonal-ventral sulcus, callum partial or complete. Mesoplax Zirfaea-like in young but producing dorsal covering in adult; siphonoplax variable, present or absent; no other accessory plates present. [Navea GRAY was based upon a young form. Shale- and rock-borers.] Mio.-Rec., E.Pac.-N.Pac.-Fig. E176,4; E186, 1-4. *P. conradi VALENCIENNES; Rec., USA (Calif.); E176,4a-c, mesoplax of adult (dorsal, ventral, lat.); E176,4d,e, mesoplax of young (dorsal, ventral); E186,1, adult specimens in substrata (type from VALENCIENNES), $\times 1$; E186,2*a*,*b*, adult LV ext. taken from shale and RV int. of same specimen showing muscle scars and siphonoplax, \times 3; E186,3a, dorsal view of adult showing mesoplax in position, $\times 3$; E186,3b,c, dorsal and LV int. views of adult taken from Haliotis, $\times 2$; E186,4a,b, LV ext. and RV int. of young specimen taken from shale, $\times 4.5$ (921b).
- Pholadidea TURTON, 1819, p. 147 [*P. loscombiana; OD] [=Pholadidoidea DE BLAINVILLE, 1826, p. 535 (obj.); Pholidea SWAINSON, 1835, p. 30 (obj.); Pholadideae SOWERBY, 1839, p. 81 (nom. null.); Pholideae SWAINSON, 1840, p. 364 (nom. null.); Talonella GRAY, 1851, p. 385 (type, T. tridens GRAY, 1843; OD); Cadmusia GRAY, 1852, p. 254 (obj.); Pholameria CONRAD, 1865, p. 22 (type, Pholas triquetra CONRAD, 1848, p. 127, pl.

13, fig. 3; OD); Pholididae PAETEL, 1875, p. 160 (nom. null.)]. Shell beaked anteriorly in young stage, closed by callum which extends dorsally over beaks in adult; rounded to truncate posteriorly, divided into 2 areas by prominent umbonal-ventral sulcus; posterior slope not clearly defined. Mesoplax variable, divided longitudinally in young but may be greatly produced in adult; incipient metaplax and hypoplax present or absent, not existing as separate plates but resulting from deposition of calcium in periostracum uniting valves posterior to umbos; siphonoplax commonly tubular, composed largely of periostracum and fused; siphonal tube present in most species. Apophyses short, fragile and not broadening at free end. [Shale, soft-rock and coral-borers.] Eoc.-Rec., E.Pac.-IndoPac.-E.Atl.

- P. (Pholadidea). Umbonal reflection raised well above umbos; mesoplax small, lacking basal portion; siphonoplax cuplike; siphonal tube lacking. *Eoc.-Rec.*, E.Atl.-IndoPac.—Fig. E187,1-3. *P. (P.) loscombiana TURTON, Rec., Eng.; 1a,b, adult RV ext., and LV int., showing small apophysis and large chondrophore, ×1.5; 2, dorsal view of opposed valves with mesoplax and siphonoplax in place, ×1.5; 3, lateral view of adult with siphonoplax, ×1.5 (921b).
- P. (Hatasia) GRAY, 1851, p. 385 [*Pholas melanura SOWERBY, 1834, p. 70; SD STOLICZKA, 1871, p. 21] [=Hatoisia SCHAUFUSS, 1869, p. 17 (nom. null.); Hastasia PAETEL, 1875, p. 91 (nom. null.)]. Umbonal reflection closely appressed, mesoplax in young stage flat, semicircular and in one piece, upper part, added in

adult stage, divided longitudinally, young basal part extending beyond it; siphonoplax composed largely of periostracum, variable in shape and size. Siphonal tube attached to siphonoplax. *Rec.* E.Pac.——FIG. E188,1. **P*. (*H.*) melanura (SowERBY), Panama (*Ia,b*), Mexico (*Ic*); *Ia*, adult LV ext. with siphonoplax; *Ib*, adult RV int.; *Ic*, dorsal view of adult showing extension of callum over beaks and mesoplax, all $\times 1$ (*SowERBY*), Panama; lateral view of adult showing siphonal tube attached to the siphonoplax, $\times 2$ (*921b*).

- **Ramsetia** STEPHENSON, 1941, p. 250 [**R. whitfieldi;* OD]. Shell *Martesia*-like, beaked and gaping anteriorly in young but closed by callum in adult; beaks diagonally truncated; umbonal-ventral ridge and sulcus present. Sculpture consisting of coarse concentric ridges which are crossed on anterior slope by weakened radial ribs. Accessory plates unknown. *U.Cret.*, N.Am.—Fic. El183,3. **R. whitfieldi*, Navarro Gr., USA(Tex.); 3a, LV ext. (holotype); 3b, RV ext. of another specimen; 3c, dorsal view of opposed valves; all $\times 1$ (889).
- Teredina LAMARCK, 1818, p. 438 [*Fistulana personata LAMARCK, 1806, p. 429, 1808, pl. 43, fig. 6-7; SD CHILDREN, 1823, p. 81] [=Fistulana LA-MARCK, 1806 (non LAMARCK, 1789) (obj.); Teridina Sowerby, 1839, p. 117 (nom. null.)]. Shell Teredo-like, particularly in young stage, but anterior gape closed by callum in adult; umbos covered by large, 4-lobed mesoplax which extends anteriorly; apophyses present; long, thick calcareous tube fused to valves anteriorly and in some shells divided by longitudinal partitions posteriorly; calcareous tube probably homologous with that found in some Pholadidea, to which seemingly it is most closely related. U.Cret.-M.Mio., Eu.—FIG. E189,1-6. *T. personata (LAMARCK), France(Paris Basin); 1, entire specimen; 2a,b, dorsal and ventral views of opposed valves, mesoplax removed; 3a,b, dorsal and ant. views of opposed valves showing lobed mesoplax; 4, internal view of shells showing apophyses; 5, abnormal post. end of tube with 2 openings; 6a,b, posterior ends of tubes showing internal ribbing; all $\times 1$ (259, pl. 3, fig. 10-15, 17-20).
- Xylophomya WHITFIELD, 1902, p. 75, pl. 27-29 [*X. laramiensis; OD]. Shell somewhat Xylophaga-like in general outline, anterior gape being closed by broad shieldlike plate (callum) in adult form; widely gaping posteriorly, with posterior margin of valves prolonged by thin, smooth tongue-shaped extensions, which probably fuse with lining of tube. Narrow umbonal-ventral sulcus present. Dorsal margin of RV with 4 minute toothlike denticles anterior to umbo. [Woodboring.] Cret., USA(Wyo.).—Fig. E190, I. *X. laramiensis, Laramie Gr.; 1a, outline showing form of RV; 1b, composite sketch from several



FIG. E179. Pholadidae (Martesiinae) (p. N712).

specimens to show sculpture and callum; lc, ant. end (reconstr.); ld, ant. teeth as seen on fragment chipped from between beaks; le, outline of dorsal view of ant. end; la-c, le, $\times 1$; ld, $\times 3$ (982).

Subfamily JOUANNETIINAE Tryon, 1862 [nom. correct. TURNER, 1955 (pro Jouannetinae TRYON, 1862)] Shells in young stage more or less globu-

N717



FIG. E180. Pholadidae (Martesiinae) (p. N712-N713).

lar, equivalved, beaked and widely gaping anteriorly; apophyses lacking; umbonalventral rib and sulcus present but weak; adult valves may or may not be equal; if inequivalved, callum closing pedal gape usually greatly produced anteriorly and entirely calcareous; if equivalved, callum flat and composed largely of periostracum. Rudimentary mesoplax present in some forms. Siphonoplax calcareous and variable in shape, unequal in *Jouannetia*. Foot well developed in young stage, atrophied in adult. Siphons capable of complete retraction within shell. Gills with two demibranchs. *U. Cret.-Rec.* Jouannetia DesMoulins, 1828, p. 244 [*]. semicaudata; OD] [=Iouannetia GRAY, 1840, p. 154 (nom. van.); Juanetia D'ORBIGNY, 1846, p. 737 (nom. null.); Juannetia DESMAREST, in CHENU, 1859, p. 231 (nom. null.)]. Shells in young stage equivalved, beaked and widely gaping anteriorly, closed posteriorly; mesoplax, if present, in young shell more or less semicircular in outline and located in normal position transversing both valves, but displaced in adult by unequal growth of callum on LV; callum very large, that of LV being largest and overlapping callum of RV. Siphonoplax of LV, if present, always much smaller than that of RV, L siphonoplax always smooth, while R may be pectinate or smooth. Shell with or without an inwardly projecting lamina for the attachment of posterior adductor and pedal muscles. [Shale- and soft-rock-borers.] U.Cret.-Rec., cosmop., temp. and trop. seas.

J. (Jouannetia). Shell with special lamina for attachment of muscles; margin of siphonoplax smooth. U.Cret.-Rec., cosmop. in temp. and trop. seas.—Fig. E191,1. *J. (J.) semicaudata Des-MOULINS, ?EOC., France(Mérignac, Bordeaux); 1a,b, right and left sides of complete adult showing overlap of callum from LV; *1c*, adult RV int. showing siphonoplax; *1d*, adult LV int. showing lack of siphonoplax; *1e-f*, RV int. and LV int. without callum, showing laminae for attachment of posterior adductor muscle; *1g*, ant. view of opposed valves without callum; *1h*, complete specimens as found in calcareous rock; all $\times 1$ (648).



FIG. E181. Pholadidae (Martesiinae) (p. N713-N714).



FIG. E182. Pholadidae (Martesiinae) (p. N714-N715).

- J. (Pholadopsis) CONRAD, 1849, p. 156 [*Pholadopsis pectinata; OD] [=Triomphalia Sowerby, 1849, p. 500 (type, Pholas globosa Quoy) (=Pholas globulosa QUOY & GAIMARD; SD Sowerby, 1850); Triumphalia PAETEL, 1890, p. 5 (nom. null.); Triomphala CLESSIN, 1892, p. 33 (nom. null.)]. Shells without special lamina for attachment of muscles; margin of siphonoplax pectinate; mesoplax small and displaced in adult. Paleoc.-Rec., Eu.-W.Atl.-E.Pac.-IndoPac.-Fig. E192,1. *J. (P.) pectinata (CONRAD), Rec., USA (Calif.); 1a, adult RV ext. showing callum not extending to mid-line and pectinate siphonoplax; 1b, LV int. showing greatly enlarged callum which overlaps RV, smaller smooth siphonoplax, and posterior adductor muscle scar just posterior to umbo; 1c, dorsal view of opposed valves showing greatly enlarged LV callum which has displaced mesoplax; all ×1.5 (1a,b, holotype; 1c, paratype) (921b, 922).
- Nettastomella CARPENTER, 1865, p. 202 [*Netastoma darwinii Sowerby in CARPENTER, 1865 (=Pholas rostrata VALENCIENNES, 1846, non darwinii Sowerby); OD] [=Netastoma CARPEN-TER, 1864, p. 637 (non Nettastoma RAFINESQUE, 1810¹); Netastomella PAETEL, 1875, p. 138 (nom.

null.); Nettastoma LAMY, 1926 (nom. null.)]. Large pedal gape of young only partially closed by calcareous callum which forms band along anterior margin of shell in adult, equal on both valves or much wider on LV; periostracal callum with minute central pore filling most of pedal gape in adult. Siphonoplax, present on both valves or on RV only, may be short or long, straight, diverging or tapering and tubelike. Mesoplax, if present, small and fused with dorsal extension of callum on LV. [Shale- and soft-rock-borers.] Plio.-Rec., N.Pac.-S.Atl.-S.Pac.-Fig. E193,1; E194,1. *N. rostrata (VALENCIENNES), Rec., USA(Calif.); E193,1a, large LV ext. with wide callum and short siphonoplax; E193,1b, small LV ext. with long siphonoplax; E193,1c, dorsal view of opposed valves; E193,1d, RV int. with siphonoplax broken off; E193,1e, ventral view of specimen beginning to produce siphonoplax; all ×2.5; E194,1, specimen with LV removed to show muscles, siphons and periostracal callum with open central pore, $\times 4.5$ (921b, 922).

Scyphomya DALL, 1898, p. 822 [*Pholas semicostata H. C. LEA, 1844, pl. 24, fig. 1; OD]. Shell similar to young Jouannetia (Pholadopsis). [The location of the type of P. semicostata LEA is unknown and specimens labeled with this name by DALL proved to be young J. (Pholadopsis), a genus not known to occur in the Atlantic at the time DALL was working. Scyphoma probably is a synonym of Pholadopsis.] Tert.-Rec., W.Atl.

¹ Although according to the present rules of Zoological Nomenclature a name differing in one letter is not considered a homonym, this was not the case at the time CAR-PENTER himself instituted a new name for his Netastoma. Since Nettastomella has been in general use since CARPENTER introduced it in 1865 it is being retained in accordance with Article 23b.

Subfamily XYLOPHAGAINAE Purchon, 1941

[nom. correct. TURNER, hercin (pro Xylophaginae TURNER, 1955, non LATREILLE, 1807) nom. transl. ex Xylophagidae LATREILLE, 1807 (nom. correct. SCHINER, 1868, pro family Xylophagi LATREILLE, 1807, Insecta)] [=Xylophaginidae PURCHON, 1941]

Shells small, globular, beaked and gaping anteriorly throughout life; beaks truncated at nearly right angles, giving shell a Teredolike appearance. Apophyses absent. Anterior slope sculptured with numerous rows of finely denticulated ridges, as in Teredinidae; disc and posterior slope sculptured only by growth lines and low concentric ridges; umbonal-ventral ridge and sulcus well developed; ventral condyle usually present but weak; dorsal condyle lacking; chondrophore well developed. Accessory plates consisting only of small divided mesoplax, which varies greatly in shape. Posterior adductor muscle scar large, located high on posterior slope. Foot well developed, truncate and not atrophying in adult. Siphons commonly capable of retraction within shell, and quite variable. Excurrent siphon may be shorter than incurrent siphon and in some species exists only as series of lappets on dorsal side of incurrent siphon. Gills with single demibranch. Length of the tunnel ranging from slightly longer than the shell to about ten times the length of the valves, the posterior end often lined with agglutinized particles ejected from the excurrent siphon forming a chimney similar to that in Parapholas.¹ U.Cret.-Rec.

Attempts have been made to erect several genera on the basis of dorsal plate characters and type of siphons, but KNUDSEN (1961) has shown that these do not group naturally and that on the basis of our present knowledge there is no way to divide Xylophaga. Xylophaga TURTON, 1822, p. 258 [*Teredo dorsalis TURTON, 1819, p. 185; OD] [=Xilophaga GEI-NITZ, 1845, p. 397 (nom. null.); Xylotomea DALL, 1898, p. 821 (new name pro Xylophaga TURTON [non Xylophagus MEUSCHEN, 1778; nec MEIGEN, 1803]—name not needed as Xylophaga and Xylo-

phagus are not considered homonyms); Xilotoma

GIGOUX, 1934, p. 285 (nom. null.); Protoxylophaga TAKI & HABE, 1945, p. 112 (type, X. tomlini PRA-SHAD; OD); Neoxylophaga TAKI & HABE, 1950, p.



FIG. E183. Pholadidae (Martesiinae) (p. N715).

¹ A remarkable new genus of bathyal Xylophagainae was discovered while this work was in press. An account of it is being prepared now for publication. The two species (Western Atlantic and Eastern Pacific) are very *Teredo*-like in habit, making tunnels over 15 cm. long, the posterior twothirds of which have a thin calcareous lining. If wood containing species of this genus were fossilized it probably would be impossible to distinguish them from teredinids.



FIG. E184. Pholadidae (Martesiinae) (p. N715).

46 (type, X. rikuzenica TAKI & HABE; OD); Metaxylophaga TAKI & HABE, 1950, p. 47 (type, M. supplicata TAKI & HABE; OD). Shell globose, Teredo-like, apophyses lacking, mesoplax divided and variable in shape and size. Chondrophore and internal ligament present. Siphons variable. [Small borers usually found in water-logged plant material in deep water.] U.Cret.-Rec., cosmop.-—Fig. E195,1,2. *X. dorsalis (TURTON), Rec., Scot.; E195,1a, LV ext. showing umbonal-ventral sulcus; E195,1b, LV int. showing muscle scars and umbonal-ventral ridge; E195,1c,d, ant. and dorsal views of opposed valves showing pedal gape, condyles, chondrophores, and mesoplax in place; E195,2a,b, dorsal and ventral views of mesoplax (921b).

Xylophagella MEEK, 1864, p. 34 [*Xylophaga elegantula MEEK & HAYDEN, 1857, p. 141; OD]. Shell Xylophaga-like, globose, beaks sharply truncated; umbonal-ventral sulcus and ridge present and extending from umbos in nearly straight line to ventral margin; internal ridge strongly crenate; second posterior internal ridge extending from umbos obliquely to posterior ventral margin. Accessory plates and apophyses not known. Burrows without shelly lining. U.Cret., N.Am.— Fio. E190,2. *X. elegantula (MEEK & HAYDEN), USA(Idaho); 2a, LV ext.; 2b, LV int. cast; 2c-e, post., ant., post. views of opposed valves; 2f, side view of holotype, ×1 (2a-e, ×3.5) (609). Family TEREDINIDAE Rafinesque, 1815 [nom. correct. DEKAY, 1843, p. 249 (pro Teredaria RAFI-NESQUE, 1815, p. 148)] [=Teredinites LATREILLE, 1825, p. 224; Teredinadae FLEMING, 1828, p. 409; Teredina GRAY, 1847, p. 188; Terediae CARPENTER, 1861, p. 248; Teredinadae TRYON, 1862, p. 459 (nom. null.)]

Shells greatly reduced, covering only anterior tip of long wormlike animal (Fig. E164,1a). Burrow usually with calcareous lining which varies greatly in thickness and is in some species divided or has septa at distal end. Valves divided into three parts as shown in Figure E164,1b,c. Condyles (on which valves rock during boring process), umbonal-ventral ridge and apophyses promi-Chondrophore and small internal nent. ligament present in all species examined by author. Siphons separate or united, relatively short and with pair of pallets inserted at base which serve to close end of burrow when siphons are withdrawn. Gill with only single demibranch. Intestine not transversing heart, except in Kuphinae. Visceral mass extending in loop posterior to shell, as shown in Figure E162,2. Caecum present, except in the Kuphinae. ?Cret., Paleoc.-Rec.

The classification of genera is based on the morphology of the soft parts and on the pallets. The species are usually distinguished on the basis of pallets and siphons. The shells are almost useless in classification as they are extremely variable, depending upon the age of the specimen and the ecologic conditions affecting it. Similar shell forms may appear in widely separated genera.

Though many fossil species have been named, some as early as the Lower Cre-

taceous, most have been instituted on the basis of shells and tubes only, and consequently they cannot be placed definitely in any Recent genus. Pallets of *Bankia* have been recorded from the Paleocene of Iraq (ELLIOTT, 1963, p. 315) and DURHAM & ZULLO (1961, p. 1) described a *Bankia* from the Middle Oligocene of Washington. *Nototeredo* has recently been discovered by A. M.



FIG. E185. Pholadidae (Martesiinae) (p. N715).



FIG. E186. Pholadidae (Martesiinae) (p. N716).

CVANCARA in the Cannonball Formation (Paleocene) of Morton Co., North Dakota (TURNER, 1966, p. 16, fig. 3; CVANCARA 1966, p. 350, pl. 9, fig. 12, 28). Pallets of *Bankia, Teredo, Teredora,* and *Nototeredo* are known from the Eocene of the Paris Basin, the Upper Eocene of Barton, Hampshire, England, and from Burgenland Formation, Austria. The fossil record is poor, but from what is known it may be assumed that all Recent genera existed in the Eocene and that the family was worldwide in distribution, for wherever sufficient fossilized wood is found in a marine horizon, evidence

of borers is also eventually found. Unfortunately, the characters which distinguish the species, particularly in the genus *Bankia*, are invested mainly in the periostracum which covers the calcareous portion of the pallets, and this is not preserved in fossils. Pallets, devoid of periostracum, are similar in appearance, and so it is usually impossible to relate fossil forms definitely with any one living species.

Inferred relationships of Recent genera of the Teredinidae are shown diagrammatically in Figure E196.



FIG. E187. Pholadidae (Martesiinae) (p. N716).

Subfamily TEREDININAE Rafinesque, 1815

[nom. transl. Stoliczka, 1871, p. 11 (ex Teredaria RAFINESQUE, 1815)]

Wood-borers with posterior adductor muscle much larger than anterior one and without muscular collar surrounding body posterior to shell. Calcareous tube lining burrow, varying greatly in thickness but never as heavy as in Kuphinae. Digestive tract elongate, esophagus short, anterior portion of stomach and crystalline style in front of posterior adductor muscle; caecum and intestine extending posteriorly; intestine not transversing heart but passing beneath it, around posterior adductor muscle, and opening into anal canal. Length of gills, as well as size and type of stomach and posterior caecum, variable. These are important in generic classification and probably indicate type of feeding. Pallets nonsegmental in structure, composed of calcareous base covered by periostracum; blade increased in size by addition of material over entire surface. Eoc.-Rec.

Teredo LINNÉ, 1758, p. 651 [*T. navalis; SD ICZN, 1926, opin. 94] [=Teredigenus RENIER, 1807, pl. vii (obj.) (ICZN, work rejected); Toredo MAY, 1929, p. 652 (nom. null.)]. Pallets variable in shape, but with blade always in one piece, periostracum usually thin and closely adhering to calcareous base (in some species may extend beyond calcareous portion distally as narrow border, but never forms cap, as in Lyrodus); blade usually sheathing stalk. Siphons usually separate. Young, in all species examined to date, carried in brood



FIG. E188. Pholadidae (Martesiinae) (p. N716-N717).
pouch dorsal to gills. Anatomy generally similar to *Lyrodus*. [The genus has been divided into numerous subgenera which are probably of little

value, as intergrades are constantly being found.



FIG. E189. Pholadidae (Martesiinae) (p. N717).

These, however, are listed and their type species figured.] *Eoc.*, Eu.(Eng.-Belg.-France)-*Rec.*, cosmop.

- T. (Teredo) [=Zopoteredo BARTSCH, 1923, p. 96 (type, Teredo (Zopoteredo) clappi; OD); T. (Austroteredo) HABE, 1952, p. 249 (type, Teredo (Teredo) parksi BARTSCH, 1921, p. 28; OD)]. Pallets white with thin pale yellow to dark brown periostracum covering distal portion of blade; distal margin of outer face U- or V-shaped, but varying from U-shaped to nearly straight on inner margin. Eoc.-Rec., cosmop.—Fio. E197,1. *T. (T.) navalis LINNÉ, USA(N.Y.); 1a,b, LV ext. and int.; 1c.d, pallet, outer and inner faces (923).
- T. (Coeloteredo) BARTSCH, 1923, p. 99 [*T. (C.) mindanensis; OD]. Pallet blade wedge-shaped, convex on outer surface, concave to flat on inner surface and with deep cup extending nearly to stalk, which is short and swollen at base. Rec., IndoPac.—FIG. E197,2. *T. (C.) mindanensis, Philip.; 2a,b, RV ext. and int.; 2c-e, pallet, outer and inner faces and side (holotype) (923).
- T. (Pingoteredo) IREDALE, 1932, p. 30 [*Teredo shawi IREDALE, 1932, p. 30; OD] [=Pinguiteredo HABE, 1952, p. 250 (nom. null.)]. Pallets similar in shape to Teredo (Teredo) but with thick periostracum extending beyond calcareous base, both laterally and distally (best seen with transmitted light). Rec., temp. and trop. seas.——Fic. E197,3. *T. (P.) shawi IREDALE, Australia; 3a,b, LV ext. and int.; 3c-e, pallet, outer and inner faces and side; 3f,g, pallet of young, outer and inner faces (paratypes) (923).
- Bactronophorus TAPPARONE-CANEFRI, 1877, p. 290 [nom. subst. pro Calobates Gould, 1862, p. 283 (non KAUP, 1829)] [*Teredo thoracites Gould, 1862, p. 283; OD]. Pallets asymmetrical, basal portion of blade more or less triangular, with shallow cup from which issues pustulose, calcareous, dagger-like blade. Siphons united except at tip, surrounded by wide mantle collar. Heart anterior, extending from posterior adductor muscle about 0.3 length of animal. Digestive system with globular stomach and large, thin-walled caecum. Gills broad and flattened ventrally with welldeveloped food groove. Rec., IndoPac.-FIG. E198,1. *B. thoracites (GOULD), Australia; 1a,b, RV ext. and int.; 1c,d, pallet, outer and inner faces (923).
- Dicyathifer IREDALE, 1932, p. 28 [*Teredo manni WRIGHT in CALMAN, 1920, p. 395 (=D. caroli IREDALE, 1936, p. 38, =T. manni WRIGHT, 1866, p. 565); OD] [=Pseudodicyathifer TCHANG, TSI & LI, 1958 (type, Teredo manni WRIGHT, 1866; OD)]. Pallets simple, solid, almost entirely calcareous, blade more or less triangular in outline, stalk long and heavy. Inner face of blade flat, outer face convex with shallow cup which is partially or almost completely divided by central, longitudinal ridge.

Shell with very broad anterior slope, disc narrow and posterior slope reduced in mature specimens, typical in young. Tube thick, solid and divided posteriorly. Siphons separate. Mantle collar around



Fig. E190. Pholadidae (Martesiinae) (1), (Xylophagainae) (2) (p. N717, N722).



Fig. E191. Pholadidae (Jouanettiinae) (p. N718-N719).

siphons narrow, rather muscular. Gills broad, truncated and extending from posterior tip of gonads to base of siphons. Branchial groove lateral and well developed. Labial palps attached. Stomach globular, caecum short and bulbous, intestine making simple loop around it; digestive gland large, extending posteriorly beyond caecum. Gonads mainly posterior to digestive glands. Heart anterior, about half length of animal; ventricle short and broad; auricles long, tapering and red-brown in color. Kidney large and dorsal to heart. Rec., -FIG. E199,1. *D. manni (WRIGHT), IndoPac.---Singapore; 1a,b, LV ext., int. (apophysis broken); 1c, RV ant.; 1d, LV post.; 1e,f, pallet, outer and inner faces; 1g, entire animal, showing anatomical characters of genus with section cut out, $\times 2$ (923). Lyrodus Gould in Gould & BINNEY, 1870, p. 34 [*Teredo chlorotica Gould, 1870, p. 33 (=T. pedicellata DE QUATREFAGES, 1849, p. 26, non DÖRING, 1885); OD] [=Teredops BARTSCH, 1921, p. 26 (type, T. diegensis BARTSCH, 1916, p. 48; OD); Cornuteredo Dall, Bartsch & Rehder, 1938, p. 209 (type, T. (Cornuteredo) milleri Dall, Bartsch, & Rehder, 1938, p. 210, =T. affinis DESHAYES, 1863, p. 6; OD)]. Pallets with calcareous base and pronounced brown to blackish periostracal cap which can readily be separated from base; calcareous portion narrowly to broadly rounded at distal end and commonly marked with growth lines. Distal margin of periostracal



FIG. E192. Pholadidae (Jouannetiinae) (p. N720).

cap may be straight, broadly curved, or have lateral horns; cap may be solid or have bubble-like cavity which usually breaks open in old specimens, allowing cavity to become filled with debris which solidifies and produces a knoblike process. Siphons short and separate, gills long, bladelike, stomach elongate, caecum large, intestine making simple loop around caecum. Young carried in brood pouch dorsal to gills until veliger stage. Rec., cosmop. in temp. and trop. seas .---- FIG. E200, 1-3. *L. pedicellatus (DE QUATREFAGES), Br. Is. (1), USA(Calif.) (2), USA(Hawaii) (3); 1a,b, LV ext., int.; 1c-e, pallet, outer and inner faces, lat.; 2a-e, corresponding views of holotype of L. diegensis (type species of Teredops); 3a-d, RV ext., int., outer and inner face of pallet, holotype of L. milleri (=lectotype of L. affinis, type species of Cornuteredo) (923).

Neoteredo BARTSCH, 1920, p. 69 [*Teredo (Neoteredo) reynei BARTSCH; OD]. Pallets simple, broadly oval, solid, slightly cupped at distal end and usually greatly eroded. Posterior end of animal with 2 long fleshy lappets on dorsal surface. *Rec.*, N.S. Am.-W.Afr.——Fig. E201,1; E202,1. *N. reynei (BARTSCH), Surinam; E201,1, entire animal (61 cm. long); E202,1*a,b*, RV ext., int. (apophysis lost); E202,1*c-e*, pallet, outer and inner faces, side view (holotype) (923).

Psiloteredo BARTSCH, 1922, p. 36 [*Teredo dilatata STIMPSON, 1851, p. 113 (=T. megotara HANLEY, 1848, p. 77); OD] [=Dactyloteredo Moll, 1941, p. 193 (type, Teredo megotara HANLEY, 1848, p. 77; SD Moll, 1952, p. 83)]. Pallets broad to elongate oval in outline, solid, almost entirely calcareous, and with short stalk. Blade thick at base, becoming thin at distal margin, slightly concave on inner face, convex on outer; outer face variable, usually with moderate to deep thumbnail-like depression, paddle-like, or with slight depression and 2 finger-like projections. Valves with prominent condyles; the posterior slope moderate to large and usually flaring. Tubes probably concamerated at posterior end. Siphons united for most of their length. Gills extending from base of siphons to visceral mass; intestine making simple loop around the caecum. Rec., cosmop. in temp. and trop. seas .- Fig. E162,2. P. healdi (BARTSCH), Surinam; entire animal showing major features of anatomy (923).-Fig. E203,2a-d. *P. megotara (HANLEY), Brit. Is. (lectotype); 2a,b, LV ext., RV int., 2c,d, outer and inner face of pallet (923).-Fig. E203,2e-h. P. megotara excisa (JEFFREYS), Brit. Is. (lectotype) [=deformed P. megotara]; 2e,f, LV ext., LV int. showing typical large dorsal condyle but reduced deformed posterior slope; 2g,h, outer and inner face of pallet (923).



FIG. E193. Pholadidae (Jouannetiinae) (p. N720).



FIG. E194. Pholadidae (Jouannetiinae) (p. N720).

Teredora BARTSCH, 1921, p. 26 [*Teredo malleolus TURTON, 1822, p. 255; OD] [=Malleolus GRAY, 1847, p. 188 (obj.) (non RAFINESQUE, 1815; nec EHRENBERG, 1838)]. Pallets narrowly to broadly oval in outline with short stalk; blade thin, convex on outer, concave on inner face, outer face with small to large, usually deep, thumbnail-like depression which is marked with broadly curved, concentric growth lines. Thickened area at base of pallet smooth. Stalk extending only to base of depression. Distal end of tube concamerated. Shell usually with small, high posterior slope. Siphons united. Gill lamellae bladelike, extending length of animal from base of siphons to mouth. Heart anterior, with short broad ventricle and small auricles. Stomach transitional, caecum doubling on itself. Intestine short, making only simple loop around caecum. Rec., cosmop.—Fic. E204,1,2. *T. malleolus (TURTON), Eng.; Ia,b, LV ext., RV int.; Ic-e, pallet, outer and inner face, side view; If,g, pallet, outer and inner face of lectotype (malformed); 2, semidiagrammatic view of entire animal showing anatomical characters of genus (from Sénégal) (923).

Teredothyra BARTSCH, 1921, p. 26 [*Teredo (Teredothyra) dominicensis BARTSCH, 1921, p. 26, 30; OD] [=Ungoteredo BARTSCH, 1927, p. 544 (type, Teredo (Ungoteredo) matacotana BARTSCH, 1927, p. 544; OD); T. (Idioteredo) TAKI & HABE, 1945, p. 115 (type, Teredo (Teredothyra) smithii BARTSCH, 1927, p. 540)]. Blade of pallets composed of 2 elements, basal portion forming broad to elongate cup with secondary divided conelike element within it; stalk of pallet, which is sheathed by basal cone, extending into blade only as far as base of inner cone. Siphons long and separated. Gill long, lamellae thin and bladelike; heart anterior, extending beneath posterior adductor muscle. Digestive system with globular stomach, small caecum which folds on itself, and short intestine. Rec., warm temp. and trop seas.-Fig. E205, 1,2. *T. dominicensis (BARTSCH), W.Indies; 1a,b, LV ext., int.; 1c, distal end of tube showing division and thickening; 1d,f, outer faces of pallets; 1e,g, inner faces of pallets; 1h, side view of pallet (1a-h, holotype of T. atwoodi BARTSCH, =T. dominicensis, adult); 2a,b, RV ext., int.; 2c, distal end of tube; 2d-f, pallet, outer and inner face, side



FIG. E195. Pholadidae (Xylophagainae) (p. N721-N722).



FIG. E196. Diagrammatic representation of relationships of living genera of Teredinidae (923).

view (2a-f, T. dominicensis, holotype, young specimens) (923).

Uperotus GUETTARD, 1770, p. 126 [*Teredo clava GMELIN, 1791, p. 3748; SD LAMY, 1927, p. 275] [=Fistulana LAMARCK, 1799, p. 90 (obj.) (non MÜLLER, 1776, nec BRUGUIÈRE, 1789; Fistulanigenus RENIER, 1807, pl. 7 (obj.) (ICZN, work rejected); Guetera GRAY, 1840, p. 42 (nom. nud.), 1847, p. 188 (type, Fistulana corniformis LAMARCK, 1799, =T. clava GMELIN, 1791; OD); Hyperotus HERRMANNSEN, 1847, p. 671 (nom. van.); Hyperotis PAETEL, 1875, p. 99 (nom. null.); Guettera H. ADAMS & A. ADAMS, 1856, p. 333 (nom. null.); Glumebra IREDALE, 1936, p. 42 (obj.) (type, G. elegans, =T. clava GMELIN; OD)]. Pallets oval to rectangular in outline with short heavy stalk, basal portion of blade nearly smooth, distal portion with pronounced radiating ribs. Shells with anterior and posterior slopes greatly reduced or typical in shape, with small, high posterior slope. [Species in this genus are usually obtained from dredged nuts or wood or from drift cast ashore. They are probably not an intertidal group. The anatomy of this species in this genus is very close to that of Teredora, gill extending from base of siphons to mouth (Fig. E204,2).] Rec., IndoPac.-

E.Pac.-E.Atl.——FIG. E206,1. *U. clavus (GME-LIN), Australia(Queensl.) (from a nut); la,b, RV (holotype of Glumebra elegans IREDALE), ext., int., $\times 5$; lc, cluster of tubes, $\times 0.9$; ld-f, pallet, outer and inner face, side view, $\times 3$ (435).——FIG. E206, 2a-g. U. lieberkindi ROCH (from dredged wood) off Rio de Oro, Afr.; 2a,b, RV (holotype) ext., int.; 2c-g, pallet, outer and inner face, side view (923).

Zachia BULATOV & RZHAVSHCHIKOV [RJABTSCHI-KOFF], 1933, p. 166 [*Z. zenkewitschi; SD HABE, 1952, p. 255]. Shells greatly reduced; pallets similar to Spathoteredo. [Species living in roots of Phylospadix, apparently stenomorphic and malformed.] Rec., N.Pac.—FIG. E207,1. *Z. zenkewitschi, USSR(Vladivostok); 1a, ant. view of opposed valves, ×20; 1b, RV ext., ×20; 1c,d, outer and inner face of pallet, ×40 (1a-d, holotype) (90).

Subfamily BANKIINAE Turner, 1966

Wood-borers with pallets composed of numerous segments which may be very closely packed and indistinct (e.g., Nototeredo, Spathoteredo), distinct but fused



FIG. E197. Teredinidae (Teredininae) (p. N725-N726).



FIG. E198. Teredinidae (Teredininae) (p. N726).

(e.g., Nausitora), or widely spaced and conelike (e.g., Bankia). Blade of pallet increased in size by addition of new segments at distal end. Valves similar to those of Teredininae. Paleoc.-Rec.

Bankia GRAY, 1842, p. 76 [*Teredo bipalmulata LAMARCK, 1801, p. 129; SD GRAY, 1847, p. 188] [=Xylotrya LEACH in GRAY, 1847, p. 188 (non MENKE, 1830; nec GRAY, 1842) (type, Teredo bipalmulata LAMARCK, 1801; OD); Xylotyra DE QUATREFAGES, 1849, p. 28 (nom. null.); Xylotria Deshayes, 1860, p. 114 (nom. null.); Xylotya VON MARTENS, 1880, p. 331 (nom. null.); Hylotrya CLESSIN, 1893, p. 82 (nom. null.)]. Pallets elongate, composed of numerous conelike elements built upon central stalk which extends length of blade, cones separate and easily removed from stalk, base of cones calcareous, with periostracal covering extended as border which varies greatly in width, may be smooth or fringed, and may be produced laterally as awns. [The genus has been divided into numerous subgenera on the basis of ornamentation of the periostracal border and the presence or absence of awns, but these taxa prob-



ably have small value owing to the presence of intergrades. However the subgenera are listed and a figure of the type species given.] The periostracum is not preserved in fossils, so usually the best one can do is refer to a fossil as *Bankia* sp. *Paleoc.-Rec.*, cosmop.

B. (Bankia) GRAY, 1842 [=Bankiura MOLL, 1952, p. 8, 42, 85 (obj.)]. Margin serrated on inner face, smooth on outer face and produced in unequal lateral awns, those on one side being 2 to 3 times length of other. *?Paleoc., Rec.,* IndoPac. ——FIG. E208,1. *B. (B.) bipalmulata (LA-MARCK), New Hebrides; 1a,b, pallet, outer and inner faces (920).

- B. (Bankiella) BARTSCH, 1921, p. 25-26 [*Bankia (Bankiella) mexicana (=B. gouldi BARTSCH, 1908); OD]. Margins of cones smooth, lateral awns long and thin. Margin on inner face wide, forming "web" between awns. Rec., cosmop.— FIG. E208,2. *B. (B.) gouldi BARTSCH, USA(Va.); 2a,b, pallet, outer and inner faces (920).
- B. (Clupibankia) MOLL, 1952, p. 42, 85 [*Bankia



FIG. E200. Teredinidae (Teredininae) (p. N727-N728).



FIG. E201. Teredinidae (Teredininae) (p. N728).

barthelowi BARTSCH, 1927, p. 537; OD]. Calcareous portion of cones wide on inner face so that cones overlap one another; margin serrate on outer face, smooth on inner face. *Rec.*, IndoPac.— FIG. E208,4. *B. (C.) barthelowi BARTSCH, Philip. Is.; outer face of pallet (923).

- B. (Liliobankia) CLENCH & TURNER, 1946, p. 17 [*B. (L.) katherinae (=B. campanellata MOLL & ROCH, 1931); OD]. Margin of cones wide, smooth and produced laterally to form broad triangular awns. Embryonic cones separated. Rec., subtrop. and trop. seas.——FIG. E208,5. *B. (L.) campanellata MOLL & ROCH; 5a,b, pallet, outer and inner faces (920).
- B. (Lyrodobankia) Moll, 1941, p. 200 [*Nausitora kamiyai Roch, 1929, p. 17 (=young B. carinata GRAY, 1827); SD TURNER, 1966] [=Bankiopsis CLENCH & TURNER, 1946 (type, B. (B.) caribbea (=B. carinata GRAY) (obj.);

OD)]. Margin smooth, equal width on both inner and outer faces, and produced laterally into short, blunt points. Embryonic cones closely packed and covered by periostracal cap. Rec., temp. and trop. seas.——FIG. E208,3. *B. (L.) carinata (GRAY), USA(Fla.) (3a,b), Japan (3c,d); 3a,b, pallet, outer and inner face (holotype of B. (Bankiopsis) caribbea CLENCH & TURNER) (920); 3c,d, pallet, outer and inner face (holotype of Nausitora kamiyai Roch, = young B. carinata GRAY) (923). B. (Neobankia) BARTSCH, 1921, p. 26 [*B. (N.) zeteki; OD] [=Deviobankia IREDALE, 1932, p. 33 (type, Bankia debenhami IREDALE, 1932; OD)]. Margin of cones wide, even, serrated on both inner and outer faces and not produced laterally to form awns. Rec., warm temp. and trop. seas.——Fig. E208,6. *B. (N.) zeteki, Panama; 6a,b, pallet, outer and inner faces (920). B. (Plumulella) CLENCH & TURNER, 1946, p. 22 [*B. fimbriatula Moll & Roch, 1931; OD]. Mar-

- [*5. *jimornatula* MoLL & Roch, 1951; OD]. Matgin of cones serrated on both inner and outer faces and produced laterally into long serrated awns. *Rec.*, temp. and trop. seas.——Fig. E208, 7. *B. (P.) *fimbriatula* MoLL & Roch, Haiti; 7*a,b*, pallet, outer and inner faces (920).
- Nausitora WRIGHT, 1864, p. 452 [*N. dunlopei; OD] [=Nausitoria TRYON, 1868, p. 20 (nom. null.); Naucitora SowEREY, 1887, pl. 469, fig. 3 (nom. null.); Nausitoria Roch & MOLL, 1929,



FIG. E202. Teredinidae (Teredininae) (p. N728).



FIG. E203. Teredinidae (Teredininae) (p. N728, N737).

p. 17 (nom. null.); Inequarista IREDALE, 1932, p. 37 (type, Nausitora messeli IREDALE, =N. dunlopei WRIGHT; OD); Nausitorella MOLL, 1952, p. 84 (type, T. fusticula JEFFREYS, 1860, p. 125;



FIG. E204. Teredinidae (Teredininae) (p. N729).



FIG. E205. Teredinidae (Teredininae) (p. N729-N730).

OD)]. Pallets elongate, composed of closely packed, fused, conelike elements built on central stalk; periostracal covering commonly extended as awns, particularly on proximal portion of blade, distal portion of blade with asymmetrical, papillose, calcareous covering which is usually worn off in old specimens. Siphons united for about three-fourths of their length. Gills short, broad and flat; heart small and posterior, located at anterior end of

© 2009 University of Kansas Paleontological Institute

gills posterior to visceral mass. Stomach elongate; caecum very large, intestine making simple loop around it. *Rec.*, trop. and subtrop. seas, usually in brackish water.——FIG. E209,1. *N. dunlopei, Australia; *1a,b*, LV ext., int.; *1c,d*, pallet, outer and inner faces (923).

Nototeredo BARTSCH, 1923, p. 100 [*Teredo (Nototeredo) edax HEDLEY, 1895, p. 501; OD] [=Phylloteredo Roch, 1937, p. 169 (type, Teredo norvagica SPENGLER, 1792, p. 102; OD)]. Pallets elongate oval to broadly oval in outline with short stalk; blade thin, convex on outer and concave on inner face; composed of soft, friable calcareous material laid down in closely packed segments separated by thin layers of periostracum which may extend laterally as small awns, entire surface of blade with thin layer of periostracum. Stalk extending length of blade. Siphons united for about



FIG. E206. Teredinidae (Teredininae) (p. N730).



FIG. E207. Teredinidae (Teredininae) (p. N730).

half their length. Gills about 0.4 length of animal, lamellae broadly U-shaped. Labial palps free at tips. Stomach globular, caecum large, and intestine extremely long and convoluted. Heart short, located at anterior end of gills, posterior to visceral mass; ventricle short and broad, auricles short; posterior aorta long, extending from ventricle to posterior adductor muscle. *Paleoc.-Rec.*, worldwide.——Fig. E203,1. *N. edax (HEDLEY), Rec. S.Australia; 1a,b, LV ext., int. (paratype); 1c,d, pallet, outer and inner face; 1e, post. end of young specimen (923).

Spathoteredo Moll, 1928, p. 282 [*Teredo bataviana MOLL & ROCH, 1931, p. 207; (=T. obtusa Sivickis, 1928, p. 290); SD TURNER, 1966, p. 122] [=Spathoteredo Rocн, 1937, р. 173 (obj.)]. Blade of pallets more or less rectangular in outline, truncated at anterior end and sheathing stalk for about 0.3 of its length. Stalk extending well up into blade which is thick at anterior end and tapers posteriorly. Periostracum dark brown, usually appearing as band across middle of blade on outer face, distal portion of outer face covered with pustulose, calcareous incrustation. Siphons with muscular collar at their base, united for most of their length, incurrent siphon with rather elaborate branched papillae. Gills long, narrowly U-shaped. Heart median, ventricle broad, auricles long and tapering. Stomach elongate, caecum large, gonads dorsal and posterior to it, intestine making loop around it. Rec., IndoPac.-S.Atl.-Fig. E210,1. *S. obtusa (SIVICKIS), Java; 1a,b, LV ext., int.; 1c-e, pallet, outer and inner face, side view (923).



FIG. E208. Teredinidae (Bankiinae) (p. N732-N734).

Subfamily KUPHINAE Tryon, 1862 [Kuphinae Tryon, 1862, p. 455]

Large mud- and possibly wood-borers having greatly reduced shells and strong muscular collar surrounding body at posterior end of shell; anterior and posterior adductor muscles nearly equal in size; condyles, chondrophore and ligament reduced, and posterior end of shell covered by muscular collar. Digestive tract greatly reduced, esophagus extending posterior to muscular collar, crystalline style and stomach located at posterior end of visceral mass;



Fig. E209. Teredinidae (Bankiinae) (p. N734, N736).



FIG. E210. Teredinidae (Bankiinae) (p. N737).

caecum lacking. [Unlike all other Teredinidae, the heart has a large ventricular bulb. The intestine passes through this bulb and around the posterior adductor muscle; it becomes imbedded in the thickened mantle for the length of the pericardial cavity and then opens into the epibranchial chamber behind the heart. The Kuphinae apparently are all filter-feeders.] *?Eoc., Rec.*

Kuphus GUETTARD, 1770, p. 139 [*Serpula polythalamia LINNÉ, 1758; SD GRAY, 1847, p. 188] [=Furcella LAMARCK, 1801, p. 104 (obj.); Septaria LAMARCK, 1818, p. 436 (non FÉRUSSAC, 1807) (obj.); Clossonnaira FÉRUSSAC, 1822, p. xiv (referring to cloissonnaire and Septaria LAMARCK); Clausaria MENKE, 1828, p. 73; Cloisonaria ADAMS, 1858, p. 648 (nom. van.); Cloissonaria PAETEL, 1875, p. 46 (nom. van.); Cloissonaria PAETEL, 1890, p. 6 (nom. van.); Cuphus AGASSIZ, 1846, p. 108 (nom. van.); Cyphus FISCHER, 1887,



FIG. E211. Teredinidae (Kuphinae); 1, Kuphus, entire animal, ×0.5; 2, same, morphology of soft parts (923).

p. 1158 (nom. van.); Kyphus Herrmannsen, 1847, p. 569 (nom. van.)]. Pallets simple, solid, almost entirely calcareous; blade triangular in outline with long heavy stalk, flat on inner face and with shallow cup. Shells relatively small, denticulated ridges of anterior slope greatly reduced; posterior slope reduced; tube very thick, solid, divided posteriorly. [The morphology of the soft parts is shown in Figure E211,2. Though the genus has been reported from the middle Eocene, this is on the basis of the tubes only. The pallets and shells of Kuphus have never been found as fossils.] ?Eoc., Rec., IndoPac.—Fig. E211,1,2. *K. polythalamia (LINNÉ), Rec., Solomon Is.; 1a, sketch of entire animal 50.5 cm. long, $\times 0.5$; 2a, semidiagrammatic long. sec. showing relationship of organs; 2b, ant. portion enl. (923).

Subfamily UNCERTAIN

Genera based on shells and tubes only cannot be classified as to subfamily within the Teredinidae.

Eoteredo BARTSCH, 1923, p. 98 [*E. philippinensis; OD]. Name based on shells only, distinguished by projection of apophyses from beneath shelf rather than umbos. [This is an age factor which may be found in the shells of several genera.] *Rec.*, Philip. Is.—Fig. E212,1. **E. philippinen*sis, Mindanao; 1*a,b*, LV ext., RV int. (apophysis broken) (holotype), $\times 6$ (923).

- Terebrimya STEPHENSON, 1952, p. 141 [*T. lamarana; OD]. Shells typical of family; pallets unknown. U.Cret.(Cenoman.), USA(Tex.).—Fig. E213,1. *T. lamarana, Woodbine F.(Templeton Mbr.), Lamar Co.; 1a,b, LV ext., RV ext., in matrix (holotype), ×4; 1c, tube, ×1 (890).
- Teredinopsis FUCH, 1878, p. 39 [*T. problematica; OD]. Based on shells and cluster of tubes similar to Uperotus clavus; pallets unknown. Quat., Suez. ——FIG. E214,1. *T. problematica; 1a,b, LV ext., int., X3; 1c, anterior view of opposed valves; 1d, cluster of tubes; all X3 (1a-c, holotype) (332).
- Teredolites LEYMERIE, 1842, p. 2 [*T. clavatus; OD] [=Teredolites LEYMERIE, 1841, p. 341 (nom. nud.); Teredolithes HERRMANNSEN, 1852, p. 131 (nom. null.)]. Name based on tubes only. [Close to Uperotus clavus GMELIN.] Cret., Eu.— FIG. E214,2. *T. clavatus, France(Spatangues, Dept. l'Aube); 2a,b, basal and lat. views of cluster of tubes (holotype), ×1 (540).

Teredolithus BARTSCH, 1930, p. 460. [Collective



FIG. E212. Teredinidae (Subfamily Uncertain) (p. N740).

group name for species of Teredinidae that cannot be placed generically.]

Turnus GABB, 1864, p. 145 [*T. plenus; OD]. Shell thin, pholadiform; internally bearing rib which rises in apex, and passes downward and backward to basal margin in same manner as umbonal groove and posterior to it. Accessory plates unknown. Tube simple, thin. [This genus was placed in the Teredininae by GABB and considered to be a link with the Pholadidae. Until more material is available the genus cannot be positioned.] Cret., N.Am.—Fig. E213,2. *T. plenus, USA(Calif.); (holotype), $\times 2$ (333).

INVALID GENERA

The following names for hypothetical genera are invalid (ICZN Code, 1961, Art. 1).

Bicornia May, 1929, p. 642, 665. Microvexillum May, 1929, p. 642, 665. Proteredo May, 1929, p. 664, 665.

GENERA ERRONEOUSLY ASSIGNED TO TEREDINIDAE

Polorthus GABB, 1861, p. 366 [*P. americana; OD]

[=Polarthus STOLICZKA, 1871, p. 14 (nom. null.); Kummelia STEPHENSON, 1936, p. 60 (obj.)]. Belongs to Gastrochaenidae.

Order HIPPURITOIDA Newell, 1965

[Diagnosis by N. D. NEWELL]

Rudists and pachydonts; thick-shelled, aberrant heterodonts, primitively equivalved, with few thick and amorphous hinge teeth; mainly attached and strongly inequi-



FIG. E213. Teredinidae (Subfamily Uncertain) (p. N740-N741).



FIG. E214. Teredinidae (Subfamily Uncertain) (p. N740).

valved, tending to gyrate or conical, operculate and edentulous forms resembling solitary corals. *M.Sil.-U.Cret.(Maastricht.)*.

The Hippuritoida are cosmopolitan bivalves especially characteristic of low latitudes where they dominate extensive reefs.

Superfamily MEGALODONTACEA Morris & Lycett, 1853

[Diagnosis by N. D. NEWELL]

Characters of family Megalodontidae. M. Sil.-L.Cret.

Family MEGALODONTIDAE Morris & Lycett, 1853

[nom. correct. ZITTEL, 1881 (pro Megalonidae MORRIS & LYCETT)] [Materials for this family prepared by L. R. Cox (Mesozoic) and Aurèle LARocque (Paleozoic)]

Shell mostly medium-sized to large, thick, equivalve except in some species of *Megalodon* and in *Pomarangina*, gibbose, subtrigonal or ovate, usually with prosogyrous beaks; hinge plate massive, bearing in each valve one to several cardinal teeth which are commonly rather amorphous and not all of which diverge from beak; lateral teeth present in some genera; ligament external, opisthodetic, nymphs heavy; pallial line entire; anterior adductor scar deep, situated in relatively dorsal and marginal position, just below anterior end of hinge plate; surface usually smooth or at most with weak concentric folds, but with radial ribs in a few forms. *M.Sil.-L.Cret*.

Megalodon J. DE C. SOWERBY, 1827, p. 131 [*M. cucullatus; M] [=Megaladon LINK, 1830 (nom. null.); Megalodonta GOLDFUSS, 1832 (nom. van.); Megalodus GOLDFUSS, 1837 (nom. van.) (nom RAFINESQUE, 1815); Eumegalodon GUEMBEL, 1862 (obj.)]. Shell medium-sized to large, subtrigonal or ovate, gibbose; beaks anterior, strongly prosogyrous; hinge plate very massive; cardinal teeth varying in number, from 1 or 2 in LV and 1 to 3 in RV, owing to suppression or duplication of elements of dentition; posterior adductor scar on slightly raised platform; surface smooth or concentrically rugose (Dechaseaux in Piveteau, 1952, p. 293, 333). Dev.-U.Trias.(Rhaet.).

- M. (Megalodon). Equivalve, valves more or less carinate posteriorly; LV with strong, elongate, acutely triangular, commonly grooved posterior cardinal tooth close to posterodorsal margin and tuberculiform anterior cardinal tooth (represented by 2 unequal teeth in some specimens) near anterior end of hinge plate; RV with strong, subtriangular, commonly pustulose or transversely grooved, mesially placed cardinal tooth received in deep, broad recess between 2 main teeth of LV, and in some specimens with very thin, elongate posterior cardinal; traces of elongate lateral tooth adjacent to posterior margin beyond hinge plate seen in some RV's. Dev.-Trias., cosmop.——Fig. E215,4. *M. (M.) cucullatus Sowerby, Dev., Paffrath, Ger.; LV int., showing dentition, $\times 1$ (379).
- M. (Neomegalodon) GUEMBEL, 1862, p. 362 [*Cardium triquetrum WULFEN, 1793, p. 48; SD STOLICZKA, 1871, p. 275] [=Tauroceras Schaf-HAEUTL, 1854 (non HOPE, 1840); Neomegalodus FRECH, 1904 (nom. van.)]. Equivalve or slightly inequivalve, presence of posterior carina variable; hinge plate narrowing posteriorly; LV without distinct posterior cardinal tooth but with 1 or 2 anterior teeth representing tuberculiform tooth of M. (Megalodon); when 2 such teeth are present these are commonly subequal and radially elongated; RV with variable, acutely triangular posterior cardinal tooth received in recess behind tooth or teeth of LV and with 2 anterior teeth which are commonly subequal and radially elongated. U.Trias., cosmop .- FIG. E216,1. *M. (Neomegalodon) triqueter (WULFEN), U.Trias. (Rhaet.), Aus.; 1a,b, RV int., LV int., showing dentition, $\times 1$ (Guembel, 1862).
- Conchodon STOPPANI, 1865, p. 246 [*C. infraliasicus (=Lycodus cor Schafhaeutl, 1863, p. 375); M] [=Lycodus Schafhaeutl, 1863 (non Quenstedt, 1856); Conchodus TAUSCH, 1891 (nom. van.) (non M'Coy, 1848); Lycodes DALL, 1900 (nom. null.)]. Very large, thick-shelled, about as high as long, with strongly prosogyrous and incoiled beaks and projecting anterior extremity; valves sharply carinate posteriorly; hinge plate massive; RV with massive arcuate or irregularly tripartite main tooth which is situated near anterodorsal margin and is received in broad socket in LV between arms of horseshoe-shaped tooth; in some specimens second and weaker tooth lies between this main tooth and margin in RV; posterior part of hinge plate without distinct teeth; no lateral teeth; anterior adductor scar almost marginal, just below main tooth; posterior scar not observed; surface of shell with weak concentric folds. U.Trias.(Rhaet.), Eu.(N.Alps-S. Alps-Hung.-Carpathians). - FIG. E216,3. *C. cor (Schafhaeutl), S.Alps; 3a, int. mold, $\times 0.3$





FIG. E215. Megalodontidae (p. N742-N743, N745).

(Stoppani, 1865); 3b, ant. part of RV hinge showing tripartite main tooth, $\times 0.3$ (Frech, 1904).

Cumularia SPRIESTERSBACH, 1919, p. 467 [*C. circularis; M]. Small, round-oval, not carinate; umbones depressed, well anterior; 1 stoutly triangular cardinal tooth in each valve, that in RV stronger and fitting behind tooth of LV; no laterals; anterior adductor scar small and deep, posterior scar larger, rounded. M.Dev., Eu.(Ger.).— FIG. E215,5. *C. circularis, ?Honseler beds, Schaf-



FIG. E216. Megalodontidae (p. N743, N745).

feld; 5a, LV int. mold, $\times 1$; 5b, RV dentition, enl. (872).

- Eomegalodus Spriestersbach, 1915, p. 53 [*E. fuchsi: M] [=Eomegalodon Cossmann, 1922 (nom. van.)]. Medium-sized, thick, elliptical, not carinate; umbones anterior, not prominent; lunule small; hinge very thick; LV with 2 cardinal teeth, posterior one heavy, and broad, cuneiform posterior lateral; RV with 1 strong and 1 weak cardinal and lamellar posterior lateral; lower margin of hinge plate of RV thickened into large toothlike pad which projects into LV; anterior adductor scar small, elliptical, deep, striated; posterior scar large, deep; sculpture of fine concentric lines. M.Dev., Eu.(Ger.).-Fig. E215,3. *E. fuchsi, U.Honseler beds, Lenneschiefer, Verneis, near Haspe; RV int., showing dentition and toothlike pad below hinge, $\times 1$ (871).
- Ferrazia REED, 1932, p. 480 [*F. cardinalis; M]. Equivalve; beaks subanterior, strongly prosogyre, incurved; lunule and escutcheon well defined; surface angulated and ornamented with strong radial carinae; each valve with large rounded, longitudinally oval cardinal tooth on narrow thickened hinge plate; ligament opisthodetic, parivincular. Perm., S.Am.(S.Brazil).—FIG. E216,1. *F. cardinalis, Corumbatai F., Rio Claro; 1a,b, RV ext. and hinge views, ×1 (Reed, 1932). [NEWELL]
- Krumbeckia DIENER, 1915, p. 131 [*K. tambangensis (= Pomarangina aff. haydeni DIENER, KRUM-BECK, 1914, p. 256); M]. Medium-sized, oval, gibbose, not carinate; beaks prosogyrous, at anterior 5th of length; hinge plate heavy; RV with single heavy, broadly arched tooth, almost median in position; teeth of LV and muscle scars unknown; ornament of concentric ribs. U.Trias., Indon.(Sumatra).—-Fig. E216,2. *K. tambangensis; 2a,b, ant. view of shell and RV int. showing dentition, $\times 1$ (Krumbeck, 1914).
- Megalomoidea Cox, 1964, p. 43 [*Megalomus canadensis HALL, 1852, p. 343; OD] [=Megalomus Hall, 1852 (non RAMBUR, 1842); Megalomys FISCHER, 1886 (nom. van.; non TROUESSART, 1881); Mewalomus KIRK, 1927 (nom. null.)]. Large, reniform-ovate, thick-shelled, especially in hinge region and along V-shaped area extending posteriorly from it across middle of each valve; valves not carinate; beaks anterior, prosogyrous; hinge plate massive, not undercut, broad and projecting in middle, where in each valve it bears group of transversely elongated teeth variable in number (2-6) and strength; anterior adductor scar as in typical Megalodontidae, 2 small accessory scars on its posterodorsal side; posterior adductor scar obscure; surface smooth except for growth lines (Kirk, 1927, p. 4). M.Sil.(Guelph), E.N.Am.-Alaska.—Fig. E215,2. *M. canadensis (HALL), Ont.(Elora); RV int., $\times 0.7$ (Kirk, 1927).

Pachyrisma MORRIS & LYCETT, 1850, p. 399 [*P. grande; M] [=Cardilla Lycett, 1848 (nom. nud... or error for Cardilia DESHAYES, 1835); Pachyerisma BAYAN, 1874 (nom. van.)]. Medium-sized to large, equivalve, thick-shelled, ovate to subtrigonal, with strongly prosogyrous, more or less anteriorly placed beaks; valves carinate posteriorly; hinge plate, ligamental nymph and teeth heavy; single strong, mesially placed cardinal in LV received in recess between strong posterior cardinal and weak (in some specimens ill-defined) anterior cardinal in RV; well-developed, tuberculiform lateral tooth present near each end of hinge plate in LV and received in sockets above corresponding laterals in RV; anterior adductor scar deep, situated just below anterior lateral tooth. L. Jur.-U. Jur., Eu.

- P. (Pachyrisma). Large, higher than long, beaks terminal in some but not all species; posterior adductor scar on lamina emerging from beneath hinge plate; surface smooth or with traces of radial ribbing. *M.Jur.-U.Jur.*, Eu.——FIG. E217, 2a-c. *P. (P.) grande MORRIS & LYCETT, M.Jur. (Bathon.), Eng.; 2a, RV ext.; 2b, LV hinge, post. lat. tooth broken away; 2c, RV hinge, post. lat. tooth broken away; all $\times 0.7$ (645).——FIG. E217,2d. P. sp. cf. P. (P.) beaumonti ZEUSCHNER, U.Jur.(Tithon.), Czech.; RV hinge showing lat. teeth, $\times 0.5$ (Böhm, 1870).
- P. (Durga) G. BÖHM, 1884, p. 191 [*D. nicolisi; OD]. Medium-sized, trigonally ovate, longer than high, tapering posteriorly; posterior carina sharp; posterior adductor scar not observed; surface smooth, except for growth rugae. L.Jur.(L. Lias.), Eu.(N.Italy-France).——Fig. E217,3. *P. (D.) nicolisi, N.Italy; 3a, RV ext., ×0.7; 3b, RV hinge, defective posteriorly, ×1 (Böhm, 1884).
- P. (Pachymegalodon) GUEMBEL, 1862, p. 375 [*Bucardites chamaeformis VON SCHLOTHEIM, 1820, p. 208; M] [=Pachymegalodus TAUSCH, 1890 (nom. van.)]. Medium-sized, higher than long, acutely subtrigonal; posterior carina sharp, with broad radial sulcus in front of it; posterior adductor scar on lamina, as in P. (Pachyrisma); surface smooth, except for growth rugae. L.Jur. (L.Lias.), Eu.(S.Alps).—Fic. E217, I. *P. (P.) chamaeforme VON SCHLOTHEIM, Yugosl.; 1a,b, RV ext., RV int., $\times 1$ (Tausch, 1890).
- Pachyrismella Cox, 1964, p. 43 [*Cardium septiferum BUVIGNIER, 1843, p. 230; OD]. Mediumsized, subequilateral, slightly longer than high, Cardium-like; beaks not strongly prosogyrous; hinge plate and teeth less heavy and irregular than in Pachyrisma; strong acutely angular posterior cardinal and weak or scarcely developed anterior cardinal present in both valves, main tooth of RV fitting in front of that of LV; lateral teeth and adductor scars as in Pachyrisma, posterior adductor on lamina emerging from be-

low hinge plate; radial ornament absent or obscure. U.Jur.(U.Oxford.), Eu.-SW.Asia(Lebanon). ——FIG. E218,2. *P. septifera (BUVIGNIER), U. Oxford., France; 2a,b, LV hinge, RV ext.; 2c, RV int., all ×0.7 (Buvignier, 1852). Paramegalodus Cox, new genus [cx KUTASSY, 1934,



FIG. E217. Megalodontidae (p. N745).

© 2009 University of Kansas Paleontological Institute

N747

p. 52 (nom. nud., type species cited but no generic diagnosis)] [*Dicerocardium eupalliatum FRECH, 1904, p. 51; OD]. Large, tall, trigonal, hornlike, with very prominent, terminal, pointed,

prosogyrous umbones; internal mold with rounded rib running from near anterior margin almost to umbo, then curving around and descending to posterior end of ventral margin; dentition un-



FIG. E218. Megalodontidae (p. N745-N748).

known. U.Trias.(Rhaet.), Eu.(Hung.)-Asia(Himaayas).——Fig. E218,3a. *P. eupalliatus (FRECH), Hung.; ant. view of int. mold, $\times 0.3$.——Fig. E218,3b,c. P incisus (FRECH), Hung.; 3b, post. view, 3c, RV int. mold, $\times 0.7$ (all Vigh, 1914).

- Pinzonella REED, 1932, p. 482 [*P. illusa; SD Cox, herein] [=Pinzonellopsis MENDES, 1944, p. 58 (type, Pachycardia occidentalis REED, 1929; M)]. Small for family, orbicular or ovate, strongly inequilateral, beaks fairly anterior, not strongly incurved; valves weakly carinate; hinge plate relatively broad and massive, with large, roundedtriangular cardinal tooth in each valve, that of RV fitting in front of LV tooth; weak lamellar lateral tooth close to posterodorsal margin distinguishable in LV of some specimens; surface smooth. Perm. (originally considered Trias.), Corumbatai beds, S.Am.(Brazil).—Fig. E218,1. *P. illusa, São Paulo State; 1a-d, LV ext. and int., RV ext. and int., all ×1.3 (Mendes, 1952).
- Pomarangina DIENER, 1908, p. 64 [*P. haydeni; M]. Ovate, inequilateral, moderately gibbose, thick-shelled, some specimens slightly inequivalve, with RV larger; beaks prosogyrous and incurved; valves carinate posteriorly; dentition and musculature unknown. U.Trias., Asia(Himalayas). Protodiceras G. Вöнм, 1891, p. 19 [*Megalodon pumilus GUEMBEL, 1862, p. 367 (as M. triqueter var. pumilus); OD] [=Prodiceras BERINGER, 1949 (nom. null.)]. Of small-medium size, subtrigonal, about as long as high, with strongly prosogyrous, terminal beaks; valves sharply carinate posteriorly; hinge plate and teeth heavy; LV with weak, elongate, marginal posterior cardinal tooth with its apex close to beak and horseshoeshaped anterior cardinal which is well separated from beak; between them is large, deep, triangular socket for reception of strong RV posterior cardinal, and within 2 arms of anterior tooth is socket for simple RV anterior cardinal; RV an-



FIG. E219. Megalodontidae (p. N748-N749).

terior lateral is feebly developed but posterior laterals are absent; anterior adductor scar deep, located as in *Pachyrisma*; posterior adductor scar not observed; surface smooth. *L.Jur.(L.Lias.)*, Eu. (N.Italy-France).——Fig. E219,1. *P. pumilum (GUEMBEL), N.Italy; *1a*, LV ext., *1b*, LV hinge, both ×1 (Tausch, 1890); *1c*, RV hinge, ×1 (Böhm, 1891).

Pterocardia BAYAN, 1874, p. 338 (ex FAVRE, nom. nud.) [*Cardium buvignieri Deshayes, 1857, p. 49 (syn., C. corallinum LEYMERIE, 1847, non LINNÉ, 1758); SD Cossmann, 1906, p. 292] [=Pterocardium Rollier, 1912 (nom. van.)]. Large, thick-shelled, subrectangular, higher than long, inequilateral, posteriorly sublobate; umbones prominent, beaks anterior to median, but almost orthogyrous; ornament of radial ribbing; hinge plate massive and moderately broad; LV with stoutly triangular, anteriorly placed cardinal, short anterior lateral close to it, and more elongate and distant posterior lateral; RV with 2 obliquely aligned cardinals, posterior and lower one stoutly triangular, anterior and marginal one relatively small, together with anterior and posterior laterals; posterior adductor scar on raised lamina emerging from below hinge plate. M. Jur. (Bathon.)-L. Cret. (Apt.), Eu.-SW.Asia(Syria)-Mex.-Fig. E219,2. *P. buvignieri (DESHAYES), U.Jur.(U.Oxford.), Swiss Jura; 2a,b, RV ext. and int.; 2c, LV int., $\times 0.7$ (de Loriol, 1891).

Superfamily HIPPURITACEA Gray, 1848

[nom. transl. NEWELL, 1965 (ex Hippuritidae GRAY, 1848)] [Materials for this superfamily prepared initially by COLETTE DECHASEAUX, typescript in French translated by R. C. MOORE reviewed and improved by L. R. Cox with advice received from L. J. CHUBB (mainly on occurrence of Caribbean rudists); subsequently (1965-67) extensively revised, with additions of new typescript and illustrations produced by A. H. COOGAN and B. F. PERKINS, as noted in different families. The final version has been referred to the original author to allow expression of any disagreements. The Editor is responsible for integrating the text and illustrations and for accepting the taxonomic framework adopted in the *Treatise*, but with advice received from N. D. NEWELL. Illustrations with reference number 252 are taken by permission from *Traité de paléontologie*, MASSON et CIE (DECHASEAUX, 1952).] [Diagnosis of superfamily by COLETTE DECHASEAUX]

Inequivalve bivalves, most commonly attached to substrate by either right or left valve, but in rare instances free; solitary or gregarious. Hinge with two teeth and one socket in free valve and two sockets and one tooth in attached valve, except in *Diceras*, in which right valve invariably has two teeth and left valve only one. Two adductor muscles present, inserted directly on shell wall or on projecting myophores. *U.Jur.(U.Oxford.)-U.Cret.(Maastricht.).*

INTRODUCTION

By Colette Dechaseaux

[Centre National de la Recherche Scientifique, Laboratoire de Paléontologie à la Sorbonne, Paris, France]

Members of the order Hippuritoida and superfamily Hippuritacea collectively are designated commonly as rudists. They were solitary or gregarous bivalve mollusks which generally were attached to the substrate by the extremity of one of their valves. Their highly varied external and internal morphological features separate them widely from all other representatives of the class, whether fossil or Recent.

From the time (1775) when PICOT DE LAPEIROUSE collected and figured fossil shells "called horns by the country folk because of their close resemblance to actual horns" (Hippurites) and "petrified vaseshaped oysters" (Sphaerulites) until 1825, naturalists were uncertain as to how they should be classified (Fig. E220). The diagnosis given in 1819 by LAMARCK (505, v. 6, p. 230), who introduced the term "les Rudistes," well illustrates the ignorance of contemporary scholars concerning the organization of these "shelly objects appearing to have some affinities with the oysters, but clearly distinguished from this group in that there is no trace of hinge, ligament, or muscle scars, and no indication as to where these were situated."

LAMARCK included certain brachiopods in his "rudists," but he omitted the hippurites because he considered them to be Cephalopoda. Picot de Lapeirouse was the first to include these "petrified oysters" with bivalves. Cuvier (1817) also suggested a relationship with this group, without giving convincing reasons. It was not until 1825 that Deshayes and DE BLAINVILLE established that Sphaerulites and Hippurites should be classified as Bivalvia. This conclusion was opposed, however, by various naturalists, who continued to class the rudists as brachiopods, corals, or cirripeds. The study of rudists has been continued by S. P. Woodward, Saemann, Bayle, Parona, Toucas, Douvillé, and many others, who have made great advances in understanding these fossils; even so, many problems presented by these curious forms are not yet solved.

Bivalvia-Heterodonta



FIG. E220. Morphological features of rudists (hippuritids and radiolitids).

- 1. Hippurites radiosus DES MOULINS, U.Cret. (Maastricht.), France; 1a, view of operculiform FV showing posterior myophore (left), posterior tooth (middle), anterior tooth (right), and anterior myophore, $\times 0.45$; *1b*, interior of AV from above, $\times 0.45$ (252).
- 2. Hippurites bioculatus LAMARCK, U.Cret.(L. Campan.), France (Pyrenees) (Montagne des Cornes); transv. sec. at level of AV with projecting teeth and myophore of FV, $\times 0.9$ (910).
- 3. Praeradiolites cylindraceus DES MOULINS, U. Cret. (Maastricht.), France; lat view of FV showing myophores and elongate teeth, $\times 0.5$ (911).
- 4. Radiolites angeoides PICOT DE LAPEIROUSE, U. Cret.(low.Campan.), France, Pyrenees (Montagne des Cornes); side view of both valyes,

showing on exterior of AV positions of Eb and Sb siphonal bands, $\times 0.7$ (911).

- 5. Sphaerulites foliaceus LAMARCK, U.Cret. (Cenoman.), France (Bouche-du-Rhone); transv. sec. at level of AV with projecting teeth and myophores of FV, ×0.3 (911).
- 6. Hippurites striatus DEFRANCE, U.Cret., France (Rennes-les-Bains), side view of AV with cuts for transv. secs. (not figured) near top, X1.5 (269).

[Explanation: am. pm, anterior and posterior myo-phores; Eb and Sb, siphonal bands; Ep, Sp, internal pillars farthest and nearest L; L, ligamental ridge; 1,3, anterior and posterior teeth of FV; 2, tooth of AV; 1', 3', sockets in AV for reception of correspondingly numbered FV teeth.] D'University of Kansas Paleontological Institute

The earliest known rudists are found in Upper Jurassic (Rauracian) strata in France and elsewhere, and the latest ones lived during Maastrichtian times,1 near the close of the Cretaceous Period. In intervening ages they spread widely, becoming highly diversified, and, according to present knowledge, were distributed along a belt extending between the latitudes of southern Sweden, which contains the most northerly rudist-bearing deposits, and Madagascar, which is the most southerly region where such fossils have been collected. Among the most prolific occurrences of rudists are those in Texas, Mexico, the Antilles, Portugal, France, the Alps, Italy, Yugoslavia, Turkey, Syria and Iran.

RUDIST MORPHOLOGY By B. F. Perkins²

[Louisiana State University, Baton Rouge, Louisiana]

SHELL SIZE AND SHAPE

Although the first rudists were only slightly inequivalve, their descendants very early became strongly so, with the two valves of individuals usually differing greatly from each other in size, shape, and shell wall structure. The inequivalve form in rudists was developed according to three basic plans (Fig. E221): 1) the attached valve coiled and larger of the two, the smaller, free valve flat or slightly convex and lidlike; 2) the attached valve conical and larger of the two, the smaller, free valve flat, lidlike, conical or coiled; and 3) the free valve coiled and larger of the two, the smaller, attached valve conical or only slightly coiled.

Conical or gently curved rudist shells range in length from 2 cm. (Monopleura) to more than 2 m. (Titanosarcolites). They range in diameter from about 8 mm. (Monopleura) to more than 0.6 m. (Bournonia). Coiled rudist valves range in coil diameter from about 2 cm. (Toucasia) to at least 30 cm. (Caprinuloidea). Shell wall thickness of rudists varies from less than 2 mm. (Monopleura, Toucasia) to 10 cm. or more (Durania).

Terminology of the principal sections which show the internal features and shellwall structure through different shapes of rudist shells is summarized in Figure E222.

ORIENTATION

In descriptive morphology of rudists the terms right valve (RV), left valve (LV), dorsal, ventral, anterior and posterior have been used commonly, but the application of these to many rudists is not so obvious as with normal bivalves. Use of the terms in rudist descriptions depends upon a comparison between the shells of rudists and living Chamidae.

Among living cemented Chamidae certain species are almost invariably attached by the RV or oppositely by the LV, although some species are fixed to the substrate indiscriminately by either value (1024a). Comparison of attached LV's of some specimens with attached RV's of other specimens shows that they are mirror images with similar dentition. Comparison of free left with free RV's reveals that they, also, are mirror images. The similarity of dentition in attached valves of Chamidae was first noted by MUNIER-CHALMAS (652a), who designated the commoner condition of attachment by the LV as "normal" and the contrasting condition of attachment as "inverse." He recognized that the designation of a valve as left or right does not identify its dentition. Consequently, he proposed that in attached Chamidae the free valves be designated a and the attached values β .

MUNIER-CHALMAS considered the inversion in *Chama* and conditions in the rudists as comparable. Accepting this, DOUVILLÉ (267a) recognized two series of rudists: a "normal" series in which the LV is at-

¹ It is now known that beds in Catalonia (Spain), once thought to be Danian in age and the latest known deposits containing rudists, belong in fact to the Maastrichtain, and are no younger than rudist-bearing beds of that stage found in other areas (L. P. MANGUN, 1963, 21 Sess. Internatl. Geol. Congr., Norden, 960, pt. 27, p. 59).

² The contributions by PERKINS are adapted in part from Shell Development Company reports and are published with permission of the Company. He acknowledges with gratitude the opportunity provided by Shell Development Company to carry out the work on which his contribution is based. He also acknowledges the invaluable assistance of T. D. ALTMAN, J. F. LAVERDE, and J. W. MOORE in prepartion of illustrations and of APHRODITE MAMOULDES and BER-NICE MELDE for library work.



FIG. E221. Principal rudist shell forms (FV, free valve; AV, attached valve) (Perkins, n).

- A. Toucasia patagiata WHITE, L.Cret.(Alb.), USA (Texas), ×1.
- B. Radiolites angeiodes (PICOT DE LAPEIROUSE), U. Cret.(Campan.), France, $\times 1$.
- C. Caprinuloidea sp., L.Cret.(Alb.), USA(Texas), ×0.4.
- D. Monopleura marcida WHITE, L.Cret. (Alb.), USA Texas), ×0.4.
- E. Coralliochama orcutti WHITE, U.Cret. (Senon.), Mexico, ×0.3.
- F. Sellaea sp., L.Cret. (Alb.), USA (Texas), ×0.6.



FIG. E222. Principal sections (polished or thin) through different shapes of rudist shells (pc, commissural plane) (Perkins, n).



FIG. E223. Diceras arietinum LAMARCK (Diceratidae), U.Jur.(Raurac.), France (Coulanges-sur-Yonne); 1a, LV (FV) int., 1b, RV (AV) int., $\times 0.5$ (modified after 246). [Trace of ligamental groove shown in solid, broken and dotted line. Solid segment=ligamental groove parallel to commissure and probably containing functional ligament at stage shown; broken line=segment of groove visible in this view but below the level of the commissure; dotted line=part of groove concealed in this view below umbones and probably not containing a functional ligament at stage shown. Explanation as for Fig. E220; 2', socket for reception of tooth 2.]

tached and an "inverse" series in which the RV is attached. Paleontologists generally have followed the conclusions of MUNIER-CHALMAS and DOUVILLÉ. DECHASEAUX(252), on the other hand, has interpreted the teeth in these two series as not homologous, basing her opinion on a comparison of Valletia, earliest rudist attached by the RV, with Diceras. She has pointed out that teeth of the free LV of Valletia (see Fig. E250,4a) are not comparable to those in the RV of Diceras (Fig. E223). The posterior tooth in Valletia is very weak, whereas in Diceras it is quite strong. The posterior tooth of rudists attached by the RV becomes larger in successively younger genera and at least by Albian time is as prominent as in Diceras. DECHASEAUX argued that inversion is only apparent in rudists and, consequently, she abandoned the former classification of the group into normal and inverse series.

In many rudists orientation in terms of right, left, dorsal, ventral, anterior and posterior can be made in the same manner (i.e., with the hinge line up and the beaks directed away from the observer) as for a normal bivalve. In conical forms such as the Radiolitidae and Hippuritidae, however, which show no evidence of coiling, orientation by this method is impossible. Without proof in some groups paleontologists have assumed that attachment was by the RV in Monopleuridae, Caprotinidae, Caprinidae, Hippuritidae and Radiolitidae, and by the LV in Heterodiceratinae, Plesiodiceratinae, Epidiceratinae, and Requieniidae. Based on this assumption, parts distinguished as anterior, posterior, ventral and dorsal can be determined. However, because of the uncertain identification of rightness or leftness in many rudist shells, it seems desirable to designate the two valves as attached valve (AV) and free valve (FV) in descriptions of rudist genera and species.

Anterior, posterior, dorsal, and ventral can be retained as convenient orientation terms, but it is important to recognize that these terms are applicable to conical shells only if assumption is made regarding rightness or leftness of the valves. Investigation of young shells of rudists which show no evidence of coiling in the adult may provide the ontogenetic information necessary to settle the question.

TEETH AND SOCKETS

Hinge structure is similar in all rudists. Except for *Diceras*, rudists have two teeth in the free valve separated by a socket which receives the single tooth of the attached valve. In *Diceras* two teeth are present in the attached RV and a single tooth occurs in the free LV (Fig. E223). Rudist hinge teeth vary from feeble tubercles weakly aligning the two valves to long, heavy straight or curved (Fig. E220,1a,3; E224,3) projections firmly guiding the opening and closing of the valves. The teeth and their corresponding sockets may be smooth or grooved.

Three principal notation systems for rudist dentition have been proposed, and several minor variations of these have been used (Table E1). The first system introduced by DOUVILLÉ (267a) has been used most commonly by rudist workers and has not been replaced completely by any later proposed notation system. This terminology



- FIG. E224. Morphological features of rudists (corallike shells with operculiform upper valve).
- 1. Hippuritella maestri VIDAL, U.Cret.(Santon.), France, Pyrenees (Montsech); side view of AV, ×1.7 (269).
- Distefanella lombricalis D'ORBIGNY, U.Cret. (Turon.), France (Charente); 2a-d, side views of 4 AV's showing shape variations and position of Eb and Sb siphonal bands, ×0.7 (911).
- 3. Caprinuloidea perfecta PALMER, U.Cret. (Cenoman.), Mexico; side view of both valves (caplike FV above), ×0.35 (714).

[Explanation: *Eb*, *Sb*, siphonal bands farthest and nearest ligament; *Ep*, *Sp*, internal pillars.]

apparently was not derived from nomenclature used previously for other bivalves and was not intended by DouvILLÉ to express homology. The second system used by DouVILLÉ (278a) was derived from terminology of MUNIER-CHALMAS (652b) and BERNARD (37, 40). It expressed DouVILLÉ's interpretation of the homologous relationships of rudist dentition. His last system (282) is only a slightly modified version of the second. Most other notation systems, such as that used by DI STEFANO (882a, 882b) and one used by KLINGHARDT (475), are minor variations of DouVILLÉ's first nomenclature.

DECHASEAUX (245, 246, 252) noted the impossibility of distinguishing cardinal and lateral teeth in rudists, and consequently, the difficulty of applying with certainty the dental notation of MUNIER-CHALMAS and BERNARD. She proposed using the numerical system of BERNARD, without the implications of homology, however. In this system the teeth are numbered from front to back (i.e., 1, 2, 3) and their corresponding sockets are indicated by the same numbers with the addition of a prime accent (i.e., 1', 2', 3'). By this system tooth 2 of the Diceratinae is in the free LV and teeth 1 and 3 are in the attached RV. In all other rudists teeth 1 and 3 are in the free valve (FV) and tooth 2 is in the attached valve (AV), whether the LV or RV is attached.

This simplified notation without homologous implications first used by DECHA-SEAUX is followed in the *Treatise*.

LIGAMENTAL STRUCTURES

The ligament is not preserved in fossil rudists, but its original location is marked by a ligamental groove or furrow on the exterior of the shell, a ligamental cavity within the shell wall, or a ligamental ridge or pit on the interior of the shell. The ligament was external in the most archaic rudists, but it was progressively submerged into the shell wall of other groups, and in many advanced groups it was entirely internal or lost completely.

The ligament in the Diceratidae, Requieniidae, and some Monopleuridae (e.g., *Valletia, Gyropleura*) lay in a groove parallel to the commissure. As the valves grew,

		Diceras					
			RV			LV	
		A	М	Р	A	М	P
		+	0	+	0	+	0
Douvillé, 1886 (267a)	Teeth	B'		В		Ν	
	Sockets		n		b'		Ь
Douvillé, 1918 (278a)	Teeth	AI		3b		AII	
	Sockets		AII'		AI'		3b'
Douvillé, 1935 (282)	Teeth	AI		3		AII-2	
	Sockets		AII'-2	,	AI'		3'
di Stefano, 1889, 1899 (<i>882a, 882b</i>)	Teeth	a					
	Sockets						
Klinghardt, 1928 <i>(4</i> 75)	Teeth						
	Sockets						
Dechaseaux, 1952 (252)	Teeth	1		3		2	
	Sockets		2'	-	1′	2	3'

TABLE E1. Notation Systems for Rudist Teeth and Sockets Employed by Various Authors.

EXPLANATION: +=tooth, O=socket; A, anterior; M, median; P, posterior.

the strong tangential growth component caused separation and coiling away from the commissure of the umbones and consequently the ligament was split so that only the most recently formed portion was entire and paralleled the commissure, the location of the previously formed sections remaining as a coiled groove in each valve extended from the commissure to the beak (Fig. E223). Quite probably only the un-



FIG. E225. Diagram showing effect of tangential growth component on ligament, arrows denoting increased effect (1024a).

[Explanation: L-L, longitudinal axis; T-T, transverse axis; broken lines indicate divergence of umbones induced by interumbonal growth consequent on increasing effect of tangential growth component, ——a. Primitive amphidetic ligament, longitudinally disposed and anteroposteriorly symmetrical.——b. Anteriorly separated and coiled ligament of Glossus, bilaterally but not anteroposteriorly symmetrical.

<u>b</u>₁. Ligament of Chamidae, bilaterally asymmetrical. c. Coiled ligament of Diceratidae, almost bilaterally symmetrical. c₁. Ligament of Requienta bilaterally symmetrical. ly straightened ligament of Caprina, functionless and now disposed transversely. d₁. Bilaterally asymmetrical ligament of Hippuritidae and Radiolitidae.]

	Rudists with Left Valve Attached					Rudists with Right Valve Attached					
	RV			LV			RV			LV	
A	М	Р	A	М	Р	A	М	Р	A	М	Р
+	0	+	0	+	0	0	+	0	+	0	+
B'		В		N			N		B'		В
	n		b'		b	b'		b		л	
AI		3Ь		AII			3B		AII		PII
	AII'		AI′		3b'	AII'		PII'		3b'	
AI		3		AII			3		AII		PIV
	AII'		AI'		3'	AII'		PVI'		3'	
							N		D'		D
						ď		d		n	
							N		Bı		В
						alı		al	-	N	
1		3		2			2		1		3
_	2'	-	1'	-	3'	1'	-	3'	-	2'	

TABLE E1. (continued)

split part of the ligament approximately parallel to the commissure was functional, and it is quite likely that the older functionless part disintegrated while the animal was still alive, as does the older functionless part of the ligament in some living oysters.

In all other rudists with conical, openly coiled or slightly twisted attached valves and coiled, conical, or operculiform free valves the long axis of the ligament, when present, was approximately normal to the plane of commissure. The reorientation of the ligament from a parallel-to-commissure to a normal-to-commissure structure is a result chiefly of the influence of the tangential component of growth. The effects of the tangential growth component on the ligament have been summarized diagrammatically by YONGE (Fig. E225).

In rudists with the ligament oriented normal to the commissure the ligament may have been functionless. This type of ligament, if functional, was certainly subject more to tensional stresses than to bending stresses of a parallel-to-commissure ligament. This normal-to-commissure ligament may have served only as a stringlike guide holding the dorsal margins of the valves together but not strongly counteracting contraction of the adductor muscles. In the Monopleuridae (excluding Valletia and Gyropleura) the ligament of the AV lay in a groove normal to the commissure. The ligamental groove is shallow and does not penetrate the shell wall (Petalodontia, Fig. E252,4a,b) or it is deep and penetrates the shell wall so that an internal groove or cavity is developed (Himeraelites, E252,5b).

In monopleurids with operculiform FV's (Monopleura, E250,3b; Araeopleura, E250, 2b; Petalodontia, E250,1a,b) the FV ligamental position may be marked externally by a slight infolding or notching of the shell wall, but in some no external feature can be related to the ligament. Internally a shallow rounded or elongate ligamental pit is found between the dorsal margin and the tooth socket (2'). The FV ligament in species of *Monopleura* with the FV coiled in a low spiral (E251,3a; E252,1a) is represented externally by a groove which extends from the beak to the commissure and leads internally to a shallow ligamental cavity. In the elevated FV of Himeraelites (E252.5c) an external ligamental groove extends from the beak to the commissure and opens internally into a deep ligamental pit.

In the AV of caprotinids the ligament location is marked externally by a deep groove which may open internally into a



FIG. E226. Caprinuloidea sp. (Caprinidae), L.Cret. (Alb.), USA(Texas); FV int. showing ligamental cavity, ×1.3 (Perkins, n).

ligamental cavity (Sellaea, Fig. E255,2b; Polyconites, E254,1b). A similar external groove and internal ligamental cavity are found in conical or coiled caprotinid FV's (Sellaea, Fig. 255,2a). The ligament location in caprotinids with operculate FV's may be marked externally by a short, shallow groove which corresponds internally to a ligamental pit (Polyconites, E254,1a; Chaperia, E253,1a).

The ligament position is defined in most caprinids by a shallow to deep external groove in both valves (*Caprinula*, E257,4*d*; *Caprinuloidea*, E258,3; *Planocaprina*, E259, *3a*; *Plagioptychus*, E260,2*a*; *Coralliochama*, E258,2*a*). The ligamental groove may open internally into a narrow or wide ligamental cavity (*Sabinia*, E262,3*a*,*b*; *Caprinula*, E257, *4c*; *Caprina*, E257,2*a*; *Caprinuloidea* sp., E226). In some caprinids, however, there is no external groove or internal structure which can be related to the ligament (*Dictyoptychus*, E256,2*a*-c).

In most hippuritids the ligamental position in the AV is marked by an external furrow and an internal ligamental ridge, but in some species (e.g., *Hippurites bioculata*, Fig. E220,2 and Fig. E263,1b) no internal ridge occurs and an external furrow is not developed. In other species a welldeveloped ligamental ridge is not matched by a distinct external furrow. The external furrow, when present, extends from the apex to the commissure and may be broadly (E220,1b) or narrowly rounded (E220,6). In transverse section the ligamental ridge may be a low, rounded swelling (Batolites, E237,11), a sharp triangle (Hippurites, E220, 1b) or rounded triangle (Tetracionites, E264,5), a long, parallel-sided projection with a truncated, rounded or swollen tip (Torreites, E238,5; E265), or a beaded (moniliform) ray (Barrettia, E227,2). An internal ligamental ridge and external furrow are present in the FV of some hippuritids (Hippurites, E220,1a) which correspond to the ridge and furrow of the AV. Hippuritids have been studied most commonly from transverse sections because separate, free valves are rare. As a result, little is known about the ligamental structures of the FV and only those features of the AV which are exposed in transverse sections are well known. It seems likely that the ligament in hippuritids was not functional.

An internal ligamental ridge is present in the AV of all Radiolitinae and in Sauvagesia (Sauvagesiinae), Praelapeirousia (Lapeirousiinae) and Joufia (subfamily uncertain). An external groove (Paronella, E269, 4) corresponding to the ligamental ridge is not found commonly in radiolitids. In transverse section the ridge may be long, parallel-sided (Pseudopolyslender and conites, E266,3), bilobed (Kuehnia, E267, 5), or truncate (Neoradiolites, E269,6). An internal ligamental ridge is known in the FV of Praeradiolites (E220,3; E269,2e) Eoradiolites, Sauvagesia and Joufia. The FV ligamental ridge is straight and narrow and may terminate in a ligamental pit. A ligamental ridge may be developed in the FV of other genera which have ridges in the AV. The ligament of most radiolitids probably was functionless, but in some (Praeradiolites, Eoradiolites, and others) it may have served as a stringlike guide.

SIPHONAL STRUCTURES

Structures presumably related to siphons are present in many rudists. Siphonal structures include bands, fossettes, pillars, pseudopillars and oscules. These occur in pairs when present and have been designated by DOUVILLÉ as "E" and "S" according to their positions. The posterodorsal structures



FIG. E227. Morphological features of rudists (shell structure) (hippuritids).

- 1. Pironaea polystylus (PIRONA), U.Cret. (Maastricht.), Italy; transv. sec. of type (AV) showing radial inward projecting partitions formed of bundled calcite prisms, $\times 0.5$ (269).
- 2. Barrettia monilifera WOODWARD, U.Cret. (Maastricht.), Jamaica; transv. sec. of type (AV) showing radial beaded structure in thick shell wall, $\times 0.5$ (269).

[Explanation as for Fig. E220.]

nearer the ligamental position were presumed by DOUVILLÉ to mark the location of the excurrent siphon and hence were designated "S" for sortie (French, excurrent). The ventral structures farther from the ligamental position were presumed to represent the incurrent siphon location and were named "E" for entré (French, incurrent). DOUVILLÉ's interpretation of these structures has been questioned by YONGE (1027a) who presented a biologically convincing alternative explanation (discussed elsewhere in this introduction by COOGAN). However, DOUVILLÉ'S symbols "E" and "S" have been used generally and are retained in the Treatise but modified by a lower case letter to denote the particular structure. For example, Eb and Sb mark bands, Ep and Sp denote pillars, Es and Ss indicate pseudopillars, and Ef and Sf indicate fossettes. Oscules are designated Eo and So.

Siphonal bands (Fig. E224,1,2; E254,2b) are external features of the AV (and, in some genera, the FV) of Radiolitidae, a few Requieniidae (Requienia, Toucasia) and one Caprotinidae (Horiopleura). Siphonal bands are broad to narrow, salient or superficial to deeply impressed areas with the long dimension normal to the commissure and extending from the apex of the valve to the commissure. In Requieniidae the bands are broad areas marked by slight deflections of the growth lines (Requienia) and slight depression of the area (Toucasia). The siphonal bands of Horiopleura (Caprotinidae) (Fig. E254,2b) are smooth depressed areas on an otherwise radially ribbed shell.

The siphonal bands of the AV of most Radiolitidae are smooth, shallow, depressed areas as in Radiolites (Fig. E267,2). However, in some radiolitids the bands may be finely and longitudinally costulate (Sauvagesia) (Fig. E266,4), broadly costulate (Medeella (Medeella)), marked by strongly convex-upward folds (Praeradiolites) (Fig. E269,2) or occur in deeply sunken grooves (Thyrastylon) (Fig. E243,2). The siphonal bands of Medeella (Fossulites) (Fig. E243, 1) are salient areas which mark cylindrical siphonal fossettes within the shell wall. In Tampsia (Fig. E272,2) sharp inflections define the bands and Eb is marked by a deep slit cutting the shell wall almost to the inner layer of the shell. In many radiolitids no external feature of the FV corresponds to bands of the AV, although in some genera (Hardaghia) bands are present in the FV. In Medeella (Fig. E243,1a; E267,1c) inflected crescentic slits or arches in the FV correspond to bands and fossettes



FIG. E228. Sellaea sp. (Caprotinidae), L.Cret.(Alb.), USA(Texas); long. sec. both valves showing mantleshell cavity open without tabulae (*p-c*; commissural plane), ×0.7 (Perkins, n).

of the AV and in *Thyrastylon* openings or oscules through the FV correspond to the deeply sunken bands of the AV.

In hippuritids infoldings of the AV shell wall produced ridges normal to the commissure (Fig. E220,1b,2). These ridges or **pillars** are usually three in number, one marking the ligamental position and the other two presumably siphonal in location. The pillars are matched in the FV by openings, oscules, through the valve (Fig. E263, 1a,2b).

In Parasauvagesia (Radiolitinae) and in most Lapeirousiinae development of cellular structure (Fig. E273,6) in the outer shell wall produces pillar-like ridges (termed **pseudopillars**) on the inner shall wall. Oscules in the FV correspond to pseudopillars in the AV. The function of pillars, pseudopillars, and oscules is discussed by COOGAN in "Evolutionary Trends in Rudist Hard Parts," and in the systematic sections on Hippuritidae and Radiolitidae.



FIG. E229. Eoradiolites sp. (Radiolitidae), L.Cret. (Alb.), USA(Texas); natural long. sec. of two AV's showing closely spaced tabulae in mantleshell cavity, $\times 0.7$ (Perkins, n).

MANTLE-SHELL CAVITY

The mantle-shell cavity of rudists is a single or subdivided cavity within each of the two valves. The cavities of the valves are nearly equal in size in the Diceratidae and in many Caprotinidae and Caprinidae. In the Requieniidae, Monopleuridae, Radiolitidae, and Hippuritidae the shell cavity of the AV is much more elongate normal to the commissure and is larger than that of the FV. In the shells of species which have operculiform FV's the cavity of that valve is reduced to a shallow depression. In the Caprotinidae, Caprinidae, some Requieniidae and Monopleuridae the shell cavity consists of a principal cavity which contained the visceropedal mass and gills along with accessory cavities which probably were lined only by the mantle. In rudists having relatively thin or compact shell walls (e.g., Diceratidae, Requieniidae, Monopleuridae, and Caprotinidae) the shell cavity is large in proportion to the cross-sectional area of the valve. In rudists with thick shell walls (Hippuritidae) or spongy shell wall structure (Radiolitidae, Caprinidae) the principal shell cavity may be very small in proportion to the valve's cross-sectional area.

The shell cavity may be open throughout its length from the commissure to the um-



FIG. E230. *Hippurites bioculatus* LAMARCK, U.Cret. (L.Campan.), France (Corbières); long. sec. both valves showing tabulae in mantle-shell cavity of AV, X1.3 (Perkins, n).



FIG. E231. Eoradiolites davidsoni HILL (Radiolitidae), L.Cret.(Alb.), USA(Texas); long. sec. both valves showing mantle-shell cavity size in relation to shell size, $\times 0.7$ (Perkins, n).

bonal area (Fig. E228), but in Caprinidae, Radiolitidae, and Hippuritidae the shell cavity commonly is divided by transverse tabulae concave toward the commissure (Fig. E229-E231). In caprinids in which the shell cavity is divided into a principal cavity and accessory cavities all cavities may be tabulate but the tabulae in these various spaces do not occur at common levels. The tabulae close off earlier-formed portions of the shell cavity and spaces remain as vacant chambers. In some Hippuritidae the earlierformed part of the shell cavity is filled from the umbo toward the commissure by dense shell material. The tabulae and dense shell material reduce the available space in the cavity for the animal which was small in relation to size of the shell in many caprinids, radiolitids, and hippuritids (Fig. E231).

ACCESSORY CAVITIES

Accessory cavities were first defined by DOUVILLÉ (267a) from studies of *Caprotina* (Caprotinidae). These cavities separate anterior and posterior myophore plates and teeth from the shell wall in caprotinids and caprinids. They are developed chiefly in the FV but also occur in the AV of some genera.

Accessory cavities are large in most caprotinids but may be reduced greatly (*Chaperia*, *Retha*). They are usually oval or lunate in section parallel to the commissure and in some shells are divided by thin, radial plates normal to the commissure. Accessory cavities occur in all caprotinid genera but are not limited to this family, for accessory cavities are found in *Bayleia* and *Bayleoidea* (Requieniidae), *Himeraelites* (Monopleuridae), and in most Caprinidae.

The posterior accessory cavity is connected with the posterior socket in the AV of Western Hemisphere caprinid genera (e.g., Amphitriscoelus, Coalcomana, Caprinuloidea) and has a characteristic shape in MACGILLAVRY (561) transverse section. first noted this distinction of Western Hemisphere caprinids and described the cavity as "more or less shaped like an ant's larva, or better, like the ornament one often encounters on oriental tapestry" (Fig. E241; E257,1a; E232). The AV posterior accessory cavity in some caprotinids (e.g., Sel*laea*) is connected also with the posterior socket, which, in turn, is connected to the ligamental cavity (Fig. E239,3a; E255,2b).

A myophorous accessory cavity is present in the FV of some caprotinids (e.g., Pachytraga, Fig. E253,4) and caprinids (e.g., Caprina, Fig. E256,1; Caprinula, Fig. E257, 4b; Caprinuloidea, Plagioptychus, Fig. E259, 5b). These accessory cavities are usually connected to the tooth socket (2') and may be only partially separated from the principal shell cavity. The cavity is formed by a vertical plate connecting the anteroventral margin of the anterior tooth (1) with the anteroventral shell wall. The plate does not reach the commissure in most species, so that at this level the principal cavity is not separated from the myophorous accessory cavity. The anterior muscle insertion of the FV is on the anterior or anteroventral cavity and the cavity received the anterior myophore plate of the AV when the valves were closed.

Accessory cavities occur in the AV of some hippuritids, radiolitids, and caprinids


FIG. E232. Caprinuloidea sp. (Caprinidae), L.Cret. (Alb.), USA(Texas); AV int. showing characteristic shape of posterior accessory cavity and connecting posterior socket (3') in western hemisphere caprinids, ×0.7 (Perkins, n).

between the cardinal structures and the dorsal shell wall.

DOUVILLÉ postulated that accessory cavities developed as the valve increased in height and the teeth and myophore plates became erect to the point that these structures no longer increased in size at the same rate as the shell diameter. As a result, a cavity developed between the muscle insertion surfaces and teeth on one side and the shell wall on the other. Consequently, a much larger but much less dense shell was formed.

Accessory cavities converge toward the apex of the shell. Steinkerns of the cavities appear as clusters of cones attached to each other by their bases and are the "birostres" of 18th and early 19th century French paleontologists.

PALLIAL CANALS

Longitudinal, thin-walled canals, called pallial canals, in the shell wall characterize the Caprinidae. These canals may be present in either or both valves of a shell, and although they occur only in the shell wall of most caprinids they may be in the dental apparatus of some genera (e.g., *Caprinuloidea* and *Titanosarcolites*, Fig. E232). The canals are bounded by radial, transverse and tangential plates lying normal to the commissure. The radial plates may be simple, bifurcate or many-branched, and the transverse and tangential plates may be regularly or irregularly arranged. In transverse section pallial canals may be approximately quadrangular (e.g., *Amphitriscoelus*), regularly oval to pyriform (e.g., *Coalcomana*, *Caprinuloidea*), or irregularly polygonal (e.g., *Coralliochama*). The pallial canals of some caprinids are traversed by thin tabulae concave toward the commissure.

In some shells a distinction cannot be made between pallial canals and divided accessory cavities. This observation caused DOUVILLÉ to speculate that pallial canals originated by the invasion of the pallial region by canals formed in advanced stages of the subdivision of accessory cavities.

Development of abundant pallial canals in caprinids produced a thick, spongy, porous shell wall which probably was rapidly deposited and which contained a minimum amount of calcium carbonate for its size and strength.

Pallial canals are discussed further in the section on shell-wall structures (Caprinidae).

MUSCLE INSERTIONS

The two adductor muscles in rudists were inserted on the shell wall, joined to projecting plates or myophores or within myophorous sockets. Within an individual rudist the type of muscle insertion may be different for the two valves or for the two muscles and are not necessarily symmetrical. For example, in Diceratidae the anterior muscle insertions in both valves may be on the shell wall, but the posterior insertions are on myophore plates. In Radiolitidae the FV muscle insertions are on projecting myophores but the AV insertions are on the shell wall (Table E2).

Shell-wall insertions may be superficial, on weakly to strongly depressed areas or on thickened areas.

Platelike prolongations of the cardinal platform are muscle insertion sites in some Diceratidae (e.g., *Heterodiceras*, Fig. E244, *1; Mesodiceras*, Fig. E244,2*a*,*b*), Requieniidae (e.g., *Kugleria*, Fig. E246,6*a*) and Monopleuridae (e.g., *Monopleura*, Fig. E252,1). The insertion surfaces on plates of this type are parallel or nearly parallel

	ATTACHED VALVE		FREE VALVE		
FAMILY	Anterior Insertion	Posterior Insertion	Anterior Insertion	Posterior Insertion	
Diceratidae	 Shell wall or prolongation of cardinal plat- form 	1) Plate project- ing above shell wall or 2) pro- longation of car- dinal platform	 Shell wall or on prolonga- tion of cardinal platform 	1) Plate project- ing above shell wall, 2) prolong- ation of cardinal platform, or 3) plate extending beneath cardinal platform	
Requieniidae	Shell wall	1) Shell wall or 2) on plate ex- tending beneath cardinal platform	1) Shell wall or 2) on prolonga- tion of cardinal platform	 Plate extend- ing beneath or above cardinal platform, 2) pro- longation of car- dinal platform, 3) plate separ- ated from shell wall by accessory cavity, or 4) plate parallel to shell wall and attached to it by plate normal to shell wall 	
Monopleuridae	Extension of car- dinal platform as thickened area or buttress	Extension of car- dinal platform as thickened area or buttress	Extension of car- dinal platform as thickened area, buttress or myo- phore plate	 Extension of cardinal platform as thickened area, buttress or myo- phore plate or 2) on erect separate myophore plate or lamina 	
Caprotinidae	1) Shell wall or 2) on plate sep- arated from shell wall by accessory cavity	1) Shell wall or 2) on plate sep- arated from shell wall by accessory cavity	 Shell wall or on plate separated from shell wall by accessory cavity 	Shell wall or on plate separated from shell wall by accessory cav- ity	
Caprinidae	1) Shell wall or 2) on plate sep- arated from shell wall by accessory cavity	 Shell wall or on plate separated from shell wall by accessory cavity 	1) Shell wall or 2) on plate sep- arated from shell wall by accessory cavity	1) Shell wall, 2) on plate sepa- rated from shell wall by accessory cavity, or 3) on projecting myo- phore which fits into socket of AV	
Hippuritidae	Shell wall	In socket which receives FV myo- phore	Projecting myo- phore or buttress	Myophore which fits into AV socket	
RADIOLITIDAE	Shell wall	Shell wall	Projecting myo- phore or buttress	Projecting myo- phore or buttress	

TABLE E2. Sum	amary of Muscle	Insertions	in	Rudists.
---------------	-----------------	------------	----	----------

to the commissure. These plates are attached to the shell wall along their front (for the anterior plate) and back (for the posterior plate) edges and curve around the shell cavity. Similar plates which are not connected directly to the cardinal platform are developed in the Requieniidae. These plates either pass above (e.g., RV posterior of *Requienia*, Fig. E246,1b) or below (e.g., LV posterior of *Bayleia*, Fig. E246,2a; LV posterior of *Apricardia*, Fig. E246,3) the cardinal platform. Erect myophore plates are present in many Caprotinidae (e.g., Sellaea, Fig. E255, 2b) and most Caprinidae (e.g., Amphitriscoelus, Fig. E257,1, Schiosia, Fig. E262, 5). Plates of this type are normal to the commissure and extend from the hinge to the posteroventral and anteroventral shell wall. The plates are separated from the anterior and posterior shell wall by simple or subdivided accessory cavities (described above).

Strongly projecting myophorous apophyses or myophores are characteristic of the FV of most Radiolitidae and Hippuritidae. Myophores of this sort may be elongate and toothlike (e.g., *Hippurites*, Fig. 220,1*a*) or thick-based with the tip swollen into a knob or boss (e.g., *Praeradiolites*, Fig. 220, 3). The two myophores in a shell may be similar in form and subequal in size (e.g., *Praeradiolites*, Fig. 220,3), or they may be quite unsymmetrical in size and shape as in *Hippurites* (Fig. 220,1*a*).

A muscle buttress is intermediate between an insertion on a thickened shell wall area and a well-developed projecting myophore. A buttress is an elevated or pendent structure in which the insertion surface usually is only slightly inclined to the shell wall as in the FV of Agriopleura (Fig. E237, 1). Buttresses are usually developed as extensions of the cardinal platform to which they remain attached. They are found in the FV of some Radiolitidae and in the AV of some species of Monopleuridae (Fig. E233).

In hippuritids the posterior muscle insertion area in the AV is on the inner wall of a socket dorsal to Sp (e.g., *Hippurites*, Fig. 220,1b). When the valves are closed the toothlike posterior myophore of the FV fits into the myophorous socket of the AV.

MECHANISM FOR OPENING AND CLOSING VALVES

By Colette Dechaseaux

The almost constant occurrence of attachment scars for anterior and posterior adductor muscles indicates that the rudists could open and close their valves. In all except the Hippuritidae and Radiolitidae the apparatus for this purpose, consisting of a ligament, well-developed teeth (not, however, forming long projections), and muscle scars, situated either directly on the shell wall or on more or less projecting apophyses (myophores), shows that the two valves could be opened by a hinging movement as in an ordinary lamellibranch. The form of the teeth in some shells (e.g., *Plagioptychus*) may have required a slight rotational movement of the free valve with respect to the fixed valve in order to disengage the expanded extremity of a tooth from its socket.

The problem of opening the shell is more involved when we consider the Hippuritidae and Radiolitidae, in which the teeth and myophores form elongate projections (Fig. E220,1,3). The free value in this group forms a lid to the attached valve, its long teeth and myophores being received in elongate sockets, so that only vertical movements are possible. The free valve, when raised above the fixed one, is guided by grooves along the teeth and also (in some forms) along the myophores and by corresponding ridges along the sides of their sockets (Fig. E220,1,3). It may be suggested that the free valve could be raised by increased pressure inside the shell, brought about by expansion of the soft parts such as the foot. When the valves were separated the muscles were stretched, but when internal pressure was relaxed they would resume their normal length, thus closing the shell.

MODE OF LIFE

By Colette Dechaseaux

Some rudists lived as solitary individuals (Fig. E224), whereas other were gregarious, their accumulated shells now forming dense masses called "rudist reefs." Except for certain radiolitids the form of which suggests that they lay resting on a flattened side on the sea bottom, and also some others with an equivalve shell lacking an attachment scar, and thus possibly capable of some free movement, all rudists grew attached, either intermingled with other organisms, particularly corals, or, when in an erect position, in clusters of varying magnitude. The earliest known species occur in coral reefs, forming an ele-



FIG. E233. Monopleura sp. (Monopleuridae), L. Cret.(Alb.), USA(Texas); dorsal oblique view of AV showing muscle buttresses and external ligamental groove, ×1.3 (Perkins, n).

ment of about the same importance as less specialized bivalves, gastropods, echinoderms, etc.

Hippuritidae and Radiolitidae are also associated locally with corals (as in eastern Serbia), but then other elements of the usual coral reef fauna are absent. Generally they occur in colonies of a single species or in assemblages containing only a small number of species. Near Angoulême, in France, certain Turonian beds which can be traced for several dozen meters contain only *Distefanella lombricalis* (D'ORBIGNY) (Fig. E224,2), apart from a very impoverished microfauna.

ORIGIN AND EXTINCTION

By Colette Dechaseaux

According to present knowledge, the appearance of Diceras in Late Jurassic (Rauracian) time marks the beginning of the history of the rudists, a history extending almost to the close of the Cretaceous and including the development of a host of highly varied forms. Two hypotheses have been advanced as to the origin of Diceras. According to Douvillé, its ancestor was a bivalve living where its earliest representatives are found and having some of its distinctive characters. These requisites, it seemed to him, were possessed by Pterocardium, a genus in which the ornament consists of radial costae and in which the posterior muscle was attached to a projecting lamella. He supposed that the newly hatched young of Pterocardium became

cemented to the substrate with the aid of the foot to avoid being carried away by currents during early life, and that as the shell developed it became twisted about the point of fixation so as to acquire a spiral form, the number of hinge teeth being reduced to three. Such modifications led ultimately to the genus *Diceras*.

The other hypothesis (by DECHASEAUX) is based on the tendency of the posterior elements of the hinge of Megalodon and Protodiceras to become reduced. In Megalodon (Devonian-Upper Triassic) one (or in some shells two) of these teeth are absent. In Protodiceras (Lower Jurassic) which normally has fewer hinge elements than Megalodon, a tendency toward reduction of the teeth on the posterior side occurs also, the final stage corresponding to the hinge of Diceras. Thus, beginning in the Devonian, a tendency toward development of the Diceras type of hinge is shown by Megalodon and Protodiceras. In support of this hypothesis we may note that in early growth stages of Diceras the posterior muscle was attached in the same way as in Megalodon.

Among the last surviving rudists were three radiolitids and a hippuritid which lived in Catalonia during the Maastrichtian Stage. They were not solitary bivalves, but on the contrary formed large "rudist reefs." Their abrupt extinction is the more difficult to explain since in this region deposition of calcareous sediment had continued uninterruptedly from the Coniacian onward, some species nevertheless disappearing while others persisted and new ones appeared; then, at the same moment, apparently all became extinct.

In Somalia, where the succession has been studied by TAVANI, Upper Cretaceous limestones pass without a break into lower Eocene limestone, yet no rudists occur in beds higher than Upper Cretaceous. The nature of the sediments gives no indication of a possible change in ecological conditions, so that we are entirely ignorant of factors responsible for extinction of the rudists and other groups that disappeared; more particularly, we are unable to ascertain what changes accounted for the fact that new species of these groups ceased to appear to replace those that died out. All we can say is that extinction of the group took place at this time.

CLASSIFICATION

By Colette Dechaseaux

The hypothesis is here accepted that the rudists were derived from the Megalodontidae, and they are considered to form a major taxon of the Bivalvia to which STEIN-MANN assigned the name Pachyodonta, and for which the name Hippuritoida is adopted in the Treatise. The rudists constitute the superfamily Hippuritacea. It is thought probable that the Chamacea are not descended from them but are sessile heterodonts. In early ontogeny the shell of chamids is unattached and regular both in outline and in the nature of its concentric ornament. Much has yet to be learned of the early ontogeny of the rudists, but we have no knowledge of the existence of a comparable stage in this group.

To a large extent, the classification of the rudists in families has been based on the various characters (fixation, hinge structure, etc.) which have been discussed in preceding paragraphs. Certain special internal features (accessory cavities, canals, pillars, pseudopillars) allow other families to be defined, as stated in the systematic descriptions which follow.

A tabular summary of the classification adopted in the *Treatise*, showing the number of genera and subgenera (for example, "2; 4" denoting 2 genera and 4 subgenera) in each division, and recording known stratigraphic distribution, follows.

Divisions of Hippuritacea

- Hippuritacea (superfamily) (115;3). U.Jur.(U. Oxford.)-U.Cret.(U.Maastricht.)
 Diceratidae (8). U.Jur.(U.Oxford.)-L.Cret. (Valangin.)
 Diceratinae (1). U.Jur.(U.Oxford.)-L. Kimmeridg.)
 Heterodiceratinae (3). U.Jur.(Tithon.)-L.Cret. (Valangin.)
 - Plesiodiceratinae (2). U.Jur.(Oxford.-Kimmeridg.)
 - Epidiceratinae (2). U.Jur.(Oxford.)-L.Cret. (Valangin.)
- Requieniidae (8;2). U.Jur.(Tithon.)-U.Cret. (Maastricht.)
- Monopleuridae (8). L.Cret.(Valang.)-U.Cret. (Maastricht.)
- Caprotinidae (8). L.Cret.(Neocom.)-U.Cret. (Turon.)
- Caprinidae (23). L.Cret.(Barrem.)-U.Cret. (Maastricht.)

Hippuritidae (12). U.Cret.(Turon.-Maastricht.) Radiolitidae (39: 1)*. L.Cret.(Barrem.)-U.Cret. (Maastricht.)

- Radiolitinae (14; 1). L.Cret.(Barrem.)-U.Cret. (Maastricht.)
- Biradiolitinae (7). U.Cret.(Turon.-Maastricht.)
- Sauvagesiinae (7). L.Cret.(Alb.)-U.Cret. (Maastricht.)
- Lapeirousiinae (8). U.Cret. (Santon.-Maastricht.) Subfamily Uncertain (3).

Family Uncertain (9).

EVOLUTIONARY TRENDS IN RUDIST HARD PARTS

By A. H. Coogan

[CoogAN's present affiliation is with Kent State University, Kent, Ohio. His *Treatise* contributions are based mainly on studies made while he was employed by the Humble Oil & Refining Company and Esso Production Research Company, Houston, Texas, to the staffs and management of which he acknowledges assistance and encouragement. Special appreciation is expressed to R. M. [FFFORMS, R. D. Woons, and the late H. N. FISK.]

The morphological diversity of rudists is a stony monument to the plasticity of the bivalve mantle as it operated in adapting to a variety of reef, bank, and shallow-shelf environmental niches available on extensive sea-covered continental platforms of the Late Jurassic and Cretaceous. Broadly speaking, two groups of rudists can be recognized with respect to their rapidity of morphological change. The conservative, little-changing, and for the most part older families are the Diceratidae, Requieniidae, Monopleuridae, and Caprotinidae. The more plastic, rapidly changing, adaptive families are the Caprinidae, Radiolitidae, and Hippuritidae (Fig. E234). In the conservative group distinctions between families involve slight differences in dentition and musculature, different modes of attachment, variations in shape and size, and the development of internal structures. In the more plastic families these same differences occur at the subfamily or generic level and in addition dramatic changes are observed in wall structure, mechanism of opening the valves, and development of structures for lightening and strengthening the shell and for support of the siphons.

Evolutionary trends with morphological significance can be discussed selectively in terms of dentition, ligamental and muscular supports, wall structure, siphonal structures and pillars. Several instances of parallel evolutionary trends in one or more of

^a Includes 3 radiolitids of unknown affinity.



FIG. E234. Late Jurassic and Cretaceous stratigraphic distribution of rudist families, more plastic and rapidly evolving ones distinguished by oblique-ruled pattern (Coogan, n).



FIG. E235. Diagram indicating effects of tangential components in growth of various bivalve shells— Glossidae (1), Chamidae (2), Hippuritacea (3-6) (1024a).

- 1. Glossus; 1a, lying on LV; 1b, lying on RV.
- Chamids; 2a, normal Chama viewed from dorsal side, lying on LV; 2b, inverse Pseudochama, lying on RV.
- 3. *Heterodiceras* (Diceratidae), with "normal" dentition, viewed from dorsal side, attached by LV.
- 4. Requienia (Requieniidae), with "normal" dentition, viewed from dorsal side, attached by LV.
- 5. Caprina (Caprinidae), attached by RV; 5a, C. adversa, with almost planospirally coiled LV, viewed from dorsal side; 5b, same, viewed from left side.
- 6. Hippurites sp. (Hippuritidae), attached by RV; 6a, long. sec.; 6b, posterodorsal side view showing position of Ep and Sp pillars inside shell.

[Ligament shown plain where exposed, indicated by broken line where enclosed by shell. Arrows mark locations of inhalant and exhalant apertures. Explanation: *am*, *pm*, anterior and posterior myophores; *Ep*, *Sp*, internal pillars; *lig*, ligament.]



these features are known from different families and subfamilies. YONGE (1024a) has recently emphasized a highly developed tangential component of shell growth in rudists and an associated lateral extension and coiling of the umbonal regions of the shell with attachment as the cause of great bilateral asymmetry in rudists (Fig. E235).

DENTITION

Across the whole spectrum of rudist families runs a trend toward modification of dentition from the "primitive" diceratid type (Fig. E236,2), which itself is a modification of heterodont dentition by reduction in tooth number, to extremes of the caprinid, radiolitid, and hippuritid dentitions.

From the simple, slightly unequally sized teeth of *Diceras* a trend in the radiolitids is directed toward enlargement and elongation of the FV teeth accompanied by reduction in size or loss of the AV tooth, or both. For example, in the oldest radiolitid genus, Agriopleura (Fig. E237,1), the FV teeth are already elongate. *Eoradiolites*, a younger genus, has similar FV teeth, as does Praeradiolites (Fig. E220,3), but has a narrow finger-like AV tooth (Fig. E237,2). A reduction in the AV tooth occurs in the bioradiolitine line (e.g., Distefanella, Fig. E237, 8) and complete loss of the tooth in other bioradiolitines (e.g., Biradiolites, Fig. E237, 4). A parallel evolutionary trend of reduction and loss of the AV tooth occurs in the Lapeirousiinae (e.g., Dubertretia, Fig. E237, 7). In the hippuritids the FV teeth are elongate (e.g., Hippurites, Fig. E220,1a), as in the radiolitids, and the AV tooth is reduced in size but not lost (e.g., Hippurites, E220,2; Barrettia, Fig. E237,10).

(On facing page).

FIG. E236. Morphological features of rudists (diceratids).

- 1. Diceras rotundatum BAYLE, U.Jur.(Raurac.), France (Coulanges-sur-Yonne); 1a, exterior, front view (AV at left) of type specimen showing strongly coiled beaks, ×0.7; 1b, interior of FV showing single tooth (2), ×0.7 (246).
- 2. Diagrammatic sketches of interiors of FV (2a) and AV (2b) showing teeth and sockets and muscle insertions (246).

[Explanation as for Fig. E220; 2', socket corresponding to tooth 2.]

In the Caprinidae distinct trends are less clearly discernible among the considerable diversity of tooth types. In some genera the teeth are large and porous (e.g., *Caprinuloidea*, Fig. E237,3), and located nearly in the center of the shell. In others they are reduced, apparently solid, and placed marginally (e.g., *Caprinula*, Fig. E237,5).

LIGAMENT SUPPORTS

Ligament supports of calcite and in some fossils calcite molds or casts of the flexible ligament are preserved in many rudists. In the primitive diceratid condition the ligament was coiled. In fact, it was already greatly modified from the primitive amphidetic ligament (Fig. E225). A general trend toward reduction in size of ligamental supports partly results from the strong tangential growth component and consequent interumbonal growth of the ligament which may become functionless. The ligament moves to the outside of the shell as rudists evolved from slightly unequally coiled diceratid-requieniid shape to extremely unequal vaselike forms of the radiolitids and hippuritids. Among radiolitids an internal ligament support occurs (e.g., Eoradiolites, Fig. E237,2), which becomes reduced in size and eventually is lost in branches of three separate radiolitid subfamilies. The bioradiolitines, which probably evolved from one of the radiolitine genera, have no internal ligament ridge (e.g., Biradiolites, Fig. E237,4; Chiapasella, Fig. E238,1). In the Sauvagesiinae the ligamental ridge is present in the older genus Sauvagesia (Fig. E238,4) but is lost in other genera (e.g., Durania, Fig. E237,9; Tampsia, Fig. E238, 2). In the Lapeirousiinae a similar loss occurs. Praelapeirousia has a weak ligament ridge and other genera lack it entirely (e.g., Lapeirousia, Dubertretia, Fig. E237,7). In the caprinids the ligament has a strong external expression in the form of a groove and commonly is curved internally. The hippuritids, starting from a Turonian shell with a relatively small ligament ridge formed by infolding of the shell wall (e.g., Hippurites, Fig. E220,1b), developed enormously elongate and thick ligament pillars (e.g., Vaccinites, Fig. E237,6; Torreites, Fig. E238,5). In another hippuritid line the

Bivalvia—Heterodonta



FIG. E237. Morphological features of rudists (dentition).

- 1. Agriopleura blumenbachi (STUDER) (Hippuritidae), L.Cret.(Barrem.), France (Brouzet); side view of FV showing projecting teeth, ×0.6 (911).
- Eoradiolites davidsoni (HILL) (Radiolitidae), L.Cret.(mid.Alb.), USA(Texas); transv. sec. AV, ×1.9 (Coogan, n).
- Caprinuloidea sp. (Caprinidae), U.Cret. (Cenoman.), Mexico; schematic transv. sec. FV (714).
- Biradiolites canaliculatus D'ORBIGNY (Radiolitidae), U.Cret.(Coniac.), France; transv. sec. AV, ×0.6 (277).
 - (Continued on facing page).

ligament ridge was modified to a thin bulbous pillar (compare *Batolites*, Fig. E237,11, and *Pironaea*, Fig. E238,6). In a parallel line of evolution (*Praebarrettia*, Fig. E238,3 to *Barrettia*, Fig. E237,10) the ligament support was drawn out gradually until it became narrowed into a moniliform ray.

MUSCLE SUPPORTS

Adductor muscle supports of calcite, the **myophores**, are relatively stable morphological characters in the rudists. In the conservative diceratids the muscles are attached to part of the cardinal area or connect with it (e.g., *Diceras*, Fig. E236,2). Modifications of this scheme occur in the requieniids. As the shape of the AV valve changed markedly to vaselike, the myophores shifted laterally (e.g., *Eoradiolites*, Fig. E237,2; *Hippurites*, Fig. E220,2), while the apophyses became massive, grooved, elongate downward projections of the FV (Fig. E220, 1a,3).

In the radiolitids the elongation of the FV myophores occurs early in the Cretaceous. Agriopleura (Fig. E237,1), a Barremian and younger genus slightly evolved from the monopleurids, has short massive apophyses. In younger radiolitids (e.g., Praeradiolites, Fig. E220,3, Albian) the apophyses are elongate smooth and displaced 90 degrees from the ligament crest (Fig. 238,4). Still younger genera evolved highly serrated lateral apophyses margins as can be seen in Dubertretia (Fig. E237,7) and Dechaseauxia (Fig. E239,1b). The earlier evolutionary imprint of twisting still may be manifest internally in highly specialized genera and where it is marked by a greater extension of the anterior apophysis in the radiolitids (e.g., *Chiapasella*, Fig. E238,1) and hippuritids (e.g., *Praebarrettia*, Fig. E238,3; *Torreites*, E238,5).

Adductor muscle supports in the caprotinids and caprinids took an entirely different turn. In these families the development of marginal accessory cavities and canals between the body cavity and anterior wall provided a thin, long interior plate or wall for muscle attachment which can be seen in *Sellaea* (Fig. E239,3) and *Schiosia* (Fig. E239,2). In the caprotinids this wall became a projecting plate in *Polyconites* (Fig. E262,4b) the posterior myophore was a raised apophysis in the FV that fits into an alveole in the AV.

WALL STRUCTURE

Wall structure is a useful basis for classification in rudist families and accordingly several trends are discussed here briefly.

The radiolitids, which characteristically have a celluloprismatic wall with a thick outer layer of hollow prisms, display a major trend toward less dense, more open network outer shell walls in younger taxa. Early genera (e.g., Agriopleura, Fig. E240, 5; Sphaerulites, Fig. E240,2) have a compact reticulate outer wall. Younger genera (e.g., *Eoradiolites*, Fig. E240,1) have a compact to loosely open rectangular network. Sauvagesia (Fig. E238,4), Chiapasella (Fig. E238,1) and others have an open polygonal network. More complicated mixed wall structure of compact and open occurs in some later Cretaceous genera (e.g., Joufia, Fig. E240,6, and *Colveraia*, Fig. E240,4). Wall structure appears to be a relatively

- (FIG. E237).
- 5. Caprinula sp. (Caprinidae), U.Cret.(Cenoman.), Eu.; schematic transv. sec. FV (252).
- 6. Vaccinites marticensis DOUVILLÉ (Hippuritidae), U.Cret.(Coniac.), France; transv. sec. at level of AV with projecting teeth and posterior myophore of FV, $\times 1$ (910).
- Dubertretia kelleri Cox (Radiolitidae), U.Cret. (Maastricht.), Syria; transv. sec. at level of AV viewed toward commissure, ×0.9 (468).
- Distefanella salmojraghii PARONA (Radiolitidae), U.Cret., Italy; transv. sec. AV, ×0.6 (719).
- 9. Durania cornupastoris DES MOULINS (Radioliti-

dae), U.Cret.(Turon.), France; transv. sec. at level of AV with projecting teeth and myophores of FV, $\times 0.6$ (268).

- Barrettia monilifera WOODWARD (Hippuritidae), U.Cret. (Campan.), W.Indies; transv. sec. AV, ×0.3 (269).
- 11. Batolites organisans DE MONTFORT (Hippuritidae), U.Cret. (Santon.), S.France (Pyrénées, Rennes-les-Bains); transv. sec. at level of AV with projecting teeth and posterior myophore of FV, $\times 2$ (269).

[Explanation as for Fig. E220; also Es, Ss, pseudopillars.]



FIG. E238. Morphological features of rudists (ligament supports).

- 1. Chiapasella cubensis RUTTEN (Radiolitidae), U.Cret.(Maastricht.), Cuba; transv. sec. at level of AV with projecting teeth and myophores of FV, $\times 1.5$ (810).
- Tampsia bishopi STEPHENSON (Radiolitidae), U. Cret.(?Maastricht.), Mexico, 2a, colony viewed from above, ×0.17; 2b, transv. sec. ant. part of AV, ×1 (886).
- 3. Praebarrettia sparcilirata (WHITFIELD) (Hippuritidae), U.Cret. (Maastricht.), Cuba; transv. sec. AV, ×0.3 (67).

conservative character which nevertheless has a certain adaptive potential.

Among the caprinids the pattern of marginal canal development in the shell wall shows a remarkable tendency to repeat a sequence of increasing complexity in several lines of caprinid evolution (MACGILLAVRY, 561). Early caprinid genera in different lines commonly have simple undivided or bifurcating radial plates that make a pattern of marginal pyriform canals. As the plates became increasingly polyfurcated,

- Sauvagesia sharpei (BAYLE) (Radiolitidae), U. Cret.(Turon.), Port.; transv. sec. at level of AV with projecting teeth and myophores of FV, ×0.6 (268).
- Torreites sanchezi (DOUVILLÉ) (Hippuritidae), U.Cret., Cuba; transv. sec. AV, ×0.6 (281).
 Pironaea polystylus (PIRONA) (Hippuritidae),
- Pironaea polystylus (PIRONA) (Hippuritidae), U.Cret.(Maastricht.), Italy; transv. sec. at level of AV with projecting teeth and posterior myophore of FV, ×0.3 (269).
- [Explanation as for Fig. E220.]

rows of marginal polygonal canals appeared on the periphery of the shell. In the Early Cretaceous of the Western Hemisphere, marginal canal development can be traced in the sequence of genera Amphitriscoelus, Planocaprina, Coalcomana, and Caprinuloidea (Fig. E241), spanning the Aptian to late Albian. In the Eastern Hemisphere an analogous sequence of canal development occurs in mainly the Cenomanian genera Caprina, Schiosia, Orthoptychus, and Sphaerucaprina (Fig. E241). Similar de-



FIG. E239. Morphological features of rudists (muscle insertions).

- 1. Dechaseauxia costata TAVANI (Radiolitidae), U.Cret.(Maastricht.), Somalia; 1a, side view of AV, $\times 0.2$; 1b,c, transv. sec. AV, $\times 3.3$, $\times 4.6$ (904).
- 2. Schiosia schiosensis Вöнм (Caprinidae), U.Cret., Alps; schematic transv. sec. FV (Dechaseaux, after Parona).
- 3. Sellaea orbignyi DI STEFANO (Caprotinidae), U. Cret. (Cenoman.), Italy; 3a,b, schematic transv. secs. AV and FV (Dechaseaux, after di Stefano).

velopment of canal patterns in the line (Fig. E260,4)-Caprinula (Fig. Offneria E257,4b) and the line Plagioptychus (E260,2b)-Mitrocaprina (E260,3) confirm the highly adaptive nature of the development of multiple marginal canals by polyfurcation of radial plates. The superficial homeomorphy between genera such as Sphaerucaprina and Caprinuloidea or Caprina and Planocaprina was a source of taxonomic confusion among workers who first tried to identify Western Hemisphere rudists.

SIPHONAL STRUCTURES

External opening to the shallow sea of predators, contaminants, and fluctuating salinities and oxygen content is served by the siphons. Expected adaptations induced by environmental pressure are well displayed in siphonal structures of the radiolitids and hippuritids. In the radiolitids the siphonal positions are marked by bands or grooves in both valves; this is the usual morphological expression of the siphons. In a few genera of different subfamilies additional intramural siphonal structures are developed. Yonge's (1027a) stimulating comparison of chamid and rudist soft parts calls for a different interpretation of the position of siphonal openings than commonly accepted (KLINGHARDT, 475). YONGE recognized water currents and cleaning currents (Fig. E242) but did not place them necessarily as coincident with the position of the siphonal bands or the pillars E and S.

In the radiolitine genus *Medeella* (Fig. 243,7) the siphonal supports take the form of cylindrical structures within the AV outer wall. As continuation of this feature, cylindrical fossettes are developed in the AV and operculiform arches in the FV of *Medeella (Fossulites)*(Fig. E243,1). Similar protective structures for the FV siphons develop in the bioradiolitine genus *Thyrastylon* (Fig. E243,2). The AV bands in

(Continued.)

- 4. Polyconites operculatus ROULLAND (Caprotinidae), L.Cret., Eu.; interior FV (Dechaseaux, after 267b).
- [Explanation as for Fig. E220.]



FIG. E240. Morphological features of rudists (Radiolitidae) (wall structure).

- 1. Eoradiolites davidsoni (HILL), L.Cret.(mid. Alb.), USA(Texas); part of transv. sec. showing AV inner and outer wall structure, X2 (Coogan, n).
- 2. Sphaerulites patera ARNAUD, U.Cret. (low. Turon.), France; 2a, AV from above, ×0.3; 2b, side view of AV siphonal bands, ×0.3 (23).
- 3. Hardaghia quadrata TAVANI, U.Cret. (Maastricht.), Somalia; AV from above, ×0.7 (904).
- 4. Colveraia variabilis KLINGHARDT, U.Cret. (Maas-

this genus are deeply sunken and in the FV the brim of the valve forms oval oscules above the AV siphonal bands. The subfamily Lapeirousiinae is characterized by intramural siphonal structures. In the AV these structures generally consist of tubular bands of polygonal cells (e.g., *Vautrinia*, Fig. E243,5-6) called pseudopillars. In the FV there are oscules or openings for the siphons.

Finally, an analogous development of oscules occurs in the hippuritid genus *Yvaniella* (Fig. E243,3-4) where a tubercle on the FV surface is traversed by two large tricht.), Italy; transv. sec. FV near commissure viewed from above, $\times 0.5$ (475).

- 5. Agriopleura blumenbachi (STUDER), L.Cret. (Barrem.), Switz.; transv. sec. at level of AV with projecting teeth and myophores of FV, ×0.7 (Pictet & Campiche, in 911).
- 6. Joufia reticulata Вöнм, U.Cret. (Maastricht.), Italy; transv. sec. at level of AV with projecting teeth and myophores of FV, ×0.2 (853).

[Explanation as for Fig. E220.]

canals. It is noteworthy that intramural siphonal structures are a Late Cretaceous phenomenon.

HIPPURITID PILLARS

The basic hippuritid stock, exemplified by *Hippurites*, has three extensions of the AV wall internally which are called pillars (Fig. E220,1b). The arrangement of the three pillars (usually lettered L, S (sortie) and E (entrée) following Douvillé carries through from Turonian to Maastrichtian in widespread and morphologically conservaEUROPE

NORTH AMERICA



FIG. E241. Morphological features of rudists (wall structure). Marginal canals and ventral radial plates in four European and four North American caprinid genera; AV transverse sections, $\times 0.9$ (Coogan, n).

VENTRAL



FIG. E242. Morphological features of rudists, AV interiors of *Hippurites (1)* and *Radiolites (2)* with indications of inhalant and exhalant water currents (full-line arrows) and cleaning currents (brokenline arrows), possible disposition of visceral mass and foot marked by light broken lines, teeth sockets solid black (1024a). [Explanation: am, pm, anterior and posterior myophores; lig, ligament.]

tive genera such as Hippurites, Hippuritella (Turon.-Maastricht., Fig. E263,4), and Vaccinites (Turon.-Maastricht., Fig. E237, 6). A trend toward increasing the number and length of pillars in both European and American lines of hippuritids is recognized. In the European line the increase in pillar number begins in *Batolites* (Fig. E237,11) which has numerous folds that do not project as far inward as the three pillars In Pironaea (Campan.-L, S, and E. Maastricht., Fig. E227,1), there are more than 12 pillars of lengths equal to those of L, E, and S. Many of these accessory pillars are elongate and reach 0.7 the distance to the center point of the AV. In the American line the marked increase in pillar number (15 to 20) occurs in *Praebarrettia* (Santon.-Maastricht., Fig. E238,3). The pillars extend toward the center and become narrow and beadlike (moniliform) in late growth stages. The final stage of this development occurs in *Barrettia* (Campan.-Maastricht.) where the AV is filled with 60 or more elongate beaded pillars or rays (Fig. E237,10). Lengthening of the pillars may occur independently of increase in pillar number as is evident in *Vaccinites* and *Torreites* (Fig. E238,5).

SYSTEMATIC DESCRIPTIONS

Family DICERATIDAE Dall, 1895

[Materials for this family prepared by COLETTE DECHASEAUX and A. H. COOGAN (subfamily divisions not recognized by DECHASEAUX, introduced by COOGAN)]

One value or both hornlike, coiled, with umbo directed anteriorly and outward. Valves generally subequal, attached by RV or unequal, attached by LV with free valve more or less operculiform. Surface ornamented by striae or finely radiating ribs. AV with two unequal teeth, small one anterior and large one posterior, separated by horseshoe-shaped socket; FV with strong conical tooth bearing small socket on its anterior face, bordered behind by large socket. Anterior muscle inserted in each valve to shell wall, posterior muscle insertion on plate that projects above shell (except in Heterodiceratinae in which AV muscles were attached to elongations of cardinal platforms). Long ligamentary groove between beak and most posterior element of hinge. U.Jur.(Oxford.)-L.Cret. (Valangin.).

This most ancient family of the rudists comprises genera or subgenera which are defined partly by mode of attachment of the shell. Fixation by the right valve is observable only in *Diceras*, whereas fixation is by the left valve in *Epidiceras* and *Heterodiceras*.

Subfamily DICERATINAE Dall, 1895

[nom. transl. COOGAN, herein (ex Diceratidae DALL, 1895)]

Shell attached by RV (AV), which has large conical posterior tooth; LV (FV) tooth hook-shaped. U.Jur.(U.Oxford.-L. Kimmeridg.).

N777



FIG. E243. Morphological features of rudists (siphonal structures).

- Medeella (Fossulites) undaesaltus Astree (Radiolitidae), U.Cret.(Coniac.), France (Aude); 1a, oblique side view of both valves, ×0.7; 1b, side view of AV, ×0.7; 1c, transv. sec. AV, ×0.7 (24).
- 2. Thyrastylon adhaerens (WHITFIELD) (Radiolitidae), U.Cret. (Maastricht.), Jamaica; 2a, adjoined shells, one at left showing oscules (So and Eo) in FV, $\times 0.7$; 2b, both valves, FV with Eo and So oscules, $\times 0.7$; 2c, transv. sec. AV, $\times 4$ (131).
- 3. Yvaniella maestrichtiensis (MILOVANOVIĆ) (Hippuritidae), U.Cret. (Maastricht.), Yugosl.; vertical sec. FV and upper part of AV, $\times 0.7$ [c, canal of central excrescence; p, pore] (624).

- Same, E.Serbia; oblique view of both valves, ×0.6 (628).
- 5-6. Vautrinia syriaca (VAUTRIN) (Radiolitidae), U. Cret. (Maastricht.), Syria; 5, transv. sec. part of AV at level of pseudopillar, weathered, showing small columns in relief above prismatic tissue, ×0.7 (933); 6a, lat. view AV, ×0.3 (933); 6b, transv. sec. AV, ×0.5 (933).
- Medeella sp. (Radiolitidae), U.Cret., France; transv. sec. AV showing part of cylindrical siphonal structure, ×0.6 (24).

[Explanation: c, canal; Eb, Sb, siphonal bands; Eo, So, oscules; Ep, Sp, internal pillars farthest and nearest L; L, ligament ridge; p, pore.]



FIG. E244. Diceratidae (Diceratinae) (4); (Heterodiceratinae) (1-3), (Epidiceratinae) (5) (p. N778-N779). [Explanation: am, pm, anterior and posterior myophores; 1, 3, anterior and posterior teeth of FV; tooth of AV; 1', 3', sockets in AV for reception of correspondingly numbered FV teeth; 2', socket for reception of tooth 2.]

Diceras LAMARCK, 1805, p. 299 [*D. arietinum; M] [=Diceratia OKEN, 1815 (nom. van.) (ICZN rejected publ.); Dicerata RAFINESQUE, 1815 (nom. van.)]. Shell robust, valves subequal, both with partially coiled beaks. U.Jur.(U.Oxford.-L.Kimmeridg.), Eu.-N.Afr.—FIG. E244,4. *D. arietinum, Raurac, France (Saint-Mihiel); 4a,b (LV=FV), ×1 (246). [Also Fig. E236,1-2; E223,1a,b.]

Subfamily HETERODICERATINAE Pchelintsev, 1959

[nom. transl. Coogan, herein (ex Heterodiceratidae PCHELINTSEV, 1959)]

Valves large, inequivalve, attached by LV (AV); RV (FV) smaller, may be operculiform, posterior tooth in RV large, trapezoidal to triangular, projecting upward; LV (AV) tooth arcuate, muscles attached to elongation of cardinal platform. U.Jur. (Tithon.)-L.Cret.(Valangin.).

Heterodiceras MUNIER-CHALMAS in HEBERT, 1870, p. 116 [*Diceras luci DEFRANCE, 1819, p. 177; M] [=Pseudodiceras GEMMELLARO, 1876, p. 50 (type, Diceras carinatum GEMMELLARO; SD Cox herein)]. FV small, may be operculiform, both muscle insertions of FV on elongations of cardinal platform and curved outer edge of body cavity, not on prominent myophore. U.Jur.(Tithon)-L. Cret.(Valangin.), Eu.-USSR.—FIG. E244,1a. *H. luci (DEFRANCE) communis (BöHM), Jur.(Portland.), France; LV, $\times 0.5$ (246).—FIG. E244, lb,c. H. sp.; diagram showing features of hinge; lb,c, AV, FV (252).

Mesodiceras PCHELINTSEV, 1959, p. 82 [*M. enissalense; OD]. Differs from Heterodiceras in having operculiform FV and posterior muscle insertions of FV attached to cardinal platform by narrow subdental bridge. U.Jur.(Oxford.-Kimmeridg.), USSR(Crimea).—FIG. E244,2. *M. enissalense; int. view, 2a,b, AV, FV, ×0.7 (722).

Paradiceras PCHELINTSEV, 1959, p. 96 [*Chama speciosa MÜNSTER in GOLDFUSS, 1837, p. 205; OD]. FV not operculiform, posterior cardinal tooth trapezoidal to triangular, posterior muscle insertions of AV on elongation of cardinal platform, anterior separate. U.Jur.(Tithon.), Eu.-USSR (Crimea).—FIG. E244,3. P. alsuense PCHELINTsev; 3a, AV, $\times 0.7$; 3b, both valves diagram. (722).

Subfamily PLESIODICERATINAE Pchelintsev, 1959

[nom. transl. Coogan, herein (ex Plesiodiceratidae PCHELINTSEV, 1959)]

Shell irregular, attached by larger LV (AV). RV (FV) usually operculiform, beaks moderately curved, posterior muscle sertion of FV extending toward and behind posterior tooth, posterior cardinal tooth strongly curved, reaching laterally nearly across valve. U.Jur.(Oxford.-Kimmeridg.).

Plesiodiceras MUNIER-CHALMAS, 1882, p. 478 [*Diceras valfinense Böhm, 1881, p. 160; OD]. FV with large cardinal and smaller but prominent anterior tooth; posterior muscle insertion on cardinal platform, extending behind posterior tooth. U. Jur. (Up. Oxford. - Kimmeridg.), Eu. — FIG. E245,2a. P. sp., diagram showing features of FV hinge (246). — FIG. E245,2b,c. P. muensteri (GOLDFUSS), Kimmeridg., France; 2b,c, AV, FV, ×1 (246).

Eodiceras PCHELINTSEV, 1959, p. 37 [*Diceras ursicinum THURMANN, 1852, p. 278; OD]. Shell small, moderately inequivalve; FV hinge primitive, posterior tooth large, transversely elongate subtriangular, anterior muscle insertion extending partly onto hinge area. U.Jur.(Oxford.), Switz.-USSR.—FiG. E245,1b,c. *E. ursicinum (THURMANN), Lusit., Crimea; 1b, ant., 1c, post., ×1 (722).—FiG. E245,1a. E. eximium (BAYLE), Jur. (Kimmeridg.), Switz.; FV, ×1 (de Loriol in 722).

Subfamily EPIDICERATINAE Rengarten, 1950

[nom. transl. Coogan, herein (ex Epidiceratidae Rengarten, 1950)]

Shell with triangular to oval outline, weakly inequivalve, attached by LV (AV), dentition massive, close to megalodontid, cardinal area flattened, teeth and sockets set obliquely. U. Jur.(Oxford.) - L. Cret. (Valangin.).

- Epidiceras DOUVILLÉ, 1936, p. 332 [*Diceras sinistrum DESHAYES, 1824, p. 466; SD DECHASEAUX, 1952, p. 326]. Shell large, posterior part of valves flattened, furrowed; FV operculiform or elevated, smaller than AV. U.Jur.(Oxford.-Kimmeridg.), Eu.-USSR.—FIG. E244,5. *E. sinistrum (DES-HAYES), Raurac., France; FV, X1 (246).
- Megadiceras PCHELINTSEV, 1959, p. 72 [*Diceras beyrichi porrecta Вöнм, 1883; OD]. Much larger than Epidiceras, beaks drawn out, posterior muscle insertion in FV extended under cardinal area. U.Jur.(Tithon.)-L.Cret.(Valangin.), Eu.-USSR.



FIG. E245. Diceratidae (Plesiodiceratinae) (p. N779). [Explanation: *am*, *pm*, anterior and posterior myophores; 1, 3, anterior and posterior teeth of FV; 2', socket in FV for reception of tooth 2 of AV.]

Family REQUIENIIDAE Douvillé, 1914

[=Bayleidae MUNIER-CHALMAS, 1873 (rejected under Code Art. 23,b)] [Materials for this family prepared by Colette Dechaseaux and B. F. Perkins]

Inequivalve, attached by coiled LV (AV) which invariably is larger than operculiform RV (FV); hinge of *Diceras* type, with single tooth in LV (AV) and two teeth in RV (FV), although toothlike thickening behind posterior socket of LV (AV) may be present in some shells (*Requienia, Matheronia*),



FIG. E246. Requieniidae (p. N781, N783). [Explanation: 1, 3, anterior and posterior teeth of FV; 2, tooth of AV.]

posterior tooth of RV (FV) generally more developed than anterior; siphonal bands more or less clearly present on posterior side of LV (AV); anterior muscle insertion on shell wall in LV (AV) and either on shell wall or prolongation of cardinal platform in RV (FV); posterior muscle inserted to shell wall in LV (AV) or on myophore plate beneath cardinal platform and on variously developed plate in RV (FV). U.Jur.(Tithon.)-U.Cret.(Maastricht.).

Genera comprised by the family Requieniidae are distinguished from one another by relative size of the teeth and by form and position of the posterior muscle insertions. They retain some features of the Diceratidae, but new characters make their appearance in them, for example, so-called siphonal bands (*Requienia, Toucasia*) and accessory cavities (*Bayleia*). These occur also in other rudist families, siphonal bands being a constant feature of the Radiolitidae and accessory cavities constituting an essential attribute of the Caprotinidae.

Requienia MATHERON, 1843, p. 102 [*Chama ammonia Goldfuss, 1837, p. 205; OD] [=Requienites MATHERON, 1843 (obj.)]. Highly inequivalve; AV coiled in spiral of several whorls; FV forming flat spiral; ornament of growth wrinkles and fine radial ribs; sinuosities of growth lines on posterior side of AV define 2 siphonal bands; slight thickening behind posterior socket in AV of some species suggests tooth; AV muscle attachments on shell wall; FV anterior muscle insertion on shell wall, posterior muscle insertion on plate projecting above cardinal platform; pallial line entire. L.Cret.(Valangin.)-U.Cret.(Senon.), Eu.-N.Afr.-S.Am.-N.Am.-E.Afr.—FIG. E247,3. *R. ammonia (GOLDFUSS), L.Cret. (U.Barrem.), France (Brouzet); both valves, $\times 0.5$ (278a).—Fig. E246,1. R. sp., diagrams showing features of hinge, 1a,b, AV and FV int., ×0.7 (252).

Apricardia GUÉRANGER, 1853, p. 36 [*A. carinata; M]. External shell form as in *Toucasia*; AV hinge unknown; posterior tooth of FV large; posterior muscle insertion in both valves on plate passing below cardinal platform, plate of FV small and oblique to valve surface. U.Cret.(Cenoman.-Senon.), Eu.-N.Afr.-E.Afr.-Syria-Mexico.——FIG. E246,3. A. sp., diagram showing features of FV hinge, ×0.7 (252).

Bayleia MUNIER-CHALMAS, 1873, p. 74 [*B. pouechi; OD]. External shell form, AV hinge and AV arched ligament ridge as in *Toucasia*; FV large coil; anterior muscle insertion on shell wall in both valves; AV posterior muscle insertion on plate passing beneath cardinal platform; FV posterior muscle insertion on projecting plate thickened distally and attenuated proximally; FV with 3 small posterior accessory cavities, 1 below ligament and 2 others separated by muscle attachment plate. U.Cret.(Campan.-Maastricht.), S. France-Alg.—Fig. E246,2. Bayleia sp., diagram showing features of hinge; 2a, AV; 2b, FV, $\times 0.7$ (252).

- **Bayleoidea** PALMER, 1928, p. 35 [*B. clivi; OD]. External shell form similar to that of *Toucasia*; AV loosely coiled, keeled; FV nonspiral semioperculiform; hinge greatly reduced; AV posterior muscle insertion on projecting plate, FV posterior muscle insertion on thin(?) plate separated from shell wall by accessory cavity; anterior muscle insertions unknown. U.Cret.(Turon.), Mexico.— FIG. E246,4. *B. clivi; both valves, $\times 0.7$ (Perkins, n; courtesy L. G. Hertlein).
- Kugleria BOUWMAN, 1938, p. 41 [*Toucasia steinmanni SCHNARRENBERGER, 1901, p. 20; SD PER-KINS herein]. External shell form similar to that of Toucasia; AV usually carinate, spirally coiled; FV flattened with several spiral whorls; posterior tooth of FV large and strongly projecting, anterior tooth reduced; FV posterior muscle insertion on plate forming extension of cardinal platform, anterior muscle insertion larger than posterior. U.Cret.(Cenoman.), Eu.(Italy)-W.Indies(Trinidad. —FIG. E246,6. K. macgillauryi BOUWMAN, Trinidad; 6a, FV int.; 6b, FV post. profile; 6c, FV ext., $\times 1$ (after 78).—FIG. E247,4. *K. steinmanni (SCHNARRENBERGER), Italy(Appennines); ant. view of both valves, $\times 0.5$ (834a).
- Matheronia MUNIER-CHALMAS, 1873, p. 74 [*Caprotina virginiae GRAS, 1852, p. 32; OD]. Inequivalve, AV low spiral coil, FV operculiform or convex; AV with small posterior tooth; FV anterior tooth weak or absent, FV posterior tooth large and projecting; FV muscle insertions on prolongation of cardinal platform; shell wall thick and lamellose. U.Jur.(Tithon.)-U.Cret.(Cenoman.), Eu.
- M. (Matheronia). AV muscle insertions on shell wall except in earliest known species, M. (M.) salevensis JOUKOWSKY & FAVRE, Tithon., Alps, in which posterior AV muscle insertion on myophore plate of Diceras type. L.Cret.(Valangin.)-U.Cret.(Cenoman.) (but unknown Hauteriv. Alb.), Eu.—Fig. E247,5a. M. (M.) munieri PAQUIER, L.Cret.(Barrem.), France; ext. of both valves, $\times 0.5$ (278a).—Fig. E247,5b.c. *M. (M.) virginiae (GRAS), L.Cret.(Urgon.), France; 5b-c, AV and FV int., $\times 0.5$ (after 716b).
- M. (Monnieria) PAQUIER, 1898, p. 343 [*Monnieria romani PAQUIER; M]. AV commonly keeled, ornamented with concentric wrinkles in some species; AV muscle insertions on shell wall. U.Jur.(Tithon.), S.France.—Fig. E247,2. *M. (M.) romani (PAQUIER), France(Gard); 2a,b,

AV int., ext., $\times 0.75$; 2c,d, AV and FV int. (diagram.), $\times 0.4$ (after 716a).

- M. (Hypelasma) PAQUIER, 1898, p. 846 [*Hypelasma colloti PAQUIER, 1898; M]. Very inequivalve; AV anterior muscle insertion on shell wall, posterior muscle insertion on weakly developed plate passing under cardinal platform (*Diceras* type). U.Jur.(*Tithon.*), Eu.(S.France).——FiG. E247,1. *M. (H.) colloti (PAQUIER), France (Gard); Ia,b, both valves and AV int., ×0.75 (after 716a).
- **Pseudotoucasia** DOUVILLÉ, 1911, p. 82 [**Toucasia* santanderensis DOUVILLÉ, 1889, p. 632; M]. Posterior muscle insertion of FV on plate lying parallel to shell wall surface and attached to shell wall by plate normal to the surface; teeth as in *Toucasia*. L.Cret.(Apt.), Eu.(Spain).—FIG. E249,1. *P. santanderensis (DOUVILLÉ); oblique section RV showing elevated myophore plate, $\times 0.5$ (after 267c).
- Toucasia MUNIER-CHALMAS, 1873, p. 74 [*Requienia carinata MATHERON, 1843, p. 104; OD] [=Caprotina d'Orbigny, 1842 (suppression proposed) ICZN pend.]. Valves keeled, carinate, or frilled with shallow siphonal bands on posterior side of AV; Diceras-type hinge but AV tooth less projecting and AV anterior socket shallower than in Diceras; anterior muscle insertions on shell wall in both valves, slightly depressed in AV; FV posterior muscle insertion on plate projecting obliquely from shell wall, with upper edge free or attached to lower surface of cardinal platform; posterior part of AV posterior muscle insertion on shell wall, anterior part raised and forming plate which passes under cardinal platform, as in Diceras. L.Cret.(Barrem.)-U.Cret.(Cenoman.), Eu.-N.Afr.-N.Am.-Fig. E246,5; E249,2. *T. carinata (MATHERON); E246,5, both valves, $\times 0.7$ (Dechaseaux, n); E249,2a,b, AV and FV int., ×1.5; E249,2c, FV transv. sec. showing post. myophore, ×0.5 (E249,2a,b, after 716b; E249,2c, after 267c).---Fig. E248,1. Toucasia sp.; 1a,b, AV and FV int. (diagram) showing hinge features (252).

Family MONOPLEURIDAE Munier-Chalmas, 1873

[=Gyropleuridae MAcGILLAVRY, 1935] [Materials for this family prepared by COLETTE DECHASEAUX and B. F. PERKINS]

Inequivalve (except Valletia); RV (AV) attached, larger; LV (FV) with two equal or unequal teeth; RV (AV) with single tooth; muscle insertions generally on extensions of cardinal platform. L.Cret. (Valangin.)-U.Cret.(Maastricht.), U.Eoc.

Monopleura MATHERON, 1843, p. 105 [*M. varians; SD KUTASSY, 1934, p. 113][?=Dipilidia MATH-ERON, 1843, p. 111 (type, D. unisulcata)]. AV



FIG. E247. Requieniidae (p. N781, N783).



FIG. E248. Requieniidae (p. N783). [Explanation: 1,3, anterior and posterior teeth of FV; 2, tooth of AV.]

conical, spirally twisted; FV operculiform or coiled in low spiral; exterior ornamented with unequal ribs extending from apex to commissure; 2 teeth of FV conical, subequal; single tooth of AV oval in section, usually transverse to cardinal platform; ligamental groove arched according to degree of spiral twisting or coiling; muscle insertions in both valves on prolongations of cardinal platform. L. Cret. (low. Valangin.) - U. Cret. (Maastricht.), Eu.-N.Am.-Jamaica.-Fig. E250, 3a; E252,1. *M. varians, Barrem., France (Brouzet); E250,3a, both valves, $\times 1$; 252,1a,b, AV and FV int., $\times 1$ (both after 278a).—Fig. 250, 3b. M. marcida WHITE, Alb., USA(Texas); dorsal view of both valves, $\times 1$ (Perkins, n).-FIG. E251,3. Monopleura sp.; 3a,b, FV and AV int. (diagram.) showing hinge features (252).

- Araeopleura Cox, 1965, p. 731 [pro Stenopleura POČTA, 1889, p. 35 (non Stebbing, 1888)] [*Plagioptychus angustissimus Роста, 1887, р. 204; SD KUTASSY, 1934, p. 127]. AV compressed coil, flattened along anterior-posterior axis; FV claviform; FV teeth weak, separated by deep socket, muscle insertions on thickened areas of shell wall extending from cardinal platform along margins of body cavity; AV teeth and muscle inunknown. U.Cret.(Cenoman.), sertions Eu. (Czech.).——Fig. E250,2. *A. angustissimus (Počта); 2a,b, AV ant., FV int., ×1 (741c).
- Gyropleura DOUVILLÉ, 1887, p. 768 [*Requienia cenomanensis D'ORBIGNY, 1850, p. 261; OD]. AV exogyriform; FV operculiform or coiled in low spiral; teeth anterior, FV teeth subequal, small; AV posterior muscle insertion on plate posterior to posterior socket and forming extension of cardinal platform. L. Cret. (Valangin) - U. Cret. (Maastricht.), Eu.-Jamaica-N.Am.(Texas).—FIG. E250,5. Gyropleura sp.; 5a,b, FV and AV int. (diagram.) showing hinge features (252).
- Himeraelites DI STEFANO, 1889, p. 1 [*Monopleura (Himeraelites) vultur; SD KUTASSY, 1934, p. 123]. AV conical, straight; FV curved, elevated,

beak overhanging AV; FV, teeth subequal, AV tooth round to oval in section; cardinal platform extended toward valve interior in both valves; FV posterior muscle insertion on exterior surface of elevated plate or lamina. U.Cret.(Cenoman.), Eu.(Italy)-Mexico.-Fig. 252,5a. *H. vultur (DI STEFANO), Sicily; both valves, $\times 0.5$ (882a). -Fig. 252,5b,c. H. douvillei (di Stefano), Sicily; 5b,c, AV and FV int., $\times 0.75$ (after 882a). Paramonopleura Korobkov in Korobkov & Maka-RENKO, 1967, р. 135 [*P. ukrainica Коковкоv & MAKARENKO; OD]. Shell small; AV exogyroid, with cuneiform tooth, 1' circular, 3' divided by low ridge; FV operculiform, tooth 1 high, curved, tooth 3 marginal, biapical, socket deep. U.Paleoc., Cherkasskaya Oblast, USSR.—Fig. E251,1. *P. ukrainica; 1a,b, FV and AV ext., X2.7; 1c,d, FV and AV int., ×5.3 (Korobkov & Makarenko, 1967). [B. F. PERKINS. See additions, p. N868]

Petalodontia Počta, 1889, p. 61 [*Hippurites gemari GEINITZ, 1840, p. 60; SD KÜHN, 1932, p. 121]. Differs from Monopleura in having FV anterior tooth much larger than posterior; FV muscle insertions on myophore plates which are joined to teeth and project around sides of body cavity. U.Cret.(Cenoman.), Eu.(Czech.)-Mexico. ——FIG. E250,1. P. planoperculata (Počta),



FIG. E249. Requieniidae (p. N783).



FIG. E250. Monopleuridae (p. N783-N785). [Explanation: 1, 3, anterior and posterior teeth of FV; 2, tooth of AV.]

Czech.; 1a,b, LV int. and dorsal view, $\times 1$ (741c).—Fig. E252,4. P. felixi DouvILLÉ, Mexico (Coalcoman); 4a,b, transv. secs. parallel to commissure at level of AV with projecting teeth of FV myophore well below and close to it, $\times 0.5$ (after 270a).

- Simacia Počta, 1889, p. 39 [*S. minima; M]. AV conical, curved or coiled, small; AV tooth broad, swollen; anterior socket rounded and deep, posterior socket lacking; FV unknown. U.Cret. (Cenoman.), Eu.(Czech.).—Fig. E252,2. *S. minima; 2a,b, AV lat. and int. views, ×1.5 (after 741c).
- Valletia MUNIER-CHALMAS, 1873, p. 74 [*V. tombecki; OD]. Externally similar to Diceras; FV anterior tooth much larger than posterior; muscle insertions in both valves on extensions of cardinal platform. L.Cret.(Valangin.), Eu.—FIG. E250,4; E252,3. *V. tombecki, Alps; E250,4a,b, FV and AV int., X1 (Dechaseaux, n); E252,3a,b, AV and FV int., X0.75 (after 652a).—FIG. E251,2. Valletia sp.; FV and AV int. (diagram.) showing hinge features (252).

Family CAPROTINIDAE Gray, 1848

[nom. correct. GILL, 1871 (pro Caprotinadae GRAY, 1848)] [=Heterocaprinidae MUNIER-CHALMAS, 1873] [Materials for this family prepared by COLETTE DECHASEAUX and B. F. PERKINS]

Inequivalve; RV (AV) attached; LV (FV) with two subequal or unequal teeth; RV (AV) with single tooth; LV (FV) with cavities (accessory cavities) between shell wall and posterior muscle insertion and in some species between anterior muscle insertion and shell wall; similar but smaller cavities may be present in the AV. L.Cret. (Neocom.)-U.Cret.(Turon.).

Caprotina D'ORBIGNY, 1850, p. 236 [*Caprina striata D'ORBIGNY, p. 170; ICZN pend.¹] AV conical, spirally twisted, anterior muscle insertion on extension of cardinal platform along shell wall, posterior muscle insertion on posterior surface of plate extending from cardinal platform to posterior shell wall, posterior accessory cavity shallow and undivided; FV conical, strongly coiled, teeth not well developed, anterior muscle insertion on extension of cardinal platform and posterior on plate, separated from shell wall by two accessory cavities. L.Cret.(Neocom.)-U.Cret.(Turon.), Eu-

¹ The genus *Caprotina*, as erected by D'ORBIGNY in 1842, contained 10 nominal species none of which is included in the genus by modern authors, and it would be a senior synonym of *Toucasia* MUNER-CHALMAS, 1873, by strict application of the International *Code*. It would only be retained in the sense in which it has come to be used by attributing it to D'ORBIGNY, 1850, and by declaring *C. striata* to be its type species, setting aside any prior designations. An application to this effect is being submitted to the International Commission. [Note by L. R. Cox.]

N.Afr.—FIG. E253,2. *Caprotina* sp.; 2*a,b*, FV and AV int. (diagram.) showing hinge features (252).

- Chaperia MUNIER-CHALMAS (1873, nom. nud.), 1882, p. 493 [*Caprina costata D'ORBIGNY, 1839, p. 107; OD]. Differs from Caprotina in having slightly convex, operculiform FV; posterior accessory cavities of FV small and inconspicuous. U. Cret. (Cenoman.), Eu. (S. France)-Mexico.— FIG. E253,1. *C. costata (D'ORBIGNY), France; Ia,b, FV and AV int., X2; Ic, cluster of individual shells, X1 (695).
- Horiopleura MUNIER-CHALMAS in DOUVILLÉ, 1889, p. 639 [*Monopleura lamberti MUNIER-CHALMAS in Douvillé; SD PAQUIER, 1905, p. 56] [=Oriopleura DE LACVIVIER, 1884 (nom. nud.)]. AV exogyriform, ornamented with radial ribs except on siphonal bands which are smooth; AV posterior muscle insertion on a thickened platform somewhat projecting over body cavity, normal to straight line formed by tooth, sockets, and anterior muscle insertion platform; FV operculiform with a narrow, shallow posterior accessory cavity. ?L. Cret.(Barrem.), L.Cret.(Apt.)-U.Cret.(Cenoman.), Eu.-N.Afr.-India-Mexico.-Fig. E254,2a,c. *H. lamberti (MUNIER-CHALMAS), Alb., Spain (Pyrenees); 2a,b, AV int. and ventral ext., $\times 0.75$; 2c, AV vert. sec., X0.4 (2a,b, after 267d; 2c, after 561).—FIG. E254,2d. H. baylei (COQUAND), Apt., Spain(Pyrenees); FV int., X0.75 (after 267d).
- Pachytraga PAQUIER, 1900, p. 337 [*Sphaerulites paradoxa Pictet & CAMPICHE, 1869, p. 48; SD PAQUIER, 1905, p. 61]. AV conical, spirally twisted, tooth strongly projecting, posterior muscle insertion on posterior face of vertical plate connecting posteroventral side of tooth with posteroventral shell wall, posterior accessory cavity present, anterior muscle insertion on thickened area of shell wall, anterior accessory cavity may be present and divided into large canals by radial plates; FV conical, openly coiled, anterior tooth much larger than posterior, anterior muscle insertion on anterior face of plate connecting large anterior tooth with anteroventral shell wall, anterior accessory cavity simple and shallow or subdivided into large shallow canals by radial plates, posterior muscle insertion on shell wall, vertical plate connects ventral edge of anterior tooth with shell wall at ventral margin of posterior muscle insertion forming a large cavity connected to tooth socket but separated from shell cavity. L.Cret.(Urgonian facies), Eu.(S. France-Switz.-Bulg.)-Jamaica.-FIG. E253,4; E254,3. *P. paradoxa (PICTET & Самрісне); E253,4, FV int. (diagram.), ×0.7 (Dechaseaux, n); E254, 3a, b, AV sec. and ant. accessory cavities (canals), $\times 0.5$ (716c).



FIG. E251. Monopleuridae (p. N783-N785). [Explanation: 1, 3, anterior and posterior teeth of FV; 2, tooth of AV.]

- Polyconites ROULLAND, 1830, p. 166 (genus without nominal species) [*P. operculatus Douvillé, 1887, p. 778 (=Radiolites polyconilites D'ORBIGNY, 1842, p. 181); SM] [=Polyconilites D'ORBIGNY, 1842 (nom. van.); Heterocaprina MUNIER-CHAL-MAS, 1873 (obj.)]. AV conical, resembling Monopleura, tooth transverse, muscle insertions on thickened areas of shell wall, no accessory cavities; FV operculiform, anterior muscle insertion extends from cardinal platform along the shell wall, posterior muscle insertion on a recumbent plate projecting posteriorly from cardinal platform, several accessory cavities as in Caprotina. L.Cret.(Apt.)-U.Cret.(Cenoman.), Eu.-Syria.-Fig. E254,1. *P. operculatus (Douvillé), Cenoman., France; 1a,b, FV and AV int., ×0.75 (after 267b). [Also, Fig. E229,4.]
- Praecaprotina YABE & NAGAO, 1926, p. 126 [*Horiopleura yaegashii YEHARA, 1920, p. 39; OD]. AV



FIG. E252. Monopleuridae (p. N783-N785). [Explanation: am, pm, anterior and posterior myophores; 1, 3, anterior and posterior teeth of FV; 2, AV tooth.]

irregularly conical, tooth strongly projecting, anterior muscle insertion on extension of cardinal platform on thickened area of shell wall, posterior muscle insertion extends as erect plate from tooth to posteroventral shell wall, large posterior accessory cavity may be divided in early stages by radial plates; FV convex, teeth subequal, elongate anterior muscle insertion extends from cardinal platform along shell wall and is separated from it by shallow groove, posterior muscle insertion on thin nearly vertical plate, large posterior accessory cavity extends from dorsal to ventral border, vertical plate connects ventral edge of anterior tooth with shell wall at ventral margin of posterior muscle insertion forming large cavity connected to socket but separated from shell cavity as in Pachytraga. L.Cret., Japan.-Fig. E255,3. *P. yaegashii (YEHARA); 3a,b, AV and FV int., ×0.75 (after 1009a).

- Retha Cox, 1965, p. 731 [pro Ethra MATHERON, 1878 (non LAPORTE, 1833)] [*Ethra munieri MATHERON; SD PAQUIER, 1905, p. 59]. Valves in elongate loose spiral, FV larger, AV with deep ligamental furrow; AV tooth slightly projecting, anterior muscle insertion on thickened area of shell wall, posterior muscle insertion on posterior face of plate extending from cardinal platform to posteroventral shell wall, posterior accessory cavity wide and shallow; FV muscle insertions on thickened areas of shell wall extending from cardinal platform, no accessory cavities, vertical plate connects posteroventral edge of anterior tooth with shell wall at ventral margin of posterior muscle attachment forming large cavity connected to socket but separated from shell cavity as in Pachytraga. L.Cret.(Urgonian facies), Eu.(S.France). -FIG. E253,3; E255,1. *R. munieri (MATH-ERON);E253,3a,b, FV and AV int., ×1 (253,3a, Dechaseaux after Paquier; E253,3b, 716c); E255, 1, both valves, $\times 0.5$ (600b).
- Sellaea DI STEFANO, 1889, p. 20 [*Caprotina zitteli DI STEFANO, 1889, p. 28; SD KUTASSY, 1934, p. 142]. Both valves conical, AV straight, FV coiled; AV anterior muscle insertion on extension of cardinal platform and separated from shell wall by large accessory cavity divided by vertical radial plates into small cavities which in turn may be subdivided into small canals by 2 sets of vertical plates lying parallel to the shell wall, posterior myophore plate extending from tooth to posterior shell wall; FV with 1 elongate deep anterior accessory cavity and 2 smaller but deep posterior accessory cavities. L.Cret.(Albian)-U.Cret.(Cenoman.), Sicily-Apennines-USA(Texas)-Mexico.— FIG. E255,2a,b. *S. zitteli (DI STEFANO),



N787

FIG. E253. Caprotinidae (p. N785, N787). [Explanation: 1, 3, anterior and posterior teeth of FV; tooth 2 of AV; 2', socket of FV corresponding to tooth 2 of AV; am, pm, anterior and posterior myophores.]

Cenoman., Sicily; 2a,b, FV int., AV sec., $\times 0.75$ (after 882a).——FIG. E255,2c. Sellaea sp., Alb., USA(Texas), both valves, post. ext., $\times 0.5$ (Perkins, n).

Family CAPRINIDAE d'Orbigny, 1850

[=Caprinellidae GILL, 1871; Trechmannellidae Cox, 1933; incl. Anomoptychidae Vokes, 1967] [Materials for this family prepared by COLETTE DECHASEAUX and B. F. PERKINS with acknowledgment of assistance by L. R. Cox]

Inequivalve, RV (AV) attached, some species attaining large size; teeth and myophores well developed, massive in some species; accessory cavities present in most



FIG. E254. Caprotinidae (p. N785, N787).

N789



FIG. E255. Caprotinidae (p. N787, N789).

genera; pallial canals in pallial region of one or both valves. L.Cret.(Urgonian facies)-U.Cret.(Maastricht.).

In the Caprinidae generic distinctions have been based mainly upon the form and disposition of the pallial canals and accessory cavities. Both the canals and accessory cavities may vary in shape and arrangement, depending upon the distance from the apex that a section is made, and such variations rarely have been taken into account in the definition of caprinid genera. Many of the presently rather arbitrarily defined caprinid genera must be restudied before a phylogenetically sound classication of the assemblage can be derived.

[In original manuscript (modified inappreciably by L. R. Cox) DECHASEAUX divided caprinid genera into four informal groups, as follows: 1) forms considered to be most typical representatives of the family (Caprina, Caprinula, Neocaprina, Orthoptychus, Paracaprinula, Plagioptychus, Praecaprina, Sphaerucaprina), 2) variants possibly representing expression of regional differentiation (Amphitriscoelus, Antillocaprina, Caprinuloidea, Coalcomana, Kipia, Mitrocaprina, Offneria, Planocaprina, Sabinia, Schiosia), 3) forms considered to exhibit approach to the Radiolitidae (Coralliochama, Dictyoptychus, Ichthyosarcolites, Titanosarcolites), and 4) imperfectly known

forms questionably assignable to the Caprinidae only because of the presence of accessory cavities or canals (Bicornucopina, Cryptaulia, Immanitas, Lithocalamus, Palus). In my opinion and that of PERKINS, it is sufficient simply to record the grouping of genera as listed and preferably to arrange systematic descriptions alphabetically after the type genus. Group 4 of DechaseAux is given under the heading "Superfamily and Family Uncertain."—EDITOR.]

Caprina C. D'ORBIGNY, 1822, p. 105 [*C. adversa; SD PAQUIER, 1905, p. 69] [=Gemellaria MUNIER-CHALMAS, 1873, p. 75 (type, Caprina communis GEMMELLARO, 1865); Cornucaprina FUTTERER, 1892, p. 87 (type, Schiosia carinata Вöнм, 1892)]. AV conical, straight, smaller than FV, which is conical and strongly coiled; AV with projecting tooth anterior to ligamental groove, anterior muscle insertion on thickened area of shell wall, posterior insertion on suberect plate separated from shell wall by accessory cavity divided into smaller cavities by simple radial vertical plates; FV anterior muscle insertion on plate connecting anterior tooth with shell wall, large anterior accessory cavity divided by thin, vertical radial and transverse plates, posterior muscle attachment on shell wall, vertical plate connects anteroventral edge of anterior tooth with ventral shell wall forming a large cavity separated from body cavity; FV with one or two series of pyriform pallial canals in anterior, ventral and posterior regions. L.Cret.(Urgonian facies)-U.Cret.(Cenoman.), Eu.-N.Afr.-N.Am.—Fig. E256,1; E257,2. *C. adversa, Cenoman., France; E256,1, FV sec., ×0.8; E257,2a, AV sec., $\times 0.5$; E257,2b, both values, $\times 0.11$ (E256,1; E257,2a, after 267c; E257,2b, 695).

Amphitriscoelus HARRIS & HODSON, 1922, p. 130 [*A. waringi; M]. Both valves elongate, incurved but not coiled, small; AV tooth narrow, elongate in section, anterior socket large, posterior socket small but joined to large accessory cavity which is undivided, pallial canals more or less rectangular or rounded-triangular limited to anterior, dorsal and posterior regions; FV with small anterior accessory cavity, vertical wall joins anterior tooth with anteroventral border of posterior muscle insertion forming cavity separate from shell cavity, pallial canals same shape and arrangement as in AV. L.Cret.(Apt.), Trinidad-USA(Texas).-FIG. E257,1. *A. waringi, Trinidad; 1a,b, AV sec., viewed from apex so that posterior is on left, and FV sec., $\times 0.7$ (Perkins, n).

Antillocaprina TRECHMANN, 1924, p. 407 [*Caprinella occidentalis WHITFIELD, 1897, p. 193; M¹]. AV more or less conical, FV with coiled beak; FV with conical anterior tooth and crescentic or sigmoidal posterior tooth; internal ligamental groove; no accessory cavities; both valves with numerous small, mostly tabulate, polygonal or oval canals in inner shell wall layers, in teeth and in myophorous plates. U.Cret.(U.Senon.-Maastricht.), W.Indies(Antilles).—Fic. E257,3. *A. occidentalis (WHITFIELD), Maastricht., Jamaica; 3a, both valves, $\times 0.2$; 3b,c, AV oblique view and FV int., $\times 0.3$ (911a).

Caprinula D'ORBIGNY, 1847, p. 269 (genus without nominal species); 1850, p. 187 [*Caprina boissyi D'ORBIGNY, 1839, p. 169; SM]. AV conical, straight; FV conical, loosely coiled; muscle insertions as in Caprina; anterior and posterior accessory cavities in both valves and divided by thin radial vertical plates; vertical plate divides cavity joined to socket from shell cavity as in Caprina; pallial canals include inner polygonal series and outer pyriform series, polygonal series decreases in diameter from interior of valves outward. L.Cret.(Alb.)-U.Cret.(Cenoman.-Turon.), Eu.-Syria-N.Am.-Fig. E257,4. *C. boissyi (D'ORBIGNY), Turon., France; 4a,b, FV secs. near commissure and nearer apex, $\times 1$; 4c, AV sec. near commissure, $\times 1$ (after 267c); 4d, both valves, $\times 0.5$ (695).

Caprinuloidea PALMER, 1928, p. 59 [*C. perfecta; OD]. AV greatly elongated, straight to curved; FV much smaller, open to tightly coiled; teeth in both valves large and projecting, those of FV commonly strongly curved; AV tooth, sockets, and posterior accessory cavity similar to those of Amphitriscoelus; FV with vertical plate joining anterior tooth with ventral shell wall forming cavity separated from body cavity, no accessory cavities; pallial canals in both valves throughout shell wall, generally comprise inner polygonal series and outer pyriform series, rounded or polygonal canals may be present in myophorous plates and in teeth; shell cavity, tooth sockets, accessory cavity, and pallial canals may be tabulate. L.Cret. (Alb.), Mexico-USA (Texas)-W. Indies (Cuba-Jamaica).-FIG. E258,3. *C. perfecta, Mexico; FV int. (plate joining ant. tooth with shell wall broken), ×0.7 (Perkins, n). [Also Fig. E224,3.] Coalcomana HARRIS & HODSON, 1922, p. 132 [*Caprina ramosa Вöнм, 1898, p. 327; M]. Resembles Caprinuloidea in external form and internal structures; differs in having pyriform pallial only. L.Cret.(Alb.)-U.Cret.(Cenoman.), canals

¹ The genus was founded on specimens misidentified by TRECHMANN as Caprinella occidentalis and which Dr. L. J. CHUBB is describing as a new species, but the conception of the genus is not affected. [Note by L. R. COX.]



Fig. E256. Caprinidae (p. N790, N795).



FIG. E257. Caprinidae (p. N790, N792-N793).

Coralliochama WHITE, 1885, p. 9 [*C. orcutti; M]. Inequivalve; AV conical, tall; FV convex, beak broad and incurved; ligament marked by inflection of outer shell wall layer into inner layer; AV muscle insertions on shell wall, no accessory cavities; AV shell wall with small polygonal, closely tabulate canals throughout; FV anterior tooth joined to ventral shell wall by vertical plate as in *Plagioptychus*, no accessory cavities; FV shell wall with wide inner area of polygonal canals and marginal series of radially elongated pyriform canals, closely tabulate as in AV. U.Cret.(Senon.), USA(Calif.)-Mexico.— FIG. E258,2. *C. orcutti, Mexico (Baja Calif.); E258,2a, both valves, $\times 0.3$; E258,2b,c, AV and FV transv. secs., $\times 0.7$ (Perkins, n).



Fig. E258. Caprinidae (p. N792-N795).



FIG. E259. Caprinidae (p. N795-N797). [Explanation: am, anterior myophore; L, ligamental ridge.]

- Dictyoptychus Douvillé, 1905, p. 178 [pro Polyptychus Douvillé, 1904, p. 248 (non Huebner, 1816)] [*Polyptychus morgani Douvillé, 1904; M] [=Anomoptychus Douvillé, 1906, p. 56 (obj.); Trechmanella Cox, 1933, p. 388 (obj.)]. Very large, inequivalve; AV conical, slightly incurved, with 2 longitudinal swellings possibly representing siphonal bands; FV much depressed, with eccentric summit; ligamental structures absent, hinge teeth produced, myophorous plates elongate; FV with large accessory cavity behind anterior myophore; AV with accessory cavities outside cardinal structures; AV with thick compact external layer and internal layer with narrow elongate canals separated by bifurcate radial plates as in Plagioptychus. U.Cret.(U.Senon.), SW.Asia (Iran).—Fig. E256,2. D. persica (Cox); 2a, both valves, $\times 0.16$; 2b, FV transv. sec., $\times 0.5$; 2c, transv. sec. at level of AV with projecting teeth
- and myophores (inner black areas) of FV, $\times 0.5$ (2a, 176; 2b,c, after 176). Ichthyosarcolites DESMAREST, 1817, p. 51 [*1. tri-
- angularis; M] [=Ichthyosarcolithus HERMANN-SEN, 1846 (nom. van.); Caprinella D'ORBIGNY, 1847, p. 269 (obj.)]. Very large, inequivalve, strongly carinate; AV curved or loosely coiled with whorls not in contact; FV curved in same direction as AV, smaller; teeth of FV fused with myophores to form single plate which fits into notches in AV shell cavity wall, radiolitid fashion; no ligament; shell cavity obliquely tabulate with tabulae of AV sloping away from commissure toward convex side and those of FV sloping away from commissure toward concave side; both valves with small, rounded-polygonal canals irregularly distributed and few large round canals in some areas, canals not tabulate. L.Cret. (Urgonian facies)-U.Cret.(Turon.), Eu.-N.Afr.-?Iran-Canada-Cuba. -FIG. E258,4. *I. triangularis, Cenoman.; 4a, both valves, $\times 0.2$; 4b, transv. sec., $\times 0.3$ (695). Kipia HARRIS & HODSON, 1922, p. 133 [*K. trinitaria; M]. AV conical, short; FV capuloid; both valves with rectangular pallial canals formed by simple, thin radial plates and restricted to anterior and ventral shell wall, which is thin where pallial canals are lacking, myophores imperfectly known. L.Cret.(Apt.), W.Indies(Trinidad).—-Fig. E259, 1. *K. trinitaria; 1a,b, FV from above (shell wall eroded) and transv. sec., $\times 1.5$ (388a).
- Mitrocaprina BöHM, 1895, p. 102 [*Coralliochama bayani DOUVILLÉ, 1888, p. 725; OD]. Very inequivalve; AV smaller, more or less exogyriform, attachment area very large; FV slightly to highly elevated, coiled; AV posterior muscle insertion on obliquely erect plate, posterior accessory cavity present and not always separated from posterior tooth socket, no pallial canals; FV teeth projecting slightly, no accessory cavities, pallial canals comprise 1 or 2 inner rows of polygonal canals and 1 or more outer rows of pyriform or radially elon-

gate canals. U.Cret.(Turon.-Maastricht.), Eu.-W. Indies(Jamaica-Cuba).—Fig. E259,2a. *M. bayani (DOUVILLÉ), Turon., France; FV int., $\times 0.7$ (267c).—Fig. E259,2b,c. M. vidaldi DOUVILLÉ, Turon., Spain; 2b,c, FV and AV int., $\times 1$ (272). —Fig. E260,3. M. tschoppi (Palmer), Maastricht., Cuba; transv. sec., at level of FV with projecting tooth of AV, $\times 0.5$ (561).

- Neocaprina PLENIČAR, 1961, p. 41 [*N. nanosi; OD]. Known only from transverse sections of FV; anterior muscle insertion larger than posterior; anterior and posterior accessory cavities divided into smaller rectangular or oval cavities by thin radial vertical plates; pallial canals rectangular in section and formed by simple radial plates which bifurcate near outer shell wall anteriorly and posteriorly. U.Cret. (Cenoman.-Turon.), Eu. (Yugosl.).—-Fig. E259,6. *N. nanosi, Turon.; 6a,b, FV transv. sec. and hinge area sec., $\times 1$ (741b).
- Offneria PAQUIER, 1905, p. 82 [*O. rhodanica; OD]. External form resembling Praecaprina; AV conical, FV curved; cardinal apparatus and myophore arrangement similar to those of Praecaprina; AV with elongate, curved posterior accessory cavity divided by thin radial plates and in some species by discontinuous plate parallel to shell wall, anterior accessory cavity divided similarly, marginal canals when present in ventral areas indistinguishable from subdivided accessory cavities; FV with marginal canals usually around entire valve but may be missing in ventral area, polygonal and pyriform canals present but arrangement irregular. L.Cret.(Urgonian facies), Eu.(S.France).-—Fig. E260,4a,b. *O. rhodanica; 4a,b, FV and AV transv. secs., ×0.75 (after 716c).---Fig. E260, 4c. O. interrupta PAQUIER; FV transv. sec., X0.75 (after 716c).
- Orthoptychus FUTTERER, 1892, p. 91 [*O. striatus; M]. AV conical, small; FV strongly inflated with beak incurved; distinguished from *Sphaerucaprina* by presence in FV posterior shell wall of some septa transverse to radial plates. *U.Cret.* (*Cenoman.*), Eu.(Alps-Apennines).—FIG. E260, 1. *O. striatus; 1a,b, FV and AV int., ×0.5 (332a).
- Paracaprinula PIVETEAU, 1939, p. 34 [*P. syriaca; M]. Resembles Plagioptychus externally but less inequivalve; anterior pallial canals polygonal as in Caprinula, posterior canals of very unequal size limited by more or less oblique transverse plates. U.Cret.(Maastricht.), SW.Asia(Syria).— FIC. E259,4. *P. syriaca; 4a, both valves, ×0.2; 4b, shell wall transv. sec., ×2 (741a).
- Plagioptychus MATHERON, 1843, p. 114 [*P. paradoxus; SD KUTASSY, 1934, p. 172]. AV conical and straight or low and twisted; external ligamental groove; FV strongly convex with recurved beak; AV tooth erect and strongly projecting, muscle insertions on shell wall, no pallial canals;

FV muscle insertions on thickened plates projecting above cardinal platform, anterior tooth smaller than posterior, separated by deep socket, vertical plate extending from anterior tooth to ventral shell wall forming cavity separate from shell cavity as in *Caprina*, pallial canals comprise single series of pyriform canals in oldest species but in other species radial plates branch, forming several series of more or less pyriform canals, no accessory cavities. *U.Cret.(Cenoman.-Maastricht.)*,



FIG. E260. Caprinidae (p. N795-N797). [Explanation: 2, tooth of AV.]

© 2009 University of Kansas Paleontological Institute

Eu.-N. Afr.-Mexico-W.Indies(Jamaica-Cuba). — FIG. E259,5. P. arnaudi DOUVILLÉ, TUron., France; 5a,b, AV and FV int., $\times 0.7$ (267c).—FIG. E260,2a. *P. paradoxus, Turon., France; both valves, $\times 0.4$ (600a).—FIG. E260,2b. P. toucasianus MATHERON, TUron., France; FV transv. sec., $\times 0.5$ (after 267c).

- Planocaprina PALMER, 1928, p. 64 [*P. trapezoides; OD]. AV conical, straight to slightly curved; FV larger, coiled in open spiral; AV tooth marginal, posterior accessory cavity large and joined to posterior socket as in Amphitriscoelus; FV anterior tooth large, curved and marginal, posterior tooth rudimentary; pyriform pallial canals occurring in single series in both valves; polyabsent. ?L.Cret.(Alb.)-U.Cret. gonal canals (Cenoman.), Mexico-?USA(Texas).-Fig. E259, 3. *P. trapezoides, Mexico; 3a, both valves, X0.3; 3b, AV transv. sec., ×1.3; 3c, FV int., ×0.7 (3a, Dechaseaux after 714; 3b,c, Perkins, n).
- Praecaprina PAQUIER, 1905, p. 72 [*P. varians; OD]. External form resembling Caprina but much smaller, FV coiling rarely more than 1 whorl, ventral region of both valves marked by longitudinal depression bordered by 2 swellings; AV tooth strongly projecting, both muscle insertions on plates projecting from cardinal platform and separated from shell wall by accessory cavities usually divided into smaller cavities by vertical radial plates; FV anterior tooth larger, erect and median in position, muscle insertions on shell wall and extend from cardinal platform, vertical plate connects anterior tooth with ventral shell wall as in Caprina, rounded or oval pallial canals formed by simple radial plates in anterior, posterior and posteroventral areas. L.Cret.(Urgonian facies), Eu.-W.Indies(Trinidad) .- FIG. E261,2; E262,2. *P. varians, France; E261,2a, both valves, $\times 0.5$; E261,2b,c, FV and AV int., $\times 0.7$; E262,2, FV transv. sec., $\times 0.75$ (716c).
- Rousselia DOUVILLÉ, 1898, p. 151 [*R. guilhoti; M]. AV straight, conical; FV strongly convex; general form and hinge resemble Monopleura; FV anterior tooth large, crescentic, near shell cavity, posterior tooth small, marginal; FV muscle insertions on raised thickened areas of shell wall; no ligamental groove or cavity; AV with rounded to polygonal, tabulate canals in some marginal areas. U.Cret.(Maastricht.), Eu.(Pyrenees).—Fig. E261,1. *R. guilhoti, Spain (Lerida); AV int., ×1 (272).
- Sabinia PARONA, 1909, p. 303 [*S. aniensis; SD KUTASSY, 1934, p. 169]. Externally resembling *Plagioptychus;* both valves without accessory cavities; AV pallial canals polygonal to rounded throughout shell wall, few pyriform canals in outer part but not forming continuous series; FV pallial canals comprise an inner wide area of polygonal canals of nearly uniform size and outer marginal row of pyriform canals. U.Cret.(Senon.),



FIG. E261. Caprinidae (p. N797).

Eu.(Apennines-W.Serbia-Turkey).—FIG. E262, 3a. *S. aniensis, Maastricht., Apennines; FV sec., $\times 0.75$ (after 719b).—FIG. E262,3b. S. sublacensis PARONA, Maastricht., Apennines; AV transv. sec., $\times 0.75$ (after 719b).

- Schiosia Böhm, 1892, p. 144 [*S. schiosensis; OD]. Very inequivalve; AV low, strongly curved; FV larger, elongate, coiled; accessory cavities present in FV and possibly also in AV; FV pallial canals include single pyriform series in anterior, ventral and posterior areas, few polygonal and rounded canals in hinge area; AV interior not known. U. Cret. (Cenoman.-Senon.), Eu.(S. Alps)-NW.Asia Minor(Bithynia).——Fic. E262,5. *S. schiosensis, Turon., S.Alps; FV transv. sec., ×0.75 (after 719a).
- Sphaerucaprina GEMMELLARO, 1865, p. 212 [*S. woodwardi; M] [=Sphaerocaprina Douvillé,

N797
1910 (nom. van.)]. AV resembling that of Caprina; FV strongly convex, caplike, beak incurved but not coiled; AV anterior muscle insertion on shell wall, posterior on curved vertical plate extending from tooth to ventral margin, large posterior accessory cavity, no pallial canals;



Fig. E262. Caprinidae (p. N797-N799).

© 2009 University of Kansas Paleontological Institute

FV with dorsal and anterior accessory cavities, vertical wall connecting anterior tooth to ventral shell wall as in *Caprina*, anterior, ventral and posterior areas with 1 or 2 rows of polygonal pallial canals and outer row of pyriform pallial canals. *L.Cret.*(*Alb.*)-*U.Cret.*(*Cenoman.*), Eu.-N. Am.-W. Indies (Jamaica).—Fig. E262,1. * *S. woodwardi*, Cenoman., Italy; *Ia,b*, AV and FV transv. secs., $\times 0.75$ (after 274a).

Titanosarcolites TRECHMANN, 1924, p. 397 [*Caprinella gigantea WHITFIELD, 1897, p. 194; M] [=Diatretus Douvillé, 1926, p. 132 (obj.)]. Very large, subequivalve, with both valves curved or coiled; dorsal and anterior surfaces with rounded longitudinal ridges separated by angular furrows, posterior and ventral surfaces with angular ridges or flanges separated by rounded grooves; ligamental groove internal, comma-shaped in transverse section; cardinal apparatus as in Antillocaprina, tooth alveoles tabulate; posterior muscle insertion in FV on raised apophysis which fits into alveole of AV, anterior muscle insertion superficial; shell cavity small, tabulate; small polygonal canals throughout shell wall, teeth and myophores; large tubular canals, rounded, oval or reniform, present on anteroventral side only. U. Cret.(Maastricht.), USA(Texas)-Mexico-W.Indies (Jamaica-Cuba-Puerto Rico-Virgin Is.). ---- FIG. E262,4a. *T. giganteus (WHITFIELD), Jamaica; AV ext., ×0.35 (980a).----Fig. E262,4b. Titanosarcolites sp.; AV transv. sec., ×0.75 (Perkins, n).

Family HIPPURITIDAE Gray, 1848

[Materials for this family prepared by COLETTE DECHASEAUX and A. H. COOGAN, with acknowledgment of assistance by L. R. Cox]

Shell conical to elongate-cylindrical and inequivalve. RV (AV) larger than LV (FV) which is operculiform, slightly convex or flat. Internally RV (AV) shell wall has compact smooth inner layer and thicker outer layer which extends toward interior in three or more folds (ligamental ridge and two or more pillars or rays). Pillar nearer ligamental ridge is designated as "S," using the notation devised by DOUVILLÉ and accepted by most authors, and the other (generally more elongate) as "E" (Fig. E237, 11). Teeth and myophore well developed. H-shaped (in transv. sec.) tooth stands between two sockets, anterior one receiving anterior tooth of LV (FV), and between it and inner wall of valve is an accessory cavity. On posterior side of RV (AV), between tooth and pillar Sp, are two sockets, that nearer tooth 2 for reception of posterior tooth of LV (AV), and that nearer

Sp is for posterior myophore of LV (FV) (Fig. E220,2). Posterior muscle insertion in RV (AV) on side of socket dorsal to Sp, and anterior muscle insertion marked by superficial scar between anterior socket and pillar Ep. Cavities or canals very rare in RV (AV). LV (FV) may be porous and commonly has two oval openings (oscules) (Fig. E263,2b). In longitudinal section RV (AV) in genera of this family shows curved partitions with concave side facing upward toward living chamber. U.Cret.(Turon.-Maastricht.).

All elements observable in morphological study of the Hippuritidae (pores, ligamental ridge, teeth, pillars) occur in combinations that permit different genera to be defined. Important for determination of genera and species is the sector (L-Sp-Ep) occupied by the three principal folds—the ligamental ridge (L) and the pillars (Sp, Ep).

The pillars, pores and oscules are the most curious features of the hippuritids, and paleontologists have long tried to interpret them. DESHAYES and WOODWARD supposed that the pillars served for muscle attachment, but suggested different ways in which this may have been accomplished. BAYLE observed that the three folds have the same structure, and he considered that the muscles were not attached to them but to the wall of the shell. Douvillé, extending the conclusions reached from his work on Sphaeru*lites* and genera of the Requientidae and Monopleuridae to *Hippurites*, suggested that the pillars correspond to siphonal zones, and accordingly designated them as "S" (sortie, excurrent) and "E" (entrée, incurrent). This opinion was accepted widely, with its implication that a hippuritid possessed two siphons serving respectively for outflow and inflow of water currents. YONGE (1024a) has advanced other interpretations based on analogies with Chama. The presence of oscules in the FV exactly above extremities of the pillars was held to support this hypothesis, for a hippuritid with closed valves could be provided continuously with water circulation through siphons opening outward at the oscules. Oscules are not a constant feature of all Hippuritidae, however, and, according to some accounts, where they exist in earlier

growth stages they may later become obliterated.

Study of the structure of the pillars by means of thin sections has led to alternative hypotheses. KLINGHARDT (475aa) and WIONTZEK (1000) observed cavities within the pillars and suggested that each pillar was a "siphonal tube" which enclosed the siphon of the living animal. No orifice, however, has been observed at the base of the pillars (Fig. E263,1c) through which a siphon could have protruded or a current of water have passed, and it seems probable that the cavities are of secondary origin.



FIG. E263. Hippuritidae (p. N801-N802). [Explanation: Eo, So, oscules; Ep, Sp, internal pillars; L, ligamental ridge.]

© 2009 University of Kansas Paleontological Institute

Actually, the pillars are folds of the external layer of the shell (MILOVANOVIĆ, 622, 625; KÜHN, 491), similar to other folds known in various hippuritids. A whole series of observations throws doubt on the existence of siphons in the hippuritids, and the hypothesis that long ones were enclosed in the pillars should be rejected.

CHUBE (131) has suggested that the sole function of the pillars was to block the oscules of the upper valve when this was pulled down tightly by the adductor muscles, thus interrupting the passage of the respiratory currents through them when necessity arose (Fig. E263, *le*). The oscules themselves, he suggested, evolved in consequence of the gregarious habit of the hippurites (and other rudists in which they are found), their presence enabling interchange of water between the mantle cavity and the sea above the animal when interchange from the side may have been difficult or impossible.

Another theory recently has been advanced by VOGEL (942), who suggested that the pillars acted as supports of sensory organs or of accessory gills. As there are no living bivalves at all like the hippuritids, it is difficult to decide what role the observed morphological characters played in the biology of the animal.

If the siphons were short or lacking, circulation of water was perhaps provided by the pores. In addition, some authors have ascribed to the pores the function of a filter that screened off impurities harmful to the animal. The arrangement of canals in the FV is complex, but their organization, especially in *Yvaniella* (Fig. E243,4) seems to indicate that water circulation was made possible to some extent by this system of perforations when the valves were closed.

As the pillars blocked the oscules completely when the shell was closed, the hippuritids must have had to raise the FV slightly to allow circulation of water for respiration and feeding. The FV is veritably a lid placed over the AV in such a manner that the long teeth and posterior myophore are engaged by the long vertical sockets of the AV. Because of this, any rocking movement about the ligament is impossible and only elevation of the FV above the AV permits separation of one from the other. This lifting could have been effected by pressure in the shell interior, produced possibly by inflation of a soft organ such as the foot.

- Hippurites LAMARCK, 1801, p. 104 [*H. bioculata; M] [=Orthoceratites LAMARCK, 1799, p. 81 (suppressed ICZN Op. 613); Cornucopina THOMson, 1802, p. 245 (generic description without nominal species); Coralliolites VON SCHLOTHEIM, 1813, p. 36 (type, C. orthoceratoides; SD Coogan, herein); Pachynus RAFINESQUE, 1815, p. 140 (obj.); Dorbignya Woodward, 1862, p. 375 (obj.); Orbignia Stoliczka, 1871 (nom. van.); Orbignya FISCHER, 1887, p. 1064 (nom. van.); non Hyppurites VON SCHLOTHEIM, 1820, p. 351]. AV nearly cylindrical, smooth, bearing 2 furrows in some but not all species; ligamental ridge short or absent; pillars Ep and Sp distinct, L absent or slightly curved to pointed inflexion of wall; sector L-Sp-Ep greater than one-quarter circumference; FV nearly flat, with 2 oscules and simple linear, well-separated pores. U.Cret.(Turon.-Maastricht), Eu.-NE. Afr. (Somalia) - Asia-N. Am. - Antilles .-FIG. E263, 1a-e. *H. bioculata, U.Cret. (Senon.), France; 1a, FV ext., ×1.3 (269); 1b, transv. sec. viewed toward commissure, AV center pseudopillars Sp and Ep dark, $\times 1.7$; 1c, detail ant. part polarized light, $\times 2.7$; 1d, pillar Sp, polarized light, ×13; 1e, long. sec. AV, pillars white, oscular indentations above pillars, $\times 2$ (942).—Fig. E263,1f. H. canaliculatus ROLLAND DU ROQUAN, U.Cret., France; linear pores in FV, $\times 7$ (269). [Also Fig. E220,1-2,6.]
- Barrettia Woodward, 1862, p. 372 [*B. monilifera; M] [=Barretia MUNIER-CHALMAS, 1873 (nom. null.)]. Adult shell very large; AV elongate, recumbent, distinguished by up to 60 or more beaded (moniliform) rays in transverse section; Sp and Ep distinguishable by their swollen extremities, that of Sp being circular and that of Ep elongate elliptical; L indentifiable by reference to teeth; portion of valve between L and siphonal pillars greater than 0.3 of shell circumference; internal layer strongly developed, forming cellular tissue between folds and tabular below shell cavity. FV convex, operculiform, consisting of central boss from which radiate numerous rods, oscule fitting over pillar Sp, no Ep oscule. U.Cret. (Campan.-Maastricht.), W.Indies-Mexico.-Fig. E263,3. *B. monilifera, Jamaica; AV from above, ×0.2 (981). [Also Fig. E227,2; E237,10.]
- Batolites DE MONTFORT, 1808, p. 334 [*B. organisans; OD] [=Batholites GABB, 1862 (nom. van.); Bihippurites FUTTERER, 1896, p. 263 (type, B. plicatus FUTTERER)]. AV long, cylindrical, slender, shaped like organ pipe; internally like Hippurites, but differs in having outer shell layer with numerous folds which, however, do not give rise to supplementary pillars projecting toward



FIG. E264. Hippuritidae 1,3-6; unrecognizable (2) (p. N802-N803). [Explanation: Ep, Sp, internal pillars; L, ligamental ridge; pm, posterior myophore; R, anterior (extra) pillar; 1,3, anterior and posterior teeth of FV.]

shell interior; 3 distinct pillars; L short, area of pillars about 0.3 of shell circumference. FV with 2 oscules and linear pores. U.Cret.(Santon.), France-Austria-USSR.—Fig. E263,2. *B. organisans, Pyrenees; 2a,b, AV ext. and FV ext. (same individual), $\times 0.7$, $\times 2$ (269). [Also Fig. E237, 11.]

- Hippuritella DOUVILLÉ, 1908, p. 268 [*Hippurites maestrei VIDAL, 1878, p. 99; OD]. Differs from Hippurites in having simple or denticulate pores in FV. U.Cret.(Turon.-Maastricht.), Eu.-N.Afr. NE. Afr.(Somalia)-Asia-N. Am.——FIG. E263,4a.
 *H. maestrei (VIDAL), Santon., France (Pyrenees); AV int. view, ×2 (269).——FIG. E263,4b. H. sulcatoides DOUVILÉ, Campan., France; polygonal pores FV, ×3.5 (269). [Also Fig. E224,1.]
 Parastroma DOUVILÉ, 1926, p. 133 [*P. sanchezi; M]. AV wall mainly of small vesicular domelike folded tabulae; rays almost effaced, stems of rays Ep and Sp rudimentary near outer shell layer, occupying more than 0.3 of shell circumference.
- FV unknown. U.Cret. (Campan. Maastricht.), Cuba.—FIG. E263,5. *P. sanchezi; details of AV wall, 5a, transv. sec., 5b, long. sec., $\times 3$ (280).—FIG. E264,6. P. guitari (PALMER), Maastricht., Cuba; transv. sec. at level of AV with projecting teeth of FV, $\times 0.4$ (561).
- Pironaea MENEGHINI in PIRONA, 1868, p. 511 [*Hippurites polystylus PIRONA, 1868, p. 508;

M] [=Pironea Meneghini, 1868 (nom. nud.); Pyronea MUNIER-CHALMAS, 1873 (nom. null.); Pironaia BLANCKENHORN, 1934 (nom. null.); Peronea WHITFIELD, 1897 (nom. null.)]. Attaining large size; surface of AV with numerous longitudinal furrows; outer shell layer with many infoldings which give rise to secondary pillars or rays, some as prominent as ligamental ridge (L) and pillars (Sp, Ep), other smaller infoldings located between the more prominent ones and between Sp and Ep; sector L-Ep-Sp less than 0.25 of circumference value. FV flattened, with denticulate pores. U.Cret.(Campan.-Maastricht.), Eu.-Afr.-Syria-Asia-N.Am.-Cuba.-Fig. E238,6. *P. polystylus (PIRONA), Maastricht., Italy; transv. sec. AV, $\times 0.3$ (269).

- Praebarrettia TRECHMANN, 1924, p. 395 [*Barrettia sparcilirata WHITFIELD, 1897, p. 245; M]. Shell moderate in size. Differs from Barrettia in having fewer (15 to 40) rays which become moniliform only in late growth stages; rays L, Sp, Ep clearly distinguished, occupying more than 0.3 of shell circumference. U.Cret.(?Santon.-Maastricht.), W. Indies-S.Am.—FIG. E264,4. *P. sparcilirata (WHITFIELD), Jamaica; AV from above, $\times 0.3$ (981). [Also Fig. E238,3.]
- Rhedensia SÉNESSE, 1939, p. 227 [*R. mutans; OD]. AV with 3 distinct pillars, Ep, Sp, and L; pillar L elongate, about equal to Ep, set at small angle

to teeth; pillars occupying more than 0.25 circumference of shell. FV pores linear, marginally subpolygonal. U.Cret.(Up.Turon.), Eu. (France).——FIG. E264,3. *R. mutans; AV transv. sec., $\times 0.7$ (839).

- Tetracionites ASTRE, 1931, p. 269 [*T. mozambicus; M]. AV small, with 4 external furrows corresponding to 4 internal folds, Ep, Sp, L, and anteriorly placed extra pillar (R); FV unknown. U.Cret.(Coniac.), France-Madag.——FIG. E264,5. *T. mozambicus; diagram. sec. AV, $\times 1.3$ (22).
- Torreites PALMER, 1933, p. 99 [*Hippurites (Vaccinites) sanchezi Douvillé, 1927, p. 27; OD]. AV cylindroconical without well-marked external furrows; internally pillars Ep, Sp, L unequal, L very long, longer than shell radius; Sp twice length of Ep; sector L-Sp-Ep about 0.25 of circumference; outer shell layer thin, forming less well-developed folds than in Batolites. FV depressed-conical, with 3 radial grooves corresponding to L, Sp and Ep without pores, imperforate outer layer and canaliferous inner laver. U.Cret. (?Santon.-Campan.), Cuba.-Fig. E265,1. *T. sanchezi (Douvillé); transv. sec. AV, ×0.6 (281). [Also Fig. E238.5.]
- Vaccinites FISCHER, 1887, p. 1064 [*Hippurites cornuvaccinum BRONN, 1831, p. 374; M] [=Pseudovaccinites Sénesse, 1947, p. 40 (type, P. pseudolatus major SÉNESSE)]. AV cylindroconical, large; 3 distinct pillars, Ep, Sp, and L occupying less than 0.25 of shell circumference; pillar L generally long, angle between L and teeth less than 45 degrees; ligamental ridge generally truncate, Sp and especially Ep tending to be contracted proximally; inner margin of outer shell layer undulating. FV flat to slightly convex; pores reticulate or denticulate, 2 oscules. U.Cret.(Turon.-Maastricht.). Eu.-Asia-N. Afr.-W. Indies.--Fig. E264,1a. V. corbaricus (Douvillé), Coniac., S. France; reticulate pores, X7 (269).--FIG. E264, 1b. V. marticensis (Douvillé), Coniac., S. France; FV ext., ×1 (910). [Also Fig. E237,6.] [SÉNESSE, who classified the hippuritids solely on the basis of shape of the FV pores, has maintained that, since their pores are polygonal, species of the group that includes the type of *Vaccinites* are more closely related to *Hippurites*. the to *Vaccinites* are more closely related to *Hippurities* than to the remaining groups included by Toucas and others in *Vaccinites*. Accordingly, he has proposed to unite all hippuritids with reticulate, subreticulate or denticulate pores in a genus named *Pseudovaccinites*. The classification of Toucas is accepted here, however.]
- Yvaniella MILOVANOVIĆ, 1938, p. 129 [pro Ivania MILOVANOVIĆ, 1936, p. 33 (non FISCHER ex BAYLE, 1885)] [*Yvania maestrichtiensis MILOVANOVIĆ, 1936; M]. AV like Hippurites. FV specialized, concave, traversed by simple canals which open on outer surface as small pores and on inner surface as enlarged funnel-shaped pores separated by minutely rugose ridges; at center of valve is tubercle traversed by 2 large canals, walls of which contain fine canals, some opening as minute pores on surface of tubercle. U.Cret. (Maastricht.), Eu.(Yugosl.).——FIG. E243,3-4.



FIG. E265. Hippuritidae (p. N803). [Explanation: am, pm, anterior and posterior myophores; Ep, Sp, internal pillars; L, ligamental ridge; 1', 3', sockets in AV corresponding to teeth in FV.]

*Y. maestrichtiensis (MILOVANOVIČ); 3, long. sec. FV (624); 4, drawing showing both values from above, $\times 0.7$ (628).

UNRECOGNIZABLE HIPPURITID GENERA

Chiapasia MÜLLERRIED, 1933, p. 268 (nom. nud.). Pseudobarrettia MÜLLERRIED, 1931, p. 255 [*P. chiapasensis (nom. nud.); OD]. Based on pathological anomaly in growth of AV pillar in individuals of a Barrettia-like hippuritid. U.Cret. (Campan.), Mexico(Chiapas).—Fig. E264,2. *P. chiapasensis; transv. sec. of AV showing pathological duplication of pillar L (scale not given, ca. $\times 1.3$ (651).

Family RADIOLITIDAE Gray, 1848

[Materials for this family prepared by COLETTE DECHASEAUX and A. H. COOGAN, with acknowledgment of assistance by L. R. Cox]

Inequivalve, RV (AV) conical, LV (FV) operculiform; surface of RV (AV) without furrows but generally with two concave, flat, or convex siphonal bands (*Eb*, *Sb*) separated by interband; ornament of siphonal bands and interband unlike that of remainder of surface (Fig. E266,4); in LV (FV), oscules present in a few genera; structure of shell characteristically celluloprismatic; outer layer thick, cellular in texture, walls of cellules formed by radial and transverse funnel-shaped plates which intersect to form hollow prisms with rec-



FIG. E266. Morphological features of Radiolitidae.

- Bournonia, U.Cret. (Maastricht.), France; 1a, B. fourtaui DouvILLÉ, transv. sec. of part of wall showing quadrangular network of celluloprismatic structure, ×0.7 (251); 1b, B. bournoni DES MOULINS, AV long. sec. showing reticulate shell wall and on inside of valve fluted groove for reception of sliding tooth of FV, ×0.7 (251).
- Lapeirousia jouanneti DES MOULINS, U.Cret. (Maastricht.), France (Charente); 2a, transv. sec. of part of shell wall showing polygonal cell structure, ×3.3; 2b, tang. sec. perpendicular to plane of 2a sec., ×3.3 (Dechaseaux, n).
- 3. Pseudopolyconites parvus MILOVANOVIĆ, Ú.Cret. (Maastricht.), Serbia; transv. sec. at level of

tangular or polygonal bases; at lip of valve these prisms form network with polygonal or quadrangular mesh (Fig. E266,1a-2a,b). Interior of RV (AV) without pillars, but in some forms with low, broad, longitudinal projections of shell wall termed "pseudopillars"; hinge, with two teeth in LV (FV) and one tooth in RV (AV); ligamental ridge present or absent; teeth and myoAV with projecting teeth and myophores of FV, $\times 0.7$ (623).

- Sauvagesia nicaisei COQUAND, var. villei ARNAUD, U.Cret.(Cenoman.), France (Charente); side view ext. AV showing longitudinally fluted surface and position of external finely ribbed *Eb* and Sb siphonal bands, ×0.7 (911).
- Joufia reticulata Вöнм, U.Cret. (Senon.), Italy; 5a,b, long. and transv. secs. of part of FV shell wall showing polygonal cell structure, ×6.7 (905).

[Explanation: L, ligament ridge; am, pm, ant. and post. myophores; Eb, Sb, siphonal bands; 1, 3, FV teeth, 2, AV tooth.]

phores of LV (FV) forming thick laminae, fluted in some species (Fig. E220,3); hinge of RV (AV) commonly reduced to sockets into which teeth of LV (FV) slide (Fig. E266,1b); muscles attached to wall of shell in RV (AV); many genera with accessory cavities outside cardinal structures (Fig. E266,3). L. Cret. (Barrem.) - U. Cret. (Maastricht.). The major features of the Radiolitidae, siphonal bands and their ornament, presence or absence of a ligamental ridge, and myophore apophyses and wall structure, are characters by which different genera in the family are distinguished. The siphonal bands and pseudopillars have structure similar to that of other parts of the shell, differing chiefly in the greater development of certain layers of cellules. The function of the pseudopillars is still uncertain; the supposition that these structures were re-



FIG. E267. Radiolitidae (Radiolitinae) (p. N806-N808). [Explanation: Eb, Sb, siphonal bands.]



FIG. E268. Radiolitidae (Radiolitinae) (p. N807-N808).

lated to respiratory or digestive organs is unproved. So far as known, however, all forms with true pseudopillars have oscules in the FV.

Subfamily RADIOLITINAE Gray, 1848

[nom. transl. Douvillé, 1903 (ex Radiolitidae GRAY, 1848)]

Wall of RV (AV) composed of quadrangular prismatic cells; posterior ligament present. L. Cret. (Barrem.) - U. Cret. (Maastricht.).

Radiolites LAMARCK, 1801, p. 130 [*Ostracites angeiodes PICOT DE LAPEIROUSE, 1781, p. 40; M] [=Euradiolites WIONTZEK, 1934, p. 11 (presumed obj.)]. AV conical, ornamented with strong longitudinal folds over whole valve, siphonal bands smooth accentuations of regular folds, outer wall structure coarsely reticulate. FV small, conical, strongly convex or rarely flat, myophore apophyses present. U.Cret.(Cenoman.-Maastricht.), Eu.-N. Afr.-NE.Asia-N.Am.—FIG. E267,2. **R. angeiodes* (DE LAPEIROUSE), U. Santon., France (Pyrenees), 2*a*, AV lat. post., $\times 0.9$; 2*b*,*c*, AV from above and below, $\times 2.2$ (23). [Also Fig. E220,4.]

Agriopleura Kühn, 1932, p. 78 [pro Agria Math-ERON, 1878, pl. C-8 (non Robineau-Desvoidy, 1830)] [*Hippurites blumenbachi STUDER, 1834, р. 107; OD] [=? Aptyxites Вонм, 1919, р. 74 (type, Radiolites muelleri WEGNER, 1905, p. 193)]. AV elongate, straight or slightly arched, commonly longitudinally ribbed; surface with 2 unequal concave furrows bordered by longitudinal swellings; siphonal bands in furrows; ligamental ridge well defined. FV wall structure poorly known, probably finely lamellar; operculiform, flat or strongly concave; hinge with 2 slender teeth, thickened areas at their base constituting muscle scars; no myophore apophyses. [Lack of myophore apophyses separates Agriopleura from other Radiolitinae.] L. Cret. (Barrem.) - U. Cret. (Maastricht.), Eu.-N.Am.-Fig. E267,3. *A. blumen*bachi* (STUDER), Barrem., France; 3*a*, FV ext., $\times 0.9$; 3*b*, both valves lat. view, $\times 0.9$ (911). [Also Fig. E237,1; E240,5.]

Eoradiolites DouvILLÉ, 1909, p. 77 [*Radiolites davidsoni HILL, 1893, p. 106; OD]. AV conical elongate, prominent smooth siphonal bands, large ribbed sockets in dorsal inner wall separated from shell cavity by lateral extension ("transverse septum") of cardinal platform from which lower valve tooth arises, outer wall of coarsely reticulate cells. FV small, operculiform, concave to flat, of fine concentric laminations, myophore apophyses present. *L.Cret.(Alb.)-U.Cret.(Turon.)*, Eu.-Afr.-Asia-N.Am.—FIG. E267,4. *E. davidsoni



FIG. E269. Radiolitidae (Radiolitinae) (p. N808-N810). [Explanation: am, pm, anterior and posterior myophores; Eb, Sb, siphonal bands; L, ligamental ridge; 1, 3, teeth of FV; 2, tooth of AV.]

(HILL), Alb., USA(Texas); 4a, both valves; 4b, AV lat. view of siphonal band Eb, $\times 0.9$ (Coogan, n). [Also Fig. E237,2; E240,1.]

- Gorjanovicia Potšak, 1968, p. 201 [*G. costata; OD]. AV elongate, cylindrical-conical, slender, longitudinal ribs salient, smooth or with fine zigzag growth lines, commonly pointed and separated by finely costulate furrows; siphonal zones large wide bands, pseudopillars clearly imprinted on internal face have special structure of folds with concave inflexions or are concentric or radially disposed. Regular shell structure lamellar, ligament triangular. FV slightly convex and costulate. Differs from Medeella in lacking external folds and in having differently shaped siphonal zones. U. Cret. (Santon.-L. Campan.), Yugosl. (Istria).— Fic. E268,1. *G. costata; 1a, lat. view, 1b, transv. sec., $\times 0.7$; 1c, tang. sec., AV, $\times 4.3$ (746b).
- Kuehnia MILOVANOVIĆ, 1956, p. 132 [*K. serbica; OD]. Known only by AV; ligamental ridge well developed, bilobate at extremity; no pseudopillars; circle of tubular cavities in inner part of thick outer shell layer, prismatic cellular structure of which is well defined. U.Cret.(Santon.-Campan. boundary), Serbia.—Fto. E267,5. *K. serbica; transv. sec. AV, ×0.45 (627).
- Medeella PARONA, 1924, p. 64 [*Radiolites zignana PIRONA, 1869, p. 419; OD]. AV elongate, cylindrical, longitudinal folds regularly costulate, shell surface covered by fine growth lines, outer wall thick; cylindrical siphonal structure in outer wall of polygonal cells, touching body cavity; myophore apophyses present. U.Cret.(Turon.-Coniac.-?Santon.), Eu.
- M. (Medeella). Siphonal bands broadly costulate; FV convex; siphons marked by inflected crescentic slits. U.Cret.(Turon-Coniac.-?Santon.) Eu.----FIG. E267,1. *M. (M.) zignana (PIRONA), Italy; 1a-c, views ventral, lat., and from above, ×0.9 (740); 1d, AV transv. sec., ×1.8 (720). [Also Fig. E243,7.]
- M. (Fossulites) ASTRE, 1957, p. 42 [*Medeella undaesaltus ASTRE, 1954; M]. Longitudinal folds mark surface, siphonal bands salient, smooth or costate, cylindrical siphonal fossettes or cavities in AV outer wall. FV operculiform, flattened, siphons marked by longitudinal arches. Fossettes distinctive. U.Cret.(L.Coniac.), France (Aude). ——Fic. E243,1. *M. (F.) undaesaltus; 1a, both valves; 1b, lat. view AV, 1c, transv. sec. AV, ×0.9 (24).
- Neoradiolites MILOVANOVIĆ, 1935, p. 97 [*N. serbicus; M]. AV conical, ornamented by fine costae, siphonal zones marked by slight inflections, valve outline irregularly circular, outer wall thick, of coarsely prismatic cells. FV capuloid, superficially like Robertella, but with ligament. U.Cret.(Maastricht.), Yugosl.—Fic. E269,6. *N. serbicus; AV transv. sec., at level of AV with projecting teeth of FV and part of dorsal overlap of FV, $\times 0.75$ (623).

- Parasauvagesia Cox, 1960, p. 428 [*P. cappadociensis; OD]. AV depressed conical, longitudinally costate, without well-differentiated siphonal bands; short ligamental ridge and 2 weakly developed pseudopillars present. FV with central domelike elevation and broad, flat brim; no oscules. U.Cret. (Campan. or Maastricht.), Turkey.—FIG. E269, 1; E270,7. *P. cappadociensis; E269,1a,b, lat. and top view, ×0.2; E269,1c, AV transv. sec. shell, ×1; E270,7. AV transv. sec., ×0.55 (199).
- **Paronella** WIONTZEK, 1934, p. 26 [*P. volzanensis; M]. AV cylindrical, transverse septum separating shell cavity from tooth sockets; teeth, myophores, outer wall structure and FV unknown; differs from Distefanella in having ligament. U.Cret.(L. Santon.), SE.Eu.(Italy).——FIG. E269,4. *P. volzanensis; AV transv. sec., ×0.75 (998).
- Praeradiolites Douvillé, 1902 [1903], p. 467 [*Radiolites fleuriaui D'ORBIGNY, 1842, p. 181; OD]. AV conical, externally with smooth folds in form of stack of inverted cones, in younger species developed into undulating chevron pattern; siphonal folds convex, plates bent upward, separated by projecting fold; outer wall structure coarsely reticulate. FV operculiform, convex to flat; myophore apophyses present. Stacked, undulating siphonal band folds distinctive. L.Cret. (Alb.)-U.Cret.(Maastricht.), Eu.-N.Afr.-NE.Asia-N.Am.--Fig. E269,2a-c. *P. fleuriaui (D'Orbig-NY), Cenoman., France (Charente); 2a,b, post. lat. and ant. views, $\times 0.75$; 2c, view from above, $\times 0.75$ (911).——Fig. E269,2d. P. toucasi (D'ORBIGNY), Santon., France; AV lat. view, ×0.75 (911).---Fig. E269,2e. P. cylindraceus (DES MOULINS), Maastricht., France; FV int., $\times 0.45$ (911). [Also Fig. E220,3.]
- **Pseudopolyconites** MILOVANOVIĆ, 1935, p. 132 [**P. parvus;* SD MILOVANOVIĆ, 1937, p. 4]. AV conical, shell surface nearly smooth, strong longitudinal folds absent, siphons marked by broad folds, internal inflexion present at incurrent position; ligamental ridge long, displaced dorsally; outer wall of 2 layers, internal prismatic and normal prismatic; siphonal zones with hornlike transverse partitions. FV weakly convex, teeth and myophores present, shell wall 2 layers. *U.Cret.(Maastricht.),* Yugosl. (Serbia).—Fig. E266,3. **P. parvus;* transv. sec. AV, $\times 1$ (623).
- **Radiolitella** DOUVILLÉ, 1904, p. 533 [*Chama forojuliensis PIRONA, 1869, p. 431; OD]. AV conical, with ligamental ridge and siphonal bands; outer wall in juvenile stages of coarse polygonal cells that become ?rectangular in adult. FV cap-shaped with strong siphonal bands. U.Cret.(Santon.-Maastricht.), Eu.(Italy-Spain).—FIG. E269,3. *R. forojuliensis (PIRONA), Maastricht., Italy; 3a, lat. view, $\times 0.75$; 3b,c, FV ext., AV transv. sec., $\times 2$ (272).

[PARONA (1923, p. 61) stated that DOUVILLÉ in designating Chama forojuliensis PIRONA as the type of Radiolitella figured a specimen from Colle di Medea in the Sorbonne (Paris) collection which corresponds with PIRONA's figures of Sphaerulites guiscardiana PIRONA, 1869, not with Chama forojuliensis PIRONA. KÜHN, 1932, accepted PARONA's evaluation listing Sphaerulites guiscardiana PIRONA (=Radiolitella forojuliensis DOUVILLÉ, non PIRONA) as the type of Radiolitella.]

Robertella Cossmann, 1904, p. 254 [pro Mouretia

DOUVILLÉ, 1903, p. 480 (non G. B. SOWERBY, 1835)] [*Mouretia arnaudi DOUVILLÉ, 1903; M] [=Sarlatia DOUVILLÉ, 1910, p. 29 (obj.)]. Nearly equivalve (AV slightly larger than FV), each



FIG. E270. Radiolitidae (Radiolitinae) (7); (Biradiolitinae) (1-3,5); (Sauvagesiinae) (4,6) (p. N810-N812). [Explanation: am, pm, anterior and posterior myophores; Eb, Sb, siphonal bands; Es, Ss, pseudo-pillars; L, ligamental ridge; 1, 3, anterior and posterior teeth of FV.]

valve capuloid in form; shell wall very thin, without well-marked siphonal bands (only 2 very weak undulations or depressions); no attachment scar at extremity of AV, shell seemingly free, resting on sea bottom; cardinal structures typically radiolitid, with ligamental ridge and myophore apophyses. U.Cret.(Santon.), France (Sarlat).— FIG. E269.5. *R. arnaudi (DOUVILLÉ); 5a, FV side view, $\times 1.5$; 5b,c, AV int. and side view, $\times 0.7$ (271).

Sphaerulites LAMARCK, 1819, p. 231 (ex DELA-MÉTHERIE, 1805, vernac.) [*S. foliaceus; M] [=Spherulites DE BLAINVILLE, 1824 (nom. null.)]. AV broad flattened sphere, external folds undulating slack; siphonal zones marked by sinuses, bordered and separated by folds; internally 2 sinus folds indenting shell cavity; shell structure probably coarsely reticulate. FV flattened, myophore apophyses present, broad, compressed. Foliaceous shape of AV distinctive. L.Cret.(Apt.)-U.Cret. (Turon.), Eu.-N.Afr.—Fig. E220,5. *S. foliaceus, Cenoman., France; AV transv. sec., $\times 0.3$ (911). [Also Fig. E240,2.]

Subfamily BIRADIOLITINAE Douvillé, 1902

RV (AV) wall of quadrangular prismatic cells, posterior ligament absent. U.Cret. (Turon.-Maastricht.).

- Biradiolites D'ORBIGNY, 1850, p. 230 [*B. canaliculatus D'ORBIGNY, 1850; SD ICZN pend.] [==Eubiradiolites COOGAN, 1966, p. 763 (obj.)]. AV conical, more or less produced, straight or arched; siphonal bands smooth, slightly depressed; 1 rib in interband; outer wall of fine cells; AV tooth absent. FV operculiform convex to concave with ornament like that of AV. U.Cret.(Turon.-Maastricht.), Eu.-N. Afr.-Asia-N. Am.-Antilles.-FIG. E270,1. *B. canaliculatus, Coniac., France; side view, ×0.75 (911). [Also Fig. E237,4.]
- Bournonia FISCHER (ex BAYLE, MS), 1887, p. 1067 [*Sphaerulites bournoni DES MOULINS, 1826 (1827), p. 271; M]. AV conical, small to very large ornamented by folds and sporadically by collared horns as in *Praeradiolites*; siphonal bands salient, undulating smooth or ribbed; anterior dorsal fold may project markedly. FV operculiform, convex. U.Cret.(Turon.-Masstricht.), Eu.-N.Afr.-Asia-W.Indies.----FIG. E270,5. *B. bournoni (DES MOULINS), Maastricht., France (Dordogne); lat. view, ×0.4 (251). [Also Fig. E266, 1.]
- Distefanella PARONA, 1901, p. 205 [*D. salmojraghii; SD PARONA, 1912, p. 283] [=Stefanella DOUVILLÉ, 1901, p. 101 (nom. van.)]. AV subcylindrical, elongate, uniformly costate, siphonal bands smooth to finely striate, outer wall thin; internally septum connects dental sockets, dorsal cavity large; AV tooth rudimentary. FV operculiform, cap-shaped. U. Cret. (Turon. - Senon.), Italy-Yugosl.-?]amaica.

-----FIG. E237,8. *D. salmojraghii, Italy; transv. sec. AV, ×0.7 (719). [Also Fig. E224,2.]

- Milovanovicia POLŠAK, 1968 [*M. heraki; OD]. AV cylindro-conical, very elongate, straight or slightly curved. External ornamentation of few large massive, elongate folds separated by deep furrows; both with fine longitudinal striae. Siphonal bands costulate as in Sauvagesia and Durania. Pseudopillars not developed, ligamental crest absent. Shell structure lamellar. FV unknown. Differs from Petkovicia in its lamellar shell structure, costulate siphonal bands, external ornamentation, and absence of pseudopillars. U.Cret. (Turon.), Yugosl. (Dalmatia).---Fig. E271,1. *M. heraki; 1a, lat. view, 1b, transv. sec. AV, ×0.53; 1c, transv. sec. showing detailed lamellar structure, ×4.8 (746a).
- Parabournonia DOUVILLÉ, 1927, p. 55 [*P. hispida; M]. Shell small; differs from *Bournonia* in having AV wall of denticulated structure of parallel plates connected by spines, according to DOUVILLÉ. Considered as indistinguishable from *Bournonia* or *Biradiolites (810). U.Cret.(Maastricht.)*, W. Indies(Cuba).—Fic. E270,3. *P. hispida; 3a, transv. sec. AV, ×0.75; 3b, detail of AV outer wall, ×3 (281).
- Synodontites PIRONA, 1867, p. 840 [*S. stoppaniana; M] [=Syndonites STOLICZKA, 1871 (nom. null.)]. AV pyramidal, elongate, base quadrangular; siphonal bands narrow, smooth; teeth displaced toward center of shell cavity, fused together except at apex. FV operculiform, flat to concave, ornamented like AV. Held to differ from Biradiolites by having fused teeth. U.Cret.(Santon.), Eu. (Italy-France).—FIG. E270,2. *S. stoppaniana, Italy; 2a, AV lat. view, $\times 0.75$; 2b,c, FV ext. and side view, $\times 0.75$ (739).
- Thyrastylon CHUBB, 1956, p. 36 [*Radiolites adhaerens WHITFIELD, 1897, p. 188; OD]. AV conical or distorted by anterior attachment; siphonal bands deeply sunken, interband rounded. FV conical, convex, brim of valve forms oval oscules above AV siphonal areas; oscules distinctive. U. Cret.(Maastricht.), Jamaica-Cuba-Guatemala-Iran. —FIG. E243,2. *T. adhaerens (WHITFIELD), Jamaica; 2a, 2 shells, upper showing oscule So in FV; lower only AV, $\times 0.7$; 2b, both valves, FV with oscules Eo and So enclosed, $\times 0.7$; 2c, transv. sec. AV, $\times 4$ (131).

Subfamily SAUVAGESIINAE Douvillé, 1908

RV (AV) wall composed of cells which are prismatic in longitudinal section but polygonal in transverse section. L.Cret. (Alb.)-U.Cret.(Maastricht.).

Sauvagesia CHOFFAT (ex BAYLE, MS), 1886, p. 31 [*Sphaerulites sharpei BAYLE, 1857, p. 638; SD DOUVILLÉ, 1903, p. 474]. AV conical to cylindroconical, ornamented with longitudinal ribs;



FIG. E271. Radiolitidae (Bioradiolitinae) (p. N810). [Explanation: Eb, Sb, siphonal bands.]

siphonal bands finely costulate folds, separated by interband that generally bears 2 costae. FV operculiform, with radial folds; ligamental ridge present, most marked in earlier forms. L.Cret.(Alb.)-U.Cret.(Maastricht.), Eu.-N.Afr.-N.Am.-Antilles. ——FIG. E238,4. *S. sharpei (BAYLE), Turon., Port.; AV, transv. sec., ×0.6 (268). [Also Fig. E2266,4.]

[The generic name Sauagesia, attributed to BAYLE, was also published in 1886 by DOUVILÉ (Bull. Soc. Géol. France, Ser. 3, v. 14, p. 393), who cited only one species, Sphaerulites lusitanieus BAYLE, 1857, as an example. DOUVILÉ was misled by a misidentified specimen, for, as pointed out by TOUCAS (919, p. 81), this species does not belong to the group to which it was intended to apply the generic name. DOUVILÉ himself (268, p. 669; also *ibid*, ser. 4, v. 2, p. 464) had previously admitted his mistake and the fact that CHOFFAT had interpreted Sauagesia correctly. The best course seems to be to attribute the name to CHOFFAT and to apply for the suppression of its publication by DOUVILÉ, should this prove to have priority.] **Apulites** TAVANI, 1958, p. 173 [*A. giganteus; M].

AV very elongate, with longitudinal costae; outer wall thin, of subquadrangular cells; siphonal zones marked by finely costate folds; ligamental ridge lacking. FV unknown. May be a biradiolitine. U.Cret.(Senon.), SE.Eu.(Italy).—Fig. E270,4. *A. giganteus; 4a, AV lat. view, $\times 0.75$; 4b, AV transv. sec., $\times 1.1$; 4c, detail of AV wall, $\times 4$ (905).

- Chiapasella Müllerried, 1931, p. 243 [*Coralliochama radiolitiformis TRECHMANN, 1924, p. 406; M]. AV conical, short, expanding rapidly, ornamented with longitudinal folds among which striated siphonal zone may be distinguished. Outer wall of irregular polygonal cells; cortex folded into wall locally along periphery. FV high and coiled as in a caprinid, convex or flattened, shell material brown, outer layer of club-shaped canals, inner layer cellular. U.Cret.(Maastricht.), Mexico-Cuba-Jamaica.—Fig. E270,6. *C. radiolitiformis (TRECHMANN), Cuba; 6a, AV transv. sec. at level of AV with projecting teeth and myophores of FV, $\times 4$; 6b, AV transv. sec. of infolding, $\times 3$ (67). [Also Fig. E238,1.]
- Dechaseauxia TAVANI, 1949, p. 21 [*D. costata; M]. AV conical to cylindrical, ornamented by salient longitudinal costae, siphonal bands narrow, marked externally by costate sulci, internally consisting of polygonal cells in regular parallel rows; siphonal zones connected next to shell cavity by 2 rows of polygonal cells; ligamental ridge absent.

FV unknown; genus distinguished by continuous 2-row polygonal wall, siphonal structure and lack of ligament. U.Cret.(Maastricht.), N.Afr.(Somalia). ——FIG. E239,1. *D. costata; 1a, lat. view, ×0.2; 1b, transv. sec. viewed toward commissure, $\times 3$; 1c, AV detail of wall structure, $\times 4.5$ (904). Durania Douvillé, 1908, p. 309 [*Hippurites cornupastoris DES MOULINS, 1827, p. 288; OD]



FIG. E272. Radiolitidae (Sauvagesiinae) (1-2,4), (Lapeirousiinae) (3) (p. N811-N813). [Explanation: Eb, Sb, siphonal bands; Eo, So, oscules; i, incisure.]

[=Duranius DOUVILLÉ, 1910 (nom. null.)]. AV cylindrical, short or elongate, siphonal bands concave, smooth or ribbed, ligamental ridge absent; bifurcating radial furrows on upper surface of outer wall in many species. FV operculiform. L. Cret.(Alb.)-U.Cret.(Maastricht.), Eu.-N.Afr.-Asia-S.Am.-N.Am.—Fig. E272,4. *D. cornupastoris (DES MOULINS), U.Cret.(Turon), France; 4a,b, FV ext, side view both valves, $\times 0.7$ (911). [Also Fig. E237,9.]

- Hardaghia TAVANI, 1949, p. 19 [*H. quadrata; M]. AV pyramidal, depressed toward quadrangular base, ornamented by thick radial ribs; siphonal bands weakly marked externally, internally Sb marked by deep sulcus; ligamental ridge lacking. FV flat, siphonal bands deep, narrow grooves; teeth and myophores absent. Distinguished by pyramidal shape and lack of cardinal apparatus. U. Cret. (Maastricht.), E. Afr. (Somalia).——Ftc. E272,1. *H. quadrata; 1a,b, FV ext. and lat. view both valves, ×0.7 (904). [Also Fig. E240,3.]
- Tampsia STEPHENSON, 1922, p. 4 [*T. bishopi; OD]. AV conical, elongate outer wall thick, cells subrectangular to polygonal, siphons marked by inflections, anterior Eb shallow and extended by narrow depressed slit that cuts outer wall to body cavity; dentition, muscle attachments unknown. FV small bosslike cap, weakly folded over AV shell cavity with thin brim over peripheral surface AV. U.Cret.(Campan.-Maastricht.), Mexico-W.Indies(Cuba).-Fig. E272,2a. Tampsia sp., Mexico (Cardenas); FV ext., $\times 0.7$ (Coogan, n; courtesy R. Meyers, Univ. Texas) .----- FIG. E272, 2b. *T. bishopi, Mexico; AV transv. sec. showing Sb and Eb inflections and incisure (i), $\times 0.7$ (Dechaseaux after Stephenson). [Also Fig. E238, 2.]

Subfamily LAPEIROUSIINAE Kühn, 1932

RV (AV) wall of irregular polygonal cells, ligamental ridge reduced or absent, siphonal zones marked by development of tubular structure (pseudopillars) in outer wall. LV (FV) with oscules marking siphonal openings. U. Cret. (Santon.-Maastricht.).

Lapeirousia BAYLE, 1878, p. 110 [*Sphaerulites jouanneti DES MOULINS, 1827, p. 246; M] [=Lapeirouseia KÜHN, 1932 (nom. van.)]. AV cylindrical to depressed convex, wall thick, pseudopillars well developed, bulge into shell cavity; externally siphonal bands indented, shell ribbed; ligamental ridge absent. FV operculiform, flat or convex, internally with 2 oscules. U.Cret.(Santon.-Maastricht.), Eu.-Asia-N.Afr.---FIG. E272,3. *L. jouanneti (DES MOULINS), U.Maastricht., France (Charente); 3a,b, side view and FV ext., ×0.33 (911). [Also Fig. E266,2.]

- Dubertretia Cox, 1965, p. 731 [pro Kelleria MILO-VANOVIĆ, 1938, p. 137 (non GURNEY, 1928)] [*Dubertretia kelleri Cox (=Lapeirousia jouanneti KELLER, 1933, non DES MOULINS sp.); OD] [=Keleria MILOVANOVIĆ, 1957 (nom. nud.)]. AV arched cone, surface with strong folds like Praeradiolites which indent half of outer wall; siphonal bands concave, pseudopillars subequal, well developed, ligamental ridge lacking, no lower valve tooth. LV unknown. U.Cret.(Maastricht.), Syria. —FIG. E273,1. *D. kelleri; 1a,b, AV transv. sec. and lat. view, $\times 0.5$ (468). [Also Fig. E237, 7.]
- Katzeria SLIŠKOVIĆ, 1966, p. 176 [*K. hercegovinaensis; OD]. AV conical-cylindrical; outer wall nearly without lamellae, those present of radiate structure; inner edge of outer wall has one row of massive prismatic cells next to inner wall; pseudopillars triangular in cross section, with radial and concentric lamellae. FV unknown. May be a bioradiolitine. Differs from Petkovicia in having prismatic cells on inner edge of outer wall. U.Cret.(low. Campan.-Maastricht.), Eu.(Yugosl.). —FIC. E273,3. *K. hercegovinaensis; AV transv. sec., ×3 (847a).
- Lapeirousella MILOVANOVIĆ, 1938, p 89 [*L. orientalis; OD]. AV conical with more or less regular longitudinal ribs; no ligamental ridge, pseudopillars weakly developed and projecting only slightly, with simpler structure than in *Praelapeir*ousia; pseudopillar Ss with large prisms at center and small ones at sides. U.Cret.(Campan.), Yugosl. (Serbia).—Fig. E273,6. *L. orientalis; AV transv. sec. pseudopillar Ss; $\times 11$ (626).
- Osculigera KÜHN, 1932, p. 165 [*O. cleggi; OD]. AV shaped like Lapeirousia, with 2 primary pseudopillars and multiple secondary warty bumps irregularly spaced in outer wall forming small swelling of inner edge where they touch shell cavity, ligamental ridge absent; FV unknown. Distinguished by multiple small pseudopillars. U. Cret.(Senon.), SW.Asia (Iran).—FIG. E273,2. *O. cleggi; AV transv. sec., ×0.5 (488).
- Petkovicia KÜHN & PEJOVIĆ, 1959, p. 979 [*P. prima; OD]. AV high-conical, strongly ribbed, not foliaceous; siphonal bands broad, flattened, separated by furrow on which is 1 rib; outer wall of shell wall very finely cellular, slight internal bulges corresponding to siphonal zones, which are differentiated within wall of shell, narrowing from interior to their outer, convex border. U. Cret.(Santon.), Yugosl.(Serbia).——Fig. E273,5. *P. prima; 5a,b, AV lat. view, and transv. sec. 2 cm. below commissure, $\times 0.75$, $\times 1.3$; 5c, drawing of 5b, $\times 1.3$ (495).
- **Praelapeirousia** WIONTZEK, 1934, p. 28 [*P. kossmati; M]. AV conical?, siphonal bands externally round projecting ribs, internally of few large cells, not swelling into shell cavity, interband broad; reduced ligamental ridge present; lower valve tooth



FIG. E273. Radiolitidae (Lapeirousiinae) (p. N813, N815). [Explanation: am, pm, anterior and posterior myophores; Eb, Sb, siphonal bands; Es, Ss, pseudopillars.]

absent. FV flat, concentrically layered; ribs few; 2 oscules mark siphonal opening. U.Cret.(Santon), Eu.-N.Afr.——FIG. E273,4. *P. kossmati; AV transv. sec., ×2 (998).

Vautrinia MILOVANOVIĆ, 1938, p. 86 [*Lapeirousia syriaca VAUTRIN, 1933, p. 31; OD]. AV conical, ornamented by ribs, no siphonal bands externally, but internally 2 prominent pseudopillars swell inner edge of wall; AV tooth unknown; outer wall of regular radial folds of complex irregular structure. FV operculiform, convex, of compact lamellae, with 2 oscules. U.Cret.(Maastricht.), SW.Asia (Syria-Turkey-Iran).—FIG. E274,2. *V. syriaca (VAUTRIN), Syria; AV transv. sec. of pseudopillar, X0.5 (933). [Also Fig. E243,5-6.]

Subfamily UNCERTAIN

Arnaudia FISCHER (ex BAYLE, MS), 1887, p. 1064 [*Hippurites arnaudi COQUAND, 1859, p. 985; M]. AV conical, ornamented by longitudinal costae; siphonal bands weak broad inflexions internally and externally; ligamental ridge lacking; outer wall thin, compact, detail structure unknown. FV operculiform, concave, ornamented with radial ribs. Long considered a hippuritid, it lacks pillars in lower valve and pores in upper valve. U.Cret. (Senon.), France (Charente).—FIG. E274,3. *A. arnaudi (COQUAND); 3a,b, side view of shell cluster and transv. sec. at level of AV with pendent teeth and post. myophore of FV, $\times 0.7$, $\times 1.1$ (269, 910).

[Arnaudia has been universally classified with the Hippuritidae since BAYLE described it and was so considered by DouvILLE (269) and Toucas (910). KÜHN (493) reexamined the type in the École des Mines in Paris and concluded that Arnaudia is a radiolitid, probably evolved from Agriopleura.]

- Colveraia KLINGHARDT, 1921, p. 23 [*C. variabilis; OD]· Shell depressed, both valves with numerous longitudinal ribs, siphonal bands convex; hinge teeth weak, muscle scars on wall of shell; outer layer of AV composed of irregular hollow prisms, that of FV not prismatic but laminated; next layer (pseudocanal layer) in FV penetrating more or less deeply into valve interior and riddled with elliptical cavities which may invade teeth and myophores. Structure of this layer constitutes an essential generic character. U.Cret.(Maastricht.), Eu.(NE.Italy).—Fig. E274,1. *C. variabilis; lat. view both valves, ×0.7 (475). [Also Fig. E240, 4.]
- Joufia Böhm, 1897, p. 180 [*]. reticulata; M]. AV conical, nearly smooth, ligamental ridge present, siphonal bands weak inflexions or lacking; outer wall of 2 layers; inner finely reticulate lamellar layer and outer layer with canals. FV oval, caplike, of 3 shell layers, inner layer of lamellar reticulate structure, middle layer of polygonal canals arranged 4 together with one in center, and outermost layer of concentric laminae; myophores present. Wall structure distinctive. U.Cret. (Senon.-Maastricht.), Eu.(Italy).-FIG. E266,5.



N815

FIG. E274. Radiolitidae (Lapeirousiinae) (2), (Subfamily uncertain) (1,3) (p. N815). [Explanation: *am, pm,* anterior and posterior myophores; *Eb, Sb,* siphonal bands; 1, 3, teeth of FV; 2, tooth of AV.]

*J. reticulata; 5a,b, FV polygonal cells long. and transv. secs., ×6.7 (905). [Also Fig. E240,6.]

UNRECOGNIZABLE RADIOLITID GENERA

Acardo BRUGUIÈRE, 1797, pl. 172 (generic name without nominal species, with illustration). Used by CUVIER in 1830 to include the genera Radiolites, Sphaerulites, Hippurites, Batolites and Calceola. Birostrites LAMARCK, 1819, p. 230 [*B. inaequiloba, an internal mold]. Held by ROQUAN (1841) to be internal mold of *Sphaerulites* and by Toucas (1907-09) of *Praeradiolites hoeninghausi*.



FIG. E275. Family Uncertain (p. N817).

Bisphaerulites BAYLE, 1857, p. 680 [nom. nud.].

- Diplidia MATHERON, 1842, p. 111 [*Diplidia unisulcata; M]. Poorly known, type species probably represented by mold of *Praeradiolites coquandi* BAYLE.
- Jodamia DEFRANCE, 1822, p. 230 [*J. bilinguis; SD KÜHN, 1932]. Internal mold, possibly of Praeradiolites (Toucas, 1907-09).
- Laskarevia MILOVANOVIĆ, 1960, p. 371 [nom. nud., generic name without nominal species].
- Rajkaia MILOVANOVIĆ, 1960, p. 367 [nom. nud., generic name without nominal species].
- Rhytoides ZEKELI, 1854, p. 206 [nom. nud., generic name without nominal species].
- Trommia KLINGHARDT, 1935, p. 38 [nom. nud., generic name without nominal species, with figure].

Family UNCERTAIN

[Materials for this section prepared by B. F. Perkins and A. H. Coogan]

- Anodontopleura FELIX, 1891, p. 167 [*A. speciosa;
 M]. Externally resembles Monopleura; hinge and muscle insertions unknown. L.Cret.(Neocom.), Mexico.—FIG. E275,6. *A. speciosa; both valves, dorsal view, ×0.5 (301a).
- Baryconites PALMER, 1928, p. 51 [*B. multilineatus; OD]. AV robust, conical, shell wall thick, externally with 2 wide flat siphonal bands separated by narrow ridge, cardinal platform large, anterior muscle insertion large and triangular, large posterior muscle insertion elongate and narrow, anterior tooth socket much larger than posterior, tooth erect and radially elongate, shell cavity small and septate, ligamental groove mostly internal; FV unknown. [This genus has been considered to be related to Polyconites and Horiopleura but irregularly spaced radial plates in dorsal shell wall suggest a possible relationship to radiolitids.] U.Cret.(Cenoman.), Mexico.-Fig. E275,5. *B. multilineatus; 5a,b, AV int., post. view, X0.35 (Perkins, n, courtesy L. G. Hertlein).
- Bicornucopina HOFMANN, 1912, p. 219 [*B. petersi; M] [=Bicornucaprina NEAVE, 1939 (nom. null.)]. Inequivalve; AV elongate, conical, slightly curved; FV strongly curved; wall of both valves with system of radial canals toward interior and smaller canals toward exterior, as in *Caprinula*; hinge insufficiently known to determine affinities. L.Cret. (mid-Neocom.), Eu.(Hung.).—Fig. E275,2. *B. petersi; AV ext., ×0.5 (412a).
- Cryptaulia Počta, 1889, p. 50 [*C. triangulum; SD KUTASSY, 1934, p. 181]. AV straight or slightly curved; longitudinal canals in shell wall; hinge unknown. U.Cret.(Cenoman.), Eu.(Czech.).
- Immanitas PALMER, 1928, p. 28 [*I. anahuacensis; OD]. Equivalve, very large, both valves curved to loosely coiled; surface with 3 ridges separated by furrows, ridges correspond to 3 cavities extending length of both valves near surface; hinge teeth rudimentary, on concave side of shell; shell



FIG. E276. Family Uncertain (p. N817). [Explanation: am, pm, anterior and posterior myophores; Eb, Sb, siphonal bands; L, ligament; 1, 3, anterior and posterior teeth of FV.]

cavity small, tabulate; shell wall composed of small, rounded or polygonal prisms often septate near interior. U.Cret.(Cenoman.), Mexico.—Fig. E275,1. *I. anahuacensis; 1a, both valves, $\times 0.2$ (714); 1b, valve sec., $\times 0.35$ (Perkins, n, courtesy L. G. Hertlein).

- Lithocalamus LUPHER & PACKARD, 1930, p. 207 [*L. colonicus; M]. Known only by AV; gregarious; hinge tooth weak; no accessory cavities; shell wall with 2 layers corresponding to inner and middle layers of *Coralliochama* shell except that cross sections of canals are more rounded and outer row of larger, elliptical canals is present. U.Cret.(Senon.), USA(Ore.).—FIG. E275,3. *L. colonicus; AV secs., ×0.5 (552).
- Palus PALMER, 1928, p. 28 [*P. corrugata; OD]. Only AV known, straight, with small tooth; muscle insertions superficial; tooth sockets reduced to grooves; shell wall composed of 3 layers, middle one with polygonal canals and possibly accessory cavities. U. Cret. (Cenoman.), Mexico.——Fig. E275,4. *P. corrugata; 4a,b, AV transv. sec. and lat. view, X1.5, X1 (Perkins, n, courtesy L. G. Hertlein).
- Pileochama PARONA, 1901, p. 211 [*P. cremai; M]. AV cylindrical, FV capuliform; resembling *Bi*radiolites except for presence of accessory cavity behind each muscle insertion of FV. ?U.Cret. (*Cenoman.-Senon.*), range poorly defined; Italy (Apennines).—FIG. E276,1. *P. cremai, transv. sec. AV, ×0.7 (719).
- **Tepeyacia** PALMER, 1928, p. 46 [**T. corrugata*; OD]. AV small, conical, flattened, ornamented externally with angular ribs; siphonal bands *Eb* and *Sb* deep grooves, ligamental ridge present, no myophores observed, hinge area weakly developed; wall of two layers; thin outer finely lamellar layer and thicker massive opaque inner layer. FV unknown. May be a monopleurid. *L.Cret.*(?*Alb.*), Mexico-W.Indies(?Cuba-?Jamaica). ——Fig. E276,2. **T. corrugata*, Mexico; transv. sec., $\times 0.7$ (714).

Subclass ANOMALODESMATA Dall, 1889

[nom. transl. et correct. KEEN, 1963 (ex Anomalodesmacea DALL, 1889)] [Diagnosis by N. D. NEWELL]

Relatively short to elongate, nestling to fossorial forms with ventrally fused mantle lobes; equivalve to subequivalve; generally approximately isomyarian; hinge margin characteristically thickened or enrolled, edentulous, or with one amorphous tooth and corresponding socket in one or each valve, lateral teeth absent; ligament opisthodetic or absent, where present associated in many genera with separate resilium and lithodesma; many genera said to have nacreous endostracum; living forms eulamellibranchiate; a few, septibranchiate. ?L.Ord., M.Ord.-Rec.

Recent and many fossil representatives, extending far back into the early Paleozoic (e.g., Rytimya, Cuneamya, Sphenolium) have radial rows of very small tubercles. It may be that this delicate ornament, easily worn away, was present in most members of the subclass. Clearly this is a group of great antiquity and possibly it should include genera placed provisionally in the Cryptodonta and elsewhere. The Anomalodesmata include many of the Desmodonten of NEUMAYR and all of PELSENEER's Septibranchiata.

Order PHOLADOMYOIDA Newell, 1965

[Diagnosis by N. D. NEWELL]

Ordinal characters same as those of subclass Anomalodesmata. ?L.Ord., M.Ord.-Rec.

Superfamily EDMONDIACEA King, 1850

[nom. transl. NEWELL, 1965 (ex Edmondiidae KING, 1850)] [Materials for this superfamily prepared by N. D. NEWELL]

Equivalve, isomyarian, generally more or less inequilateral; ovoid; ligament opisthodetic, external, short, attached in well-defined groove and supported by strong nymphs and thin hinge plate; essentially edentulous. U.Dev.-U.Perm.

Family EDMONDIIDAE King, 1850

Equivalve, evenly convex shells with incurving prosogyre or orthogyre beaks; surface generally without radial ornamentation, nearly smooth or rugose, lunule and escutcheon lacking or obscure; pallial line entire or with very shallow sinus. U.Dev.-U.Perm.

- Edmondia de Koninck, 1841, p. 66 [*Isocardia unioniformis PHILLIPS, 1936; OD] [=Allorisma KING, 1844, p. 315 (type, Sanguinolaria sulcata PHILLIPS, 1936; OD); Aediculus GISTL, 1848, p. 9 (obj.); Broeckia DE KONINCK, 1885, p. 19 (type, B. latissima; SD Newell, herein); Pseudedmondia FISCHER, 1887, p. 1100 (type, P. puzosi de Kon-INCK, =Cardiomorpha puzosiana de Kon-INCK, 1842; M); Edmondiella CHERNYSHEV, 1950, p. 74 (type, Sanguinolaria sulcata Phillips, 1836; OD); Allorismiella Astafieva-Urbajtis, 1962, p. 36 (type, "Allorisma sulcata of HIND, 1899" =Hiatella sulcata FLEMING, 1828 and Sanguinolaria sulcata PHILLIPS, 1836; OD]. Ovoid to elongate elliptical, evenly gibbous, without lateral carinae or sulci; margins closed; beaks small, prosogyre, situated one-fourth to one-third behind anterior margin; surface generally with somewhat irregular concentric ridges or growth lines; hinge plate internally reinforced by nearly parallel internal ridge. U.Dev.-U.Perm., cosmop.-FIG. F1,4a. *E. unioniformis (PHILLIPS), L.Carb., Ire.; LV ext., ×1 (Hind, 1899).—FIG. F1,4b. E. sp., L.Perm.(Getaway), Guadalupe Mts., USA(Tex.); RV int. $\times 1$ (Newell, n).
- Cardiomorpha DE KONINCK, 1841, p. 101 [*Isocardia oblonga SOWERBY, 1825; SD WOODWARD, 1854] [=Isoculia M'COY, 1862, explan. pl. 8, fig. 15 (type, *I. corrugata*; M)]. Similar to Edmondia but with very prominent, strongly prosogyre umbones and beaks; surface smooth; internal characters unknown. *L.Carb.*, Eu.-N.Am.—Fig. F1,5. *C. oblonga (SOWERBY), Ire; 5a-c, LV ext., ant., hinge views, $\times 0.5$ (Hind, 1898).

Superfamily PHOLADOMYACEA Gray, 1847

[nom. transl. N. D. NEWELL, 1965] [Materials for this superfamily prepared by N. D. NEWELL, with additions as recorded]

Equivalve, ovoid to elongate shells, generally elongate, with simple, external ligament. ?L.Ord., M.Ord.-Rec.

Family ORTHONOTIDAE S. A. Miller, 1877

[Materials for this family prepared by N. D. NEWELL and AURÈLE LA ROCQUE]

Soleniform Paleozoic bivalves characterized by concentric folds and posterior gape; lunule and escutcheon generally absent; hinge and internal characters unknown. *M.Ord.-M.Dev*.



FIG. F1. Edmondiidae (4-5); Grammysiidae (1-3,6) (p. N818, N822-N823).

Orthonota CONRAD, 1841, p. 50 [*O. undulata; SD CONRAD, 1866]. Very elongate, more than 4 times longer than height, gaping slightly posteriorly; beaks about 0.2 length behind front margin; anterior surface with concentric growth lines and, on postumbonal slope, strong concentric undulations and radial folds; ligament enclosed in linear fold on cardinal margin; edentulous. M.Ord. (Llandeil.-Caradoc.)-M.Dev.(Hamilton.), N.Am.-Eu.—Fig. F2,2. *O. undulata, M.Dev.(Hamilton.), USA(N.Y.); bivalve specimen, composite mold, $\times 1$ (379).

Palacosolen HALL, 1885, p. 483 [*Orthonota siliquoidea HALL, 1870; M]. Similar to Orthonota but with beaks nearly terminal; postumbonal slope marked by shallow diagonal sulcus and umbonal ridge; surface marked by fine growth lines which may become regular and coarse on postumbonal area; posterior end quadrately truncate, widely gaping; anterior end with narrow gape. L.Dev., M.Dev., Eu.(Ger.)-USA.—FIG. F2,1. *P. siliquoidea (HALL), M.Dev.(Hamilton.), USA(N.Y.); RV, composite ext.-int. mold, ×1 (379).

Family GRAMMYSIIDAE S. A. Miller, 1877

[=Sanguinolitidae S. A. MILLER, 1877] [Materials for this family prepared by N. D. NEWELL and AURÈLE LA ROCQUE]

Oval to elongate forms characterized by smooth surface or concentric ornamentation;

radial ribs commonly subordinate; ligament elongate; nymphs obscure; lunule and escutcheon commonly present; posterior umbonal ridge well defined in majority of genera; pallial line entire; hinge edentulous. [A poorly known, probably heterogeneous grouping of convenience.] ?L.Ord., M.Ord.-U.Perm.

- Grammysia DE VERNEUIL, 1847, p. 696 [*G. hamiltonensis (=*Pterinea bisulcata CONRAD, 1838); M]. Ovoid, gibbous; lunule and escutcheon well defined; characteristically with concentric folds and 2 oblique radial sulci with intervening fold extending backward from beaks to near middle of ventral margin; edentulous; pallial line simple, radially striate. L.Dev.-U.Dev., cosmop.—FIG. F3, 10. *G. bisulcata (CONRAD), M.Dev., USA(N.Y.); 10a,b, lat. and front views of RV int. mold, ×0.7 (379).
- Alula GIRTY, 1912, p. 3 [*A. squamulifera; OD]. Externally similar to Solenomorpha but with fine radial costellae over surface in front of posterior umbonal carina; dorsal margin gently concave, ventral margin convex; RV with single platelike anterior and posterior tooth with possibly small rounded cardinal tooth below beaks; pallial line unknown. L.Perm., N.Am.—Fig. F3,12. *A. squamulifera, Lykins F., USA(Colo.); RV ext., ×2 (Girty, 1912).



FIG. F2. Orthonotidae (p. N819).

- Cimitaria HALL & WHITFIELD, 1869, p. 66 [*Cypricardites recurvus CONRAD, 1842; SD HALL, 1885]. Shell elongate, subrectangular, falcate or trapezoid; anterior end short and rounded; posterior end elongate, truncate; umbonal ridge angular and commonly strongly defined; surface marked by strong concentric lines of growth and by fine radial costellae; lateral sulcus extends slightly backward from umbones to basal margin; hinge marked by narrow, elongate ligament groove; lunule and escutcheon well defined; internal features and hinge unknown. [Cooper, 1931.] M. Dev.-U.Dev., E.USA.—FIG. F3,7. *C. recurva (CONRAD), M.Dev.(Hamilton.), N.Y.; 7a,b, cardinal view and RV ext., $\times 0.5$ (379).
- Cuneamya Hall & WHITFIELD, 1875, p. 90 [*C. miamiensis; OD] [=Ceromyopsis MEEK, 1872, p. 327 (type, Cardiomorpha? obliquata MEEK, 1872); Sphenomya HALL, 1883, pl. 62 (type, Grammysia cuneata HALL, 1883; OD)]. Subrhomboidal, tapering backward for maximum height at prominent, nearly terminal umbones and strongly incurved beaks to obliquely truncate posterior margin; lunule and escutcheon well developed; posterior umbonal ridge rounded and broad; lateral sulcus broad, faint, oblique; anterior surface with uniform concentric ornamentation; posterior slope smooth; without marginal gape. M.Ord.(Trenton.)-M.Dev.(Hamilton.), N.Am.-FIG. F3,3. *C. miamiensis, U.Ord., USA (Ohio); 3a,b, hinge view and RV ext., $\times 1$ (381).
- **2Davidia** HICKS, 1873, p. 49 [*D. ornata; SD NEWELL, herein]. Subtriangular, with submedian beaks and rounded, nasute, anterior and posterior extremities; posterior and anterior umbonal carinae near cardinal border; surface smooth except for faint radial costellae over ?posterior end of shell. L.Ord.(Tremadoc.), Wales.—FIG. F3,4. *D. ornata, St. Davids; 4a, ?LV evt., X1; 4b, surface, enl. (406).

- **?Glossites** HALL, 1885, p. 49 [*G. lingualis; OD] [=?Elymella HALL, 1885, p. 50 (type, E. nuculoides; OD)]. Shell elliptical, beaks anterior, small, appressed; hinge line long, gently arcuate; posterior umbonal ridge rounded; surface smooth or sublamellose, with or without faint radial costellae; lunule and escutcheon distinct; muscle scars shallow. L.Dev.(Chapman Ss.), USA (Maine)-U.Dev. USA(N.Y.)-Eu.-Afr.; L.Miss., USA(Iowa-Ohio). —FIG. F3,6. *G. lingualis, U.Dev.(Chemung), USA(N.Y.); RV ext., $\times 1$ (379).
- Grammysioidea WILLIAMS & BREGER, 1916, p. 133 [*G. princiana; OD]. Similar to Grammysia, but lacks regular concentric ornamentation and either lacks radial sulcus or shows only single shallow lateral sulcus. Sil.(Clinton.)-U.Dev., USA (Nev.)-E.N.Am.-S.Am.-Eu.—FIG. F3,5. *G. princiana, L.Dev.(Moose R. Ss.), USA(Maine); RV ext., ×0.5 (986).
- ?Leinzia MENDES, 1949, p.11 [*Solenomorpha similis HOLDHAUS, 1918; OD]. Elongate pterioid, with anterior auricle; strong umbonal carina in front of narrow, flattened, smooth or carinate siphonal area; body of shell in front of umbonal carina with coarse, concentric ornamentation; LV with single cardinal socket; laterals lacking. Perm., S.Am. (S.Brazil).—FIG. F4,5. *L. similis (HOLD-HAUS), Passa Dois F.; LV ext., ×1 (Mendes, 1949). ?Palaecorbula REED, 1932, p. 63 [*P. difficilis;
- M]. Moderately inflated, 1952, p. 65 [1. ulpichi, M]. Moderately inflated, strongly inequivalve, RV smaller than LV, suboval, longer than high; anterior end projecting, sharply rounded; umbones submedian; surface ornamented with numerous, regular, sharp, equidistant, concentric ridges, some of which abruptly thin out or coalesce at weak anterior sulcus in front of which concentric ridges are only about half as numerous; lunule lacking; escutcheon well defined, narrow; interior unknown. L.Perm., India(Kashmir).—Fic. F3,9. *P. difficilis, agglomeratic slates, 9a,b, lat. and post. views of RV, $\times 1$ (Reed, 1932).
- Pholadella Hall, 1869, p. 63 [*P. newberryi; SD HALL, 1885] [=Cercomyopsis MEEK, 1871, p. 71 (type, Allorisma pleuropistha MEEK, 1871; OD); Grammysiopsis CHERNYSHEV, 1950 (type, G. irregularis; OD)]. Shell elongate, gibbous; beaks about 0.25 distance behind anterior margin; umbones and umbonal ridge prominent; anterior end rounded or obliquely truncate; laterally compressed posterior truncate; broad, lateral sulcus extending directly downward from beaks to ventral indentation; surface marked by strong concentric undulations which may be confined to anterior part of shell; distinct costae originating at umbo extend across central or greater portion of shell body, leaving anterior and cardinal area free of radial ornamentation; cardinal margin marked by broad ligament groove, lunule and escutcheon well defined; hinge, pallial and adductor impressions unknown. L.Dev. (Coblenz.), Ger.; L.Miss., E.USA; M.Penn.-

U.Penn., C.USA; U.Carb., USSR(Urals).—Fig. F3,11. *P. newberryi, L.Miss.(Waverly.), USA (Ohio); LV ext., ×1 (379).

Promacrus MEEK, 1871 p. 4 [*P. nasutus; OD]. Anterior end attenuated and produced; posterior end higher and obliquely truncated; beaks ranging in position from median to slightly anterior or posterior; umbonal ridge well defined; without lunule and escutcheon; surface smooth or in some shells with radial costellae over umbonal region;



FIG. F3. Grammysiidae (p. N819-N823).



FIG. F4. Grammysiidae (5); Megadesmidae (1-4) (p. N820, N825-N827).

hinge and pallial line unknown. L.Miss., N.Am. ——FIG. F1,6. *P. nasutus, L.Miss.(Chouteau), USA(Mo.); LV ext., ×0.6 (Meek, 1872).

- **Prothyris** MEEK, 1871, p. 4 [**P. elegans;* OD] [=*Prothyris* MEEK, 1869, p. 172 (nom. nud.)]. Elongate-oblong, smooth or weakly costellate; gaping slightly behind, or closed and widely gaping in front, where hiatus is increased by notch; beaks depressed and very near anterior end, with small ridge extending from anterior side of each beak to corner of anterior notch; dorsal margin without escutcheon or lunule; ?edentulous. *L.Dev.-U.Perm.*, W.Eu.-N.Am.-S.Am.(Brazil).
- P. (Prothyris). Without posteroventral notch or sulcus. L.Dev.-U.Perm., W.Eu.-E.USA-C.USA.

——FIG. F1,2. *P. (P.) elegans MEEK, U.Penn. (Willard Sh.), USA(Neb.); RV ext., lectotype, ×2 (Newell, n).

- P. (Paraprothyris) CLARKE, 1913 [*P. (P.) knodi;
 M]. Similar to P. (Prothyris) but with broad posterior sulcus ending in marginal notch, surface with 2 sets of concentric ornamentation forming herringbone pattern below posterior sulcus. L.Dev. (Ponta Grossa Sh.), E.Am.(Brazil).—Fig. Fl,1.
 *P. (P.) knodi; bivalved individual, LV below, ×1 (138).
- Protomya HALL, 1885, p. 52 [pro Palaeomya HALL, 1885, p. 52 (non ZITTEL & GOUBERT, 1861)] [*P. oblonga; OD]. Elongate, oval; beaks submedian, incurved, prominent; umbonal slope



FIG. F5. Morphological features of Megadesmus.—A, B. M. nobilissimus, semidiagrammatic long. sec. of LV showing shell layers, ×1.5, and long. sec. of inner layer showing lamellae secreted around sand grain, ×7.5.—C, D. M. globosus, superposed serial secs. of hinge viewed from post. end (C) and ant. view of umbonal secs. of LV showing socket (D), ×1.—E. M. nobilissimus, transv. sec. of ligament. [Explanation: a,b, outer and inner shell layers; c, periostracum; d, beak; e, tooth; f, socket; g, nymph; h, ligament groove; i, j, k, inner, outer, and periostracal layers of ligament.] (Runnegar, 1965).

gibbous above; surface with fine growth lines and strong concentric undulations; cardinal line long, nearly straight; ligament external; hinge and pallial line unknown. *M.Dev.*, USA(N.Y.).—Fig. F3,8. **P. oblonga*, Hamilton, N.Y.; LV int. mold, $\times 0.7$ (379).

Sanguinolites M'Coy, 1844, p. 47 [*S. discors; SD STOLICZKA, 1871] [=Cercomyopsis SANDBERGER, 1881, p. 247 (type, C. acutirostris; OD); Sphenotus HALL, 1885, p. 33 (type, Sanguinolites arcaeformis HALL & WHITFIELD, 1869; SD S.A.MILLER, 1889); ?Eopleurophorus ELIAS, 1957, p. 780 (type, Cypricardia? tricostata PORTLOCK, 1843; OD)]. Shell elongate; umbones small, gibbous, incurved and contiguous, placed in anterior 0.2 of shell; anterior convex part of shell with coarse concentic ornamentation, sharply set off from flattened postumbonal area by 1 or more radial carinae; lunule and escutcheon well developed; pallial line entire. U.Dev.-Perm., cosmop.—Fig. F3,1. *S. discors, L.Carb., Ire.; RV ext., ×1 (M'Coy, 1844).

Sedgwickia M'Coy, 1844, p. 61 [*S. attenuata; SD STOLICZKA, 1871] [=?Fuchsella DAHMER, 1942, p. 145 (type, Sphenotus maillieuxi Asselberghs, 1930; M)]. Elongate, more or less gibbous; anterior end rounded, posterior edge subtruncate; umbones prominent, placed well forward, slightly prosogyre; surface smooth or with low concentric ridges; defined ligament nymphs behind beaks; lunule, escutcheon and radial carinae lacking; hinge unknown, ?edentulous. [The relationship between this genus and Myonia DANA, 1847, is uncertain.] Miss.-Perm., cosmop.—Fig. F1,3. *S. attenuata, L.Carb., Marsden, Eng.; RV ext., ×1 (M'Cov, 1844).

N823

Solenomorpha COCKERELL, 1903, p. 559 [pro Solenopsis M'Coy, 1844, p. 47 (non WESTWOOD, 1840)] [*Solenopsis minor M'Coy; M]. Subcuneiform, tapering posteriorly from maximum height at beaks near anterior end; anterior end closed; posterior end gaping slightly; umbonal carina conspicuous; narrow lunule and escutcheon present; surface smooth, without radial ornamentation; hinge unknown; pallial line entire. L.Dev.-U.Perm., cosmop.——FIG. F3,2. *S. minor (M'Coy), L.Carb., Ire.; LV ext., ×1 (M'Coy, 1844).

Family MEGADESMIDAE Vokes, 1967

[nom. correct. Newell, herein (pro Megadesmatidae VOKES, 1967, nom. subst. pro Pachydomidae FISCHER, 1886, based on invalid generic name, ICZN Code, Art. 11e)] [Materials for this family prepared by N. D. Newell]

Similar to Edmondiidae but many genera more clearly adapted for burrowing; liga-



FIG. F6. Musculature and pallial lines shown on internal molds of early to late species of Megadesmus and Astarila (stratigraphic ranges indicated by heavy vertical lines).—...A. M. globosus.—.B. M. nobilisimus.—..C. M. gryphoides.—.D. A. intrepida.—.E. A. elegans.—.F. M. grandis. [Explanation: 1, ant. adductor; 2, pedal protractor; 3, ant. pedal restactor; 4, umbonal pedal retractor; 5, post. pedal retractor; 6, post. adductor.] (Runnegar, 1965).

ment short, nymphs very prominent with a single blunt tooth in RV and rarely in LV. U.Carb.-Perm.

Some of the more important features of shell structure, hingement, and musculature are illustrated in Figures F5-7, based on studies by RUNNEGAR (1965, 805a).

Megadesmus Sowerby, 1839, p. 14 [*M. globosus; SD Woodward, 1854, p. 262] [=Pachydomus Morris, 1845, p. 271 (nom. van. pro Megadesmus Sowerby, 1839, non Megadesma Bowdich, 1822); Cleobis Dana, 1847, p. 154 (type, Cleobis grandis Dana, 1847; SD Newell, 1956, p. 10)]. Large equivalve, asymmetrical shells ornamented with coarse to medium imbricate growth lamellae and fine to medium concentric ribs; with sporadic obscure radial costae; micro-ornament consisting of radial rows of minute papillae, hinge with dental process in RV produced by fold in dorsal anterior valve margin, and socket in LV resulting from depression of valve edge; ligament external, opisthodetic, parivincular, supported by strong nymphs set in well-defined escutcheon; adductors subequal, the anterior smaller; 2 pedal muscle scars (protractor and retractor) situated above anterior adductor, and single retractor adjoining posterior adductor; third retractor scar in and on anterior side of umbonal cavity; pallial line simple, radially striated; shell inside pallial line commonly pitted by insertions of mantle; shell and ligament of 3 lavers: periostracum, outer lamellar layer and inner (?nacreous) layer (Runnegar, 1965). Perm., Australia-Tasmania-India-Argentina.----Fig. F8. 4a-c. *M. globosus (Sowerby), L.Perm. (Allandale F.), Harper's Hill, Hunter Valley, New S. Wales; 4a, LV view of shells, $\times 0.5$ (Sowerby, 1838); 4b, dorsal view of lectotype, ×0.5 (Runnegar); 4c, RV ext., $\times 0.5$ (805a).—Fig. F8.4d. M. gryphoides DE KONINCK, E.Australia; latex cast of interior showing that front of dorsal margin slightly overlaps that of LV, ant. part of which fits into shallow groove in front of LV tooth, $\times 0.5$ (Runnegar, n).

Astartila DANA, 1847, p. 155 [*A. intrepida; SD STOLICZKA, 1871, p. xix]. Small, ovate shells with gently convex posterior umbonal slopes and low, forwardly directed beaks; ornament varying from regular imbricate growth lamellae to irregularly spaced concentric threads: radial ornament of low, wide costae may be present; shell surface covered with radial rows of minute papillae; ligament external and opisthodetic, attached behind welldeveloped nymphs set in narrow escutcheon: lunule usually absent; RV with single upright tooth derived from fold in valve margin; LV with deep to shallow socket of type found in Megadesmus specimens with well-developed radial ornament having weakly developed megadesmid dentition; adductor scars subequal, the anterior smaller and deeper, commonly having several lobes on the posterior-dorsal edge; a single, deep, oval pedal scar occurring above anterior adductor and a large pedal retractor scar attached to upper edge of posterior adductor; a third pedal scar on rear side of umbonal cavity; pallial line simple and radially striate. L.Perm., Australia.

[Astartila differs from Megadesmus in the following respects. 1) Because of the narrow, deep escutcheon, the upper margin of the valve behind the umbo is gently convex. In Megadesmus the escutcheon is broader and less steeply inclined so that it is mechanically possible for the umbones to project above the posterior margin of the valves. 2) Only one pedal scar occurs above the anterior adductor. The scar that is present is ovoid and deeply impressed so that it is almost certainly the scar that has been termed the anterior pedal retractor in Megadesmus. In one specimen of Astartila intrepida there is a differentiation of the edge of the adductor which may represent the protractor scar. However, as the edge of the adductor is commonly lobed, it is probable that this is merely an exaggerated development of a single lobe. The absence of a scar does not necessarily imply the absence of a pedal protractor muscle since BLOOMER (1901, p. 40) has described a species of Solem in which the protractor muscle is attached to the shert of the scare for Megadesmus or Astartila it may account for the more or less complete merging of the protractor and adductor scares (RUNRGAR, 1965, 805a).]

A. (Astartila). Species lacking well-developed radial ornamentation. L.Perm., Australia.——FIG. F8,3. *A. (A.) intrepida DANA, U.Marine, Wallongong, NewS.Wales; 3a-c, RV ext., latex cast of hinge int., shell front, $\times 1$; 3d, hinge ext., $\times 0.7$ (668).

A. (Pleurikodonta) RUNNEGAR, p. 247, 1965 [*P. elegans, OD]. Internally like A. (Astartila) but ornamented with obscure radial costae which are reflected by inflections in growth lamellae and



FIG. F7. Muscle scars and pallial lines on internal molds of representative Megadesmidae and Pholadomyidae (Runnegar, 1965).—*A. Astartila (Astartila) intrepida* DANA.—B. A. (Pleurikodonta) elegans RUNNEGAR.—C. Chaenomya leavenworthensis (MEEK).—D. Megadesmus gryphoides (DE KONINCK).—E. Chaenomya? sp.—F. Pyramus laevis (SOWEREY).—G. Myonia valida DANA.— H. Vacunella sp. cf. V. waterhousei (DUN).—I. Pholadomya gigantea (SOWEREY).—J. Vacunella curvata (MORRIS). [Explanation: a, muscles of uncertain significance; ar, anterior retractor; ava, accessory ventral adductor; g, siphonal gape; p, protractor; pd, pedal gape; pr, posterior protractor; ur, umbonal retractor.]



FIG. F8. Megadesmidae (p. N824-N826).

crenulations in valve margins; megadesmid dentition of A. (Astartila) wholly or partially replaced by costae which interlock in front of beaks. L.Perm.(M.Bowen Beds), Queensl.— FIG. F4,3. *A. (P.) elegans (RUNNEGAR); 3a-c, ventral, ant. and oblique views of latex cast, $\times 1$ (Runnegar, 1965).

Casterella MENDES, 1952, p. 100 [*C. gratiosa; M]. Similar to Megadesmus but with pallial sinus and thin hinge plate. Perm.(Corumbatai F.), S.Am. (S.Brazil).—FIG. F8,2. *C. gratiosa; 2a,b, RV ext. and hinge views, X1.5 (Mendes, 1952). ?Crassiconcha NECHAEV, 1894, p. 316 [*C. stuckenbergi; M]. Equivalve; smooth; beaks submedian; lunule and escutcheon well marked; front end projecting, narrowly rounded; lateral surfaces divided approximately into thirds by broad shallow sulci; deep pallial sinus; hinge unknown. U.Perm., Eu.(E.USSR)-E.Greenl.—FIG. F8,1. *C. stuckenbergi, Kazan., USSR; 1a, hinge view and 1b, ext., X0.7 (Nechaev, 1894).

Myonia DANA, 1847, p. 158 [*M. elongata; SD FLETCHER, 1932] [=Maeonia DANA, 1849 (nom. van. pro Myonia DANA, 1847)]. Shell elongate, lenticular, with small umbones; tapering backward as viewed from above and side; posterior end obliquely truncate; obscure sulcus extending from beaks to ventral margin, usually bounded behind by posterior umbonal ridge; cardinal teeth lacking or obscure; margins not gaping; pallial line continuous, but radially striate; mantle within pallial line attached to shell by scattered deep pits. U.Carb.-Perm., New S. Wales-Kashmir-S. Am. (Brazil)-USSR(NE.Sib.).

[Myonia is placed in the Megadesmidae rather than in the Edmondiidae because of its very strong outward rolled nymphs; at least some examples (Fig. F4,2b) show the usual cardinal boss characteristics of the subfamily.]

- M. (Myonia). Umbonal ridge rounded or with weak carina. U.Carb.-Perm., New S. Wales-Brazil-Sib.----FIG. F4,2a. *M. (M.) elongata DANA, Gerringong, New S. Wales; LV ext., $\times 0.34$ (668).----FIG. F4,2b. M. (M.) carinata, U.Marine Ser., south coast, New S. Wales; RV int., $\times 0.4$ (New-ell, n).
- M. (Pachymyonia) DUN, 1932, p. 411 [*P. morrisii ETHERIDGE, 1919; OD]. Umbonal ridge very strong, angular. Perm., New S.Wales.—FIG. F4,1. *M. (P.) morrisii (ETHERIDGE), L.Marine Ser., New S.Wales; 1a,b, RV ext., hinge view, $\times 0.5$ (Newell, n).
- Pyramus DANA, July 1847, p. 156 [*P. myiformis; SD NEWELL, 1856] [=Notomya M'COY, NOV. 1847, p. 303 (type, N. securiformis; SD STOLICZKA, 1871); Pyramia DANA, 1849 (nom. van. pro Pyramus DANA, 1847); Clarkia DEKONINCK, 1877 (obj.)]. Similar to Myonia but with slight posterior gape and shallow pallial sinus; pallial line not striate and interior of shell not pitted within pallial line; 1 large tooth in each valve below beaks. L.Perm.(U.Marine), New S.Wales; Perm.? (Corumbatai F.), S.Am.(S.Brazil).---Fig. F4,4. *P. myiformus, L.Perm.(U.Marine), Blackhead, New S.Wales; 4a,b, latex cast viewed from right; int. same, RV; both $\times 1$ (668).

Family PHOLADOMYIDAE Gray, 1847

[nom. correct. KING, 1850 (pro Pholadomyadae GRAY, 1847)] [=Arcomyidae FISCHER, 1887] [Materials for this family prepared by L. R. Cox, with additions by N. D. NEWELL]

Shell equivalve (except in Girardotia), with wide range of size, ovate, oblong or subtrigonal, subequilateral to (more commonly) strongly inequilateral, moderately to strongly inflated; most forms gaping at posterior end and some with narrower anterior gape; ostracum thin (except in some Pachymya and in Machomya), nacreous, although commonly altered in fossilization; surface bearing small pustules, aligned radially or concentrically in many forms. Hinge edentulous; cardinal margin thickened below and behind beak and bearing strong nymph in each valve for support of external, opisthodetic ligament; small internal ligament (resilium) also present below beak in Recent type species of *Pholadomya*, but not observed in any fossil forms, internal characters of most being inadequately known; pallial sinus present in most forms but absent in a few. *Miss.-Rec*.

FISCHER recognized two distinct families, Pholadomyidae and Arcomyidae, supposing the fine surface pustules present in the latter group to be absent in the former. It is now known that the surface is finely pustulose in some Lower Tertiary *Pholadomya* (Fig. F9,1f), however, and it seems probable that this delicate ornament, which is easily worn away, was present both in the holotype of the Recent type species and in numerous fossil representatives of the genus.

Pholadomya G.B. Sowerby, 1823 [*P. candida; SD GRAY, 1847, p. 194] [=Pholadomyaea FLEMING, 1828 (nom. null.); Pholadomia Swainson, 1835 (nom. null.); Phaladomya MEEK, 1858 (nom. null.); Pholadomye Deshayes, 1860 (nom. null.); Pholdomya CONRAD, 1865 (nom. null.); Pholodomya HECTOR, 1886 (nom. null.); Pholadonya DALL, 1905 (nom. null.)]. Medium-sized to large, ovate to subtrigonal, strongly inequilateral, ventricose, most so anteriorly; umbones broadly rounded to subangular, of variable prominence, more or less anteriorly placed; valves gaping posteriorly to variable extent, anterior gape narrow or absent; pustulation of surface very delicate; ornament usually strongly developed, but weak in some forms and consisting of radial ribs or ridges, commonly bearing tubercles, and of concentric undulations or rugae; pallial sinus broad, of moderate depth. U.Trias.-Rec., cosmop.

[Although several Recent species from various parts of the world have been described under *Pholadomya*, the type species is the only one resembling the numerous fossil forms in size and shape. The remainder are relatively small shells, some of which belong to the genus *Panacca* DALL (see below), while some others, particularly certain very small forms from the Antarctic, should probably be included in one or more new genera. All known Recent *Pholadomyidae* are moderately deep- to deep-water forms, whereas the Mesozoic species of the family are found commonly in shallow-water sediments. No satisfactory subgeneric classification of the numerous species of *Pholadomya* has yet been achieved and a thorough revision of the genus would result in the recognition of many more subgeneric roups than those here distinguished.]

P. (Pholadomya) [=Flabellomya ROLLIER, 1911, p. 231 (type, Lutraria ambigua J. SOWERBY, 1819, p. 48; SD Cox, herein)]. Elongate-ovate, with broad and not prominently protruding umbones; dorsal umbonal ridge, bordering an escutcheon, present or absent. U.Trias.-Rec., cosmop.——FiG. F9, Ia-d. *P. (P.) candida G.B. SOWERBY, Rec., Carib.; Ia-c, holotype, RV ext., RV int. (showing pallial line), and dorsal view of both valves (all



FIG. F9. Pholadomyidae (p. N827-N829).

 \times 0.7); 1d, hinge region of RV showing ligamental nymph and shallow rhombic subumbonal pit for internal ligament, small, obtusely angular projection of margin below it (\times 2) (Cox, n). ——Fic. F9,1e. P. (P.) ambigua (J. SOWERBY), L.Jur.(Lias.), Eng.; LV ext., \times 0.7 (Cox, n).—— Fic. F9,1f. P. (P.) leonensis STENZEL, KRAUSE & TWINING, Eoc., USA(Tex.); pustulose ornament, \times 4 (Stenzel, Krause & Twining, 1957). P. (Bucardiomya) ROLLIER in COSSMANN, 1912, p. 215 [pro Bucardia ROLLIER, 1911, p. 231 (non SCHUMACHER, 1817)] [*Pholadomya bucardium AGASSIZ, 1842, p. 77; SD Cox, herein] [=Bureiomya VORONETZ, 1937, p. 58 (type, Pholadomya polymorpha D'ORBIGNY, 1850, p. 360; SD Cox, herein)]. Subtrigonal or obliquely oval, not greatly elongated; umbones prominent and subangular in most species; no escutcheon; strength of radial ribbing very variable. L.Jur.(Toarc.)-L.Tert., cosmop.—Fig. F10,1a. *P. (B.) bucardium Agassiz, M.Jur.(Bathon.), Switz.; LV ext., $\times 0.7$ (Moesch, 1874).—Fig. F10,1b,c. P. (B.) lirata (J. SOWERBY), M.Jur.(Bathon.), Eng.; 1b,c, LV ext., both valves dorsal, $\times 1$ (Cox, n). ——FIG. F10,1d. P. (B.) margaritacea (J. Sow-ERBY), U.Eoc., Italy; RV ext., $\times 1$ (Moesch, 1874).

P. (Procardia) MEEK, 1871, p. 184 [*Isocardia?



FIG. F10. Pholadomyidae (p. N828-N830).



FIG. F11. Pholadomyidae (p. N830-N832).

hodgei MEEK, 1871, p. 183; M]. Relatively short, subtrigonal or oblong, with prominent umbones and strongly incurved, prosogyrous beaks; anterior end short, truncated, flattened or impressed, with still more impressed lunule under beaks; escutcheon distinctly bordered; flank ornamented with narrow radial costae and concentric ridges. U.Jur.(Callov.)-U.Cret.(Turon.), cosmop.—FIG. F10,2. P. (P.) decussata (MANTELL), U.Cret. (Cenoman.), Eng.; 2a-c, RV ext., both valves dorsal and ant. views, $\times 1$ (Woods, 1909).

Anomalopleuroides Cox, 1962 [pro Anomalopleura LEONARDI, 1948, p. 62 (non KLEINE, 1916)] [*Anomalopleura elisae LEONARDI, 1948; M]. Smallmedium sized, elongate-ovate, fairly strongly inflated, with wide posterior gape; umbones obtusely rounded, scarcely protruding, placed at about anterior third of length; posterior two-thirds of shell



FIG. F12. Pholadomyidae (p. N831).

ornamented with narrow, closely spaced radial ribs, anterior third with more widely spaced, oblique, steep ribs which meet last rib of radial series in acute angle; internal characters unknown. U.Trias., Austria(S.Tirol).——FIG. F11,6. *A. elisae (LEON-ARDI); LV ext., $\times 1.3$ (Leonardi, 1948).

- Argyromya FISCHER, 1887, p. 1166 [*Glycimeris margaritacea LAMARCK, 1818, p. 458; OD (cited as "Panopaea margaritacea DESHAYES")] [=Aigyromya DONCIEUX, 1911 (nom. null.)]. Mediumsized, oblong, subequilateral, moderately inflated, most so posteriorly, where very wide gape occurs; anterior gape narrow; umbones narrow, scarcely protruding; surface with irregular growth rugae; pustules minute, radially aligned, seen only in earlier growth stages; pallial sinus narrow and deep. M.Eoc., Eu.(France).—FIG. F11,1. *A. margaritacea (LAMARCK); Ia-c, RV ext., RV int., and dorsal view of both valves, all ×1 (Deshayes, 1856).
- Chaenomya MEEK, 1864, p. 42 [*Allorisma? leavenworthensis MEEK & HAYDEN, 1858; M]. Shell smooth or ornamented with concentric folds; umbones prominent, situated about 0.25 of shell length from anterior margin; subcylindrical at beaks; without lateral sulcus or ventral sinus; siphonal gape extreme, equal to cross section of shell, or flaring slightly; pallial sinus deep. Penn.-Perm., USA (Mid-Cont.); Perm., Australia.—Fic. F12,2. *C. leavenworthensis (MEEK & HAYDEN), U.Penn.; 2a,b, LV lat. and hinge view of both valves, X1; 2c, detail of shell surface, enl., (Meek, in Meek & Hayden, 1864). [NEWELL]

- Cortinia LEONARDI, 1948, p. 63 [*C. catharinae; M]. Small, obliquely oval, inequilateral, *Pholadomya*like but with obtuse ridge running from umbo toward posteroventral angle; ornamented with pustulose radial threads and with undulations which follow growth lines or are slightly oblique to them; internal characters unknown. U.Trias., Austria(S.Tirol).—FIG. F11,2. *C. catharinae; RV ext., ×2 (Leonardi, 1948).
- **Cosmomya** HOLDHAUS, 1913, p. 446 [**C. egregia;* M]. Medium-sized, moderately inflated, with broadly rounded, well protruding, rather anteriorly placed umbo; ornament consisting of posterior series of steep, oblique ribs, some zigzagging posteriorly and bending up in V anteriorly, and of anterior series of ribs which are only slightly oblique to growth lines and meet the posterior series along shallow groove descending from umbo to ventral margin; internal characters unknown. "Below Werfen beds," i.e. pre-Lower Trias.,¹ Asia(Niti Pass, Himalayas), (Dickins & Shah, 1965).
- Exochorhynchus MEEK & HAYDEN, 1864, p. 42 [*Allorisma? altirostrata MEEK & HAYDEN, 1858; M]. Similar to Wilkingia but with terminal beaks; hinge and interior unknown. Miss.-Penn., W.Eu.-N.Am.—FIG. F12,1. *E. altirostratus, U.Penn., USA(Kans.), LV ext., ×0.7 (Meek & Hayden, 1864). [NEWELL]

¹ The type species of *Cosmomya*, thought by HOLDHAUS to be derived from Jurassic rocks, is probably Permian and seems to be congeneric with *Palaeocosmomya*, fide J. M. DICKINS (ed.).

- Girardotia DE LORIOL, 1903, p. 133 [*G. elegans; M]. Small to medium-sized, oval, slightly to moderately inequilateral, gibbose, with wide posterior and narrow anterior gape; slightly inequivalve, RV smaller; umbones broadly rounded, scarcely protruding; RV with radial groove, LV with ridge in some species and groove in others, running from umbo to posterior part ventral margin; ornament consisting of narrow concentric ribs present on entire surface or on anterior part only, and of concentric ridges; internal characters unknown. M.Jur.-U.Jur.(Bajoc.-Kimmeridg.), Eu. -FIG. F11,3. *G. elegans, U.Jur.(Oxford.), France; 3a,b, RV ext., and dorsal view of both valves showing gape, both $\times 1$ (de Loriol, 1903). Goniomya Agassiz, 1841, p. 275 [*Mya angulifera J. SOWERBY, 1819, p. 46 (=*Mya intersectans SMITH, 1817, p. 92; SD HERRMANNSEN, 1847, p. 486)] [=Gonomya Agassiz, 1838 (nom. nud.); Gonyomya HAUER, 1853 (nom. van.); Gonimya NECHAEV, 1894 (nom. null.); Goniomyaa PCHEL-INTSEV, 1924 (nom. null.)]. Small to mediumsized, ovate, moderately to strongly elongate and inequilateral, with broadly rounded to subangular umbones protruding slightly above dorsal margin; beaks almost orthogyrous; inflation moderate; posterior gape relatively wide, anterior gape narrow; diagonal ridge obtuse, rounded off; escutcheon shallow, its bordering ridges ill-defined except near umbones; anterior and posterior parts
- of surface with discordant ribbing; hinge structure unknown; pallial sinus present. L.Jur.(L. Lias.)-Eoc. G. (Goniomya) [=Lysianassa MÜNSTER, 1838
- G. (Goniomya) [=Lysianassa MUNSTER, 1838 (non EDWARDS, 1830); Rhombomya SACCO, 1901, p. 133 (type, Lysianassa rhombifera GOLDFUSS, 1840, p. 264)]. Ornament consisting of anterior and posterior series of steep oblique ribs inclined toward one another; in some species these meet along line from umbo to ventral margin forming series of V's, and in others they are separated by intervening rib parallel with growth lines or by almost smooth area. L.Jur.(L.Lias.)-U.Cret. (Turon.), cosmop.; Eoc., Eu.(Italy).—FIG. F11,4. *G. (G.) intersectans (SMITH), M.Jur. (Bathon.), Eng.; 4a,b, LV ext., dorsal of both valves, ×1 (Cox, n).
- G. (Deltamya) BURMEISTER, 1914, p. 21 [*D. *jboehmi*; M]. Ribs on posterior and median parts of surface parallel with growth lines, those on anterior part slightly oblique to them but weak. U.Cret.(Senon.), Eu.(Ger.).—FIG. F11,5. *G. (D.) *jboehmi* (BURMEISTER); LV ext., ×1 (Burmeister, 1914).
- Homomya AGASSIZ, 1843, p. 154 [*Mactra gibbosa J. SOWERBY, 1813, p. 91; SD HERRMANNSEN, 1847, p. 541]. Resembling *Pholadomya* (*Pholadomya*) in shape except that in some species umbones are less prominent; without radial ribbing, unless in

earliest stages of growth; hinge margin smooth, uninterrupted; pallial sinus deep. M.Trias. (Muschelkalk)-U. Jur. (Portland.), cosmop. [The commoner Muschelkalk species which have been referred to this genus seem better included in Pachymya (Arcomya).]—FIG. F13,3. *H. gibbosa (SowERBY), M.Jur. (Bathon.), Eng.; 3a,b, LV ext., both valves dorsal (holotype), ×0.7 (Cox, n).

- Machomya DE LORIOL, 1868, p. 517 [*Panopaea dunkeri D'ORBIGNY, 1850, p. 47 (pro Solen jurensis DUNKER, 1847, p. 131, incorrectly treated by D'ORBIGNY as a secondary homonym of "Panopaea jurensis BRONGNIART, 1821," presumably a mistake for Mya? jurassi BRONGNIART, 1821); M]. Resembling more compressed and elongate species of Pachymya (Arcomya) in external characters; interior of each valve with low oblique rib near anterior margin; ostracum moderately thick; details of hinge and pallial line unknown. M.lur.-U.Jur.(Bathon.-Kimmeridg.), Eu.-Fig. F13,2. *M. jurensis (DUNKER), U.Jur.(Kimmeridg.), France; 2a-c, LV ext., both valves dorsal; LV ext. showing impression of internal rib; all $\times 1$ (de Loriol, 1868).
- Molukkana KRUMBECK, 1923, p. 219 [*M. seranensis; M]. Oblong, strongly inequilateral, with broad, moderately protruding, almost orthogyrous, well anteriorly placed umbones and rounded-off diagonal umbonal ridge; ostracum thick, ligamental nymph solid; hinge edentulous; pallial line and adductor scars unknown; ornament of irregular concentric undulations. [Possibly inseparable from Pachymya (Pachymya) but imperfectly known.] U.Trias.(Nor.), Indon.
- Neoburmesia YABE & SATO, 1942, p. 251 [*N. iwakiensis; OD]. Medium-sized, elongate-oblong, with prominent, anteriorly placed, broadly rounded umbones well incurved to orthogyrous beaks; strongly inflated, most so at mid-length; posterior gape moderately wide; strong carina in each valve from umbo to posteroventral angle, delimiting broad, elongate, partly concave posterior area, while on other side of umbo weaker radial ridge delimits small anterior area; escutcheon long, narrow, bordered by distinct ridges; median part of surface bearing radial and concentric ribs with tubercles at their intersections; posterior and anterior areas with weak concentric ornament only; internal characters unknown. U.Jur., Japan.-FIG. F13,1. *N. iwakiensis; 1a,b, LV ext. and dorsal view of both valves, $\times 1$ (Tamura, 1960).
- Osteomya Moesch, 1874, p. 19 [*Mya dilata Phil-LIPS, 1829, p. 155 (cited as "dilatata"); M] [=Goniomeris CHOFFAT, 1893, p. 37 (type, G. gaudryi; M); Uromya Rollier, 1913, p. 262 (type, Mya dilata PhilliPs; SD Cossmann, 1921, p. 27); Eurychasma Cossmann, 1915, p. 9 (type, E. combesi; M)]. Medium-sized, elongate-oblong, strongly

inequilateral, with broad, only slightly protruding, opisthogyrous umbones placed from anterior third to quarter of length; some specimens upcurved posteriorly; inflation moderately strong; shell truncated vertically posteriorly and with wide gape correponding to complete cross section of shell; anterior gape absent or very narrow; ornament consisting of weak concentric undulations, irregu-



Fig. F13. Pholadomyidae (p. N832).
larly arranged except on anterodorsal part of surface; pustules relatively conspicuous, in closely spaced radial rows; internal characters unknown. *L.Jur.(Toarc.)-U.Jur.(Callov.)*, Eu.-Madag.-E.Afr. ——FIG. F14,1. *O. dilata (PHILLIPS), M.Jur. (Bajoc.), Eng.; 1a,b, LV ext., dorsal view of both valves, ×1 (Cox, n).

Pachymya J. DE C. SOWEREY, 1826, p. 1 [*P. gigas; M]. Oblong, moderately to strongly inequilateral, with broad, only slightly protruding, almost orthogyrous umbones; posterior gape slight to moderate; most species with umbonal ridge, crossing most inflated part of shell, running diagonally to posteroventral corner; pallial line distant from shell margins; pallial sinus (where known) small or absent; surface unornamented in most species except for fine, radially aligned pustules, but with concentric undulations in some Triassic forms. *M.Trias.-U.Cret.*, cosmop.

P. (Pachymya) [=Cratomya Rollier, 1913, p. 287 (type, Arcomya liesbergensis Rollier, 1913, p. 286; M)]. Medium-sized to large, with umbones placed well anteriorly; moderately to strongly inflated, with diagonal ridge prominent; escutcheon broad, scarcely impressed, bordered by obtuse umbonal ridges; ostracum relatively thick in many species; hinge margin much thickened near beak and commonly with irregular longitudinal rugosities; ligamental nymphs stout; pallial sinus small or absent. M.Trias.-U.Cret. (Cenoman.), cosmop.--FIG. F14,2a,b. *P. (P.) gigas Sowerby, U.Cret. (Cenoman.), France; 2a,b, LV ext., and dorsal view of both valves, $\times 0.5$ (d'Orbigny, 1843-47).—FIG. F14,2c. P. (P.) austinensis SHUMARD, L.Cret. (Alb.), USA (Tex.); RV int. showing hinge and pallial line, $\times 0.45$ (Stanton, 1947).---FIG. F14,2d. P. (P.) latissima (AGASSIZ), U.Jur.(Oxford), Switz.; LV int., showing pallial line, $\times 0.7$ (Rollier, 1913).

- P. (Arcomya) ROEMER (ex AGASSIZ, MS), 1839, p. 43 [*Solen helveticus ROEMER (ex THURMANN, MS), 1839; M]. Medium-sized, relatively weakly inflated; position of umbones variable; hinge structure not observed; pallial line (where known, but not seen in type species) without sinus. M. Trias.-U.Cret.(Turon.), cosmop. [The Triassic species have been included mostly in Homomya.] —FIG. F15,2a,b. *P. (A.) helvetica (ROEMER), U.Jur.(Kimmeridg.), Switz.; 2a,b, RV ext. and dorsal views of both valves, ×1 (Agassiz, 1843). —FIG. F15,2c. P. (A.) sp., U.Jur., Scot.; RV int. mold showing pallial line, ×1 (Cox, n).
- P. (Trichomyella) Cox, nom. subst. herein [pro Trichomya CRICKMAY, 1936, p. 558 (non IHERING, 1900, p. 87)] [*Trichomya amphitrite CRICKMAY, 1936; OD]. Resembling P. (Arcomya) but without diagonal ridge; radial lines of pustules conspicuous. U.Jur.(Callov.), USA (Wyo.).—FIG. F15,1. *P. (T.) amphitrite (CRICKMAY); RV ext., ×1.3 (Crickmay, 1936).

Palaeocosmomya FLETCHER, 1946, p. 401 [*P. teicherti; OD]. Medium-sized, ovate or oblong, variably elongated; with broadly rounded, unprotruding or slightly protruding umbones situated at or in front of the anterior third of length, and with feebly prosogyrous beaks; inflation moderate, posterior gape wide; escutcheon distinctly bordered; posterior 0.7 of surface bearing 2 convergent series of steep, oblique ribs which meet to form V's, anterior third with broader ribs which are only slightly oblique to growth lines; radial groove crossing latter series of ribs (that is, not marking boundary between them and V-shaped ribs) runs almost perpendicularly from umbo to ventral margin; internal characters unknown. [Regarded by DICKINS & SHAH (1965) as subgenus of Cosmomya.] Perm., Australia-Greenland.--Fro F15,7. *P. teicherti; LV ext., $\times 1$ (Cox, n).

- Panacca Dall, 1905, p. 143 [pro Aporema Dall, 1903, p. 1532 (non Scudder, 1890)] [*Pholadomya arata VERRILL, 1881, p. 301; OD] [=Notoтуа Соттон, 1931, р. 342 (поп М'Соч, 1847) (type, Pholadomya tasmanica Hedley & MAY, 1914, p. 132; OD); Panacea SALISBURY, 1932 (nom. null.)]. Shell small for family, gibbous, subtriangular, inequilateral, anterior end more or less truncated and flattened transversely; anterior margin commonly sinuate and meeting anterodorsal margin in well-defined angle; beaks slightly prosogyrous; posterior gape narrow or absent; most species ornamented with unevenly spaced, narrow radial ridges absent from anterior end of shell (one species with radial threads only); surface pustules very fine; pallial line with shallow sinus; hinge margin simple, very little thickened; ligament entirely external. Rec., cosmop. [Deep water. About seven known species are typical: Pholadomya loveni JEFFREYS and P. pacifica DALL, which some authors have included in Panacca, disagree with the above diagnosis in being less trigonal and inequilateral.]-FIG. F15,3a,b. *P. arata (VERRILL), W.Atl.; side and ant. views RV, ×1 (Verrill, 1882, 1884).—Fig. F15,3c,d. P. locardi DALL, E.Atl.; LV ext. and RV int., ×1.3 (Locard, 1898).
- Parilimya MELVILL & STANDEN, 1899, p. 202 [*Pholadomya (Parilimya) haddoni; M]. Small, oval, subequilateral, evenly and only moderately inflated; margins with narrow anterior but no posterior gape; ornament of weak radial threads; pallial line not observed; ligament entirely external; dorsal margin with toothlike thickening in front of beak in both valves. Rec., Torres Straits. Pentagrammysia CHERNYSHEV, 1950, p. 22 [*P. altaica, OD]. Superficially similar to Undulomya FLETCHER, 1946, in form and ornamentation but without posterodorsal furrows; posterior gape obscure, if present. L.Carb., Kuznetsk Basin, USSR (Sib.).—FIG. F16,4. *P. altaica; RV ext., ×1 (Ebersin,1960). [NEWELL]

Praeundulomya DICKINS, 1957, p. 10 [**P. concentrica;* OD]. Medium-sized, oblong, elongate, with broad, scarcely protruding, well anteriorly placed umbones and prosogyrous beaks; inflation moderate, posterior gape narrow; escutcheon narrow, elongate, distinctly bordered; flank with 2 dorsal grooves like those of *Undulomya* but shallower; ornament consisting of irregular undula-



FIG. F14. Pholadomyidae (p. N833-N834).

Bivalvia—Anomalodesmata



FIG. F15. Pholadomyidae (p. N834-N835, N837-N838).

Pholadomyoida—Pholadomyacea



FIG. F16. Pholadomyidae (p. N834, N837-N838).

tions, which, although almost concentric, are slightly oblique to growth lines on most parts of surface; V-shaped ribs absent; internal characters unknown. L.Perm., Australia-?Kashmir-S. Am.(Peru).-Fig. F15,6. *P. concentrica, W. Australia; 6a,b, LV ext. (imperfect anteriorly) and dorsal view of both valves, $\times 1$ (Dickins, 1957).

Tetorimya HAYAMI, 1959, p. 159 [*T. carinata; OD]. Medium-sized, trapezoidal, highest near posterior end, well inflated, most so along diagonal (which may form distinct ridge) from umbo to

posteroventral angle of shell; posterior gape narrow or absent; umbo narrow, protruding, placed well anteriorly and incurved to prosogyrous beak; anterior part of ventral margin with broad sinus to which radial sulcus of flank corresponds; pallial line with deep sinus; surface with coarse growth rugae; internal features of hinge unknown. U.Jur., Japan-Alaska-USSR.-FIG. F15,5a. *T. carinata, Japan; RV ext., ×1 (392).—Fig. F15,5b. T. panderi (EICHWALD), Alaska; LV ext., X1 (Eichwald, 1871).

?Triplicosta COOPER, 1897, p. 333 [*Pholadomya

(Triplicosta) progressiva; M]. Medium-sized, ovate, not much elongated, gibbose, strongly inequilateral, with broadly rounded, well anteriorly placed umbones; with moderate posterior gape; ornament of rounded radial ribs which are relatively broad on the posterior part of the surface and margins and clearly arranged on the anterior part; internal characters unknown; ostracum relatively thick, not nacreous in known fossil specimens. [While included in *Pholadomya* it is also suggested that this species may be related to *Cardita* or *Petricola.*] ?Eoc., USA(Calif.).——Fic. F16,2. *T. progressiva (COOPER); 2a,b, RV ext., both valves ant., $\times 1$ (Cooper, 1897).

Undulomya Fletcher, 1946, p. 391 [*U. pleiopleura; OD]. Medium-sized, elongate-ovate, with broad, unprotruding, well anteriorly placed umbones and prosogyrous beaks; inflation moderate, posterior gape moderately wide; escutcheon shallow; dorsal part of flank with 2 grooves running from umbo to posterior margin; ornament consisting of 2 convergent series of straight or curved ribs which meet along line from umbo to ventral margin; ribs of posterior series strongly oblique to growth lines, while obliquity of anterior series is variable and they are almost concentric in some specimens; internal characters unknown. Perm., Australia-Afr. (Madag.).-FIG. F15,4. *U. pleiopleura, W.Australia; LV ext., X0.7 (Dickins, 1956).

Vacunella WATERHOUSE, 1956, p. 277 [*Allorisma curvatum MORRIS, 1845; OD]. Similar to Chaenomya but with more rounded ventral margin, maximum shell convexity near mid-length and relatively small posterodorsal gape; shell interior marked by scattered mantle insertions; edentulous; ligament nymphs heavy and rolled outward. Perm., E.Australia.—FIG. F16,3. *V. curvatum (MOR-RIS), L.Perm., Wollongong, New S. Wales; 3a, top view of LV int. mold; 3b, same, int. hinge, latex cast showing interior of amphidetic ligament; 3c, same showing pallial sinus and mantle insertions, all ×0.4 (Newell, n). [NEWELL]

Wilkingia WILSON, 1959, p. 401 [*Venus elliptica PHILLIPS, 1836; OD] [=Allorisma AUCTT. (non KING, 1850); ?Tellinomorpha DE KONINCK, 1885, p. 90 (type, T. cuneiformis; OD)]. Elongate oval, subcylindrical at beaks; beaks placed 0.2 to 0.25 behind front margin; anterior and posterior extremities rounded, dorsal and ventral margins subparallel; broad, shallow sulcus extending ventrally from umbones across anterior half of valves; escutcheon and elongate lunule present; umbonal ridge broad and poorly developed; valves marked by regular broad and rounded concentric folds; radial rows of small papilli present, especially on posterodorsal area; adductor scars shallow, without buttresses; shallow pallial sinus present; with or without narrow posterior gape; ligament nymphs short and weak; hinge edentulous. Miss.-Perm.,

cosmop.——FIG. F16,1. *W. elliptica (PHILLIPS), L.Carb., Eng.(Redesdale); 1a,b, RV and cardinal views, $\times 1$ (Wilson, 1959). [NEWELL]

Family BURMESIIDAE Healey, 1908

[Materials for this family prepared by L. R. Cox]

Medium-sized, equivalve, thin-shelled, of moderate convexity, well elongated, not strongly inequilateral; hinge line elongate, umbones broad and protruding only slightly above it; each valve with narrow, spoonlike chondrophore extending into shell cavity from below beak; no hinge teeth; pallial line and adductor scars not observed; surface elaborately ornamented with radial riblets together with concentric folds and threads, radial riblets predominating on middle of each valve; whole surface also covered with rows of minute granules. U. Trias.-L.Jur.(Lias.).

- Burmesia HEALEY, 1908, p. 58 [*B. latouchii; SD DIENER, 1923, p. 247]. Elongate-ovate, beaks very slightly anterior to mid-length; valves gaping slightly in front, more widely behind; posterior end of shell ornamented with concentric folds and subordinate radial threads, anterior end commonly bearing depressed folds which are almost perpendicular to hinge line and cross growth lines obliquely. U. Trias.-L. Jur. (Lias.), Asia(Jordan-Burma-Indonesia-Japan).—Fio. F17,1. B. lirata HEALEY, U.Trias.(Rhaet.), Burma; pair of valves, RV below, ×1 (Healey, 1908).
- Prolaria HEALEY, 1908, p. 60 [*P. sollasi; M]. Presumed posterior end of shell forming rostrumlike projection truncated at its extremity and situated in relatively dorsal position with deep sinus below it; sharp sigmoidally curved carina runs in each valve from umbo to lower corner of this projection; predominant radial ribbing confined to posteromedian part of surface; strong, irregular concentric folds with subordinate radial threads cover anterior half of surface, while posterior projection is unornamented except for growth lines. U.Trias.(Rhaet.), Asia(Burma-Armenia-Indon.).-Fig. F17,2a,b. *P. sollasi, Burma; 2a, part of RV ext., showing posterior projection, 2b, more complete but crushed RV, both $\times 1$ (Healey, 1908).——FIG. F17,2c,d. P. armenica ROBINSON, Armenia; 2c,d, RV ext. and dorsal view of both valves, post. extremity broken away, ×1 (Kiparisova, 1947).

Family CERATOMYIDAE Arkell, 1934

[=Ceromyidae FISCHER, 1887 (invalid because based on junior homonym)] [Materials for this family prepared by L. R. Cox]

Shell ovate, longer than high, inequilateral, moderately to strongly inflated, some



FIG. F17. Burmesiidae (p. N838).

specimens inequivalve; valve margins closed or with narrow posterior gape; shell wall rather thin; beaks prosogyrous; no demarcated lunule or escutcheon; ligament opisthodetic, subinternal, located between reflected and thickened posterodorsal margin of LV and overlapping margin of RV, which has subinternal thickening protruding into cavity of valve, giving rise in *Cera*- tomya and Gresslya to slit extending back from beak on internal mold of many specimens; true hinge teeth absent, replaced by thickenings or protuberances of dorsal margins; pallial line variable; surface with variously oriented plications or unornamented except for minute pustules present in some forms. U.Trias.-U.Jur., ?Mio.

The hinge apparatus is so closely similar in *Ceratomya* and *Gresslya* that their union in the same family seems justified, especially as the earlier species of *Ceratomya* (e.g., *C. petricosa* of the Lias) lack the external ribbing which renders some of the later species so much unlike *Gresslya* in appearance. Nevertheless, the two genera differ greatly in the form of the pallial line.

It seems most improbable that the Miocene genus *Ceromyella* was (as thought by its author, SACCO) a survivor of the Ceratomyidae, but, for lack of definite evidence as to its affinities, it is here listed under this family, but with a query.

Ceratomya SANDBERGER, 1864, p. 16 [nom. subst. pro Ceromya Agassiz, 1842] [non Ceromya ROBINEAU-DESVOIDY, 1830] [*Isocardia excentrica ROEMER, 1836, p. 106; ICZN pend.] [=Ceromia STOLICZKA, 1871 (nom. null.)]. Medium-sized to large, ovate, gibbose, especially anteriorly, with strongly prosogyrous and in some species incoiled, more or less anteriorly placed beaks; some specimens slightly inequivalve, with umbo of either valve extending more anteriorly than that of other; no gape of valve margins; posterodorsal margin of RV with thin outer flange separated from subinternal thickening by groove in which ligament was inserted, corresponding groove on upper (outer) side of reflected margin serving same purpose in LV; anterodorsal margin of RV much thickened below beak in some species; adductor scars small; pallial line bending up sharply posteriorly, shallowly sinuate in some species; surface smooth or (more commonly) with concentric or oblique undulations. L. Jur.-U. Jur., cosmop .--FIG. F18,1a. *C. excentrica (ROEMER), U.Jur.(L. Kimmeridg.), France; LV ext., ×1 (549).-FIG. F18,1b-d. C. aalensis (QUENSTEDT), M.Jur. (Bajoc.), France; 1b-d, LV int., RV int., and int. mold showing pallial line and adductor scars, all ×0.7 (Benecke, 1905).-FIG. F18,1e. C. petricosa (SIMPSON), L.Jur. (M.Lias.), Eng.; LV ext. of a smooth species, $\times 1.3$ (Cox, n).——Fig. F18,1f. C. bajociana (D'ORBIGNY), M.Jur.(Bajoc.), Eng.; transv. sec. through hinge region short distance behind beaks, LV and RV as oriented, former position of ligament dotted, $\times 2$ (Cox, n).

?Ceromyella Sacco, 1901, p. 133 [*C. miotaurina; M]. Like Ceratomya in shape but only 6 mm. long; internal characters unknown. Mio.(Helvet.), N.Italy.

Gresslya Agassiz, 1843, p. 202 [*Lutraria gregaria ZIETEN, 1833, p. 85; SD HERRMANNSEN, 1847, p. 490, as "Lutraria gregaria Goldfuss"] [=Gresslyia BRONN, 1848 (nom. van.); Gresslya D'OR-BIGNY, 1850 (nom. null.); Gressluya PAETEL, 1875 (nom. null.)]. Ovate, usually with cuneiform tendancy, moderately elongate, umbones not prominent, that of RV slightly higher than LV; valves with narrow posterior gape; hinge structure as defined for family, slit extending back from



FIG. F18. Ceratomyidae (p. N839-N841).

© 2009 University of Kansas Paleontological Institute



FIG. F19. Ceratomyidae (p. N841).

spicuous ornament but bearing very fine pustules or puncta radially aligned. L.Jur.-U.Jur., cosmop. ——FIG. F18,2a,b. G. peregrina (PHILLIPS), U. Jur.(Oxford), Eng.; 2a,b, LV int. mold showing pallial sinus, dorsal view of both valves showing slit extending back from beak in RV, ×1.3 (Cox, n).——FIG. F18,2c. *G. gregaria (ZIETEN), M. Jur.(Bajoc), Ger.; LV ext., ×1 (Schmidtill, 1926). ——FIG. F18,2d. G. abducta (PHILLIPS), M.Jur. (Bajoc.), Eng.; transv. sec. through hinge region short distance behind beaks, LV and RV as oriented, edge marked "X" giving rise to the slit on internal molds; ×3.3 (Cox, n).

- Pholadomyocardia SZAJNOCHA, 1889, p. 88 [*P. jelskii; M]. Large, inequivalve, gibbose, slightly longer than high; valves with a broadly trigonal body and a flattened winglike postero-dorsal extension; umbones placed well anteriorly, protruding moderately, prosogyrous, the right one higher than the left; surface with a few broad, irregular, concentric folds; internal characters unknown. Jur., S.Am.(Peru).—Fig. F19,2. *P. jelskii, 2a,b, LV ext. and ant. view of both valves, $\times 0.5$ (Szajnocha, 1889).
- Pteromya MOORE, 1861, p. 505 [*P. crowcombeia; SD STOLICZKA, 1871, p. xv]. Subovate, subequilateral or inequilateral to a varying extent, not strongly inflated, slightly to moderately inequivalve, right valve the more gibbose and with its umbo the more elevated; valve margins not gaping; umbones broad, protruding very little; posterodorsal and posterior margins forming continuous, strongly convex curve or else meeting in obtuse angle, in which case very obtuse posterior ridge may be present in one or both valves; hinge structure as in Ceratomya and Gresslya; adductor scars and pallial line not yet observed, the latter probably without a sinus; surface with concentric undulations or ridges, or merely with coarse growth threads. U.Trias.(L. Rhaet.)-L.Jur.(L. Hettang.), Eu.-Fig. F19,1a,b. *P. crowcombeia, L.Rhaet., Eng.; 1a,b, LV ext., and RV ext., of different specimens, $\times 1$ (Cox, n).—Fig. F19,1c,d, P. tatei (RICHARDSON & TUTCHER), L.Hettang., Eng.; 1c,d, RV ext. with and without posterior ridge, all $\times 1$ (Cox, n).

Family MYOPHOLADIDAE Cox, 1964

[Materials for this family prepared by L. R. Cox]

Shell medium-sized, elongate-ovate, some specimens with slight tendency to be rostrate posteriorly; umbones broadly rounded, scarcely protruding, situated anterior to mid-length and strongly incurved to slightly prosogyrous beaks; inflation of shell strong below umbones, diminishing regularly in posterior direction; valve margins with



FIG. F20. Myopholadidae (p. N842).

rather wide posterior and narrow anterior gape; ornament of narrow radial ribs which are widely separated on anterior part of surface and relatively closely arranged on median part; in some species strong and fairly closely arranged ribs continue almost to posterior extremity, but in others posterior end of shell is sparsely ribbed or almost smooth; dorsal margin of RV overlapping that of LV, with subinternal ligament lying between them, as in *Ceratomya* and *Gresslya;* sharp edge of thickening of dorsal margin of right valve which projects into cavity of valve gives rise to groove extending back from beak on internal mold, as in those two genera; adductor scars and pallial line unknown; ostracum thin, probably originally nacreous internally. *M.Jur.* (*Bathon.*)-L.Cret.(U.Alb.).

Myopholas DOUVILLÉ, 1907, p. 107 [*Pholadomya multicostata AGASSIZ, 1842, p. 52; OD]. Characters and distribution of family. M.Jur.-L.Cret., Eu. —FIG. F20,1a,b. *M. multicostata (AGASSIZ), U.Jur.(Kimmeridg.), Switz.; 1a,b, RV ext. and dorsal view of both valves, ×1 (Cox, n).— FIG. F20,1c. M. ledouxi DOUVILLÉ, L.Cret.(U. Alb.), France; dorsal view of both valves showing groove on RV of internal mold, ×1 (Douvillé, 1907).

Family PLEUROMYIDAE Dall, 1900

[nom. correct. ZITTEL, 1903 (pro Pleuromyacidae DALL, 1900, ex ZITTEL MS)] [Materials for this family prepared by L. R. Cox]

Shell of medium size, equivalve, oval, oblong or trapeziform, moderately to strongly inflated, with narrow to moderately wide posterior gape; umbones situated within anterior half and usually well toward anterior end of shell, broadly rounded, not strongly protruding; no demarcated dorsal areas; no true hinge teeth; main part of ligament external, opisthodetic, with short supporting nymphs; below and slightly anterior to the beak of each valve is short, rounded protuberance of margin, slightly hollowed out above, and behind protuberance is small niche; protuberance of RV fits above that of the left, a small internal ligament possibly occupying the space between them; postero-dorsal margin of RV overlapping that of LV; pallial sinus deep; ostracum thin, probably originally nacreous internally. Surface with or without concentric ribbing and with a delicate ornament of radial rows of minute pustules. Trias.-L.Cret.

Pleuromya Agassiz, 1842, p. 439 [*Mya gibbosa J. DE C. SOWERBY, 1823, p. 19 (=*Donacites alduini BRONGNIART, 1821, p. 555); M] [=Myacites von Schlotheim, auctt.¹; Anaplomya KRAUS, 1843, p. 130 (type, A. lutraria; M); Anoplomya KRAUS, 1850 (nom. null.); Hapalomya ROEDER, 1882, p. 102 (type, H. fragilis; M); Hapalomia ROEDER, 1882 (nom. null.); ?Fogiella KRUMBECK,

¹ This generic name, applied particularly to shells of this genus by some early authors, merely denoted a fossil *Mya* and is not available for purposes of nomenclature (Zool. Code, 1961, Art. 20).



FIG. F21. Pleuromyidae (p. N842-N843).

1913, p. 57 (type, F. deningeri; M)]. Characters of family. Trias.-L.Cret., cosmop.-Fig. F21,1a. *P. alduini (BRONGNIART), U.Jur.(U.Oxford Clay), Eng.; RV ext., $\times 1$ (19*f*).—Fig. F21,1*b*. *P*. uniformis (J.Sowerby), U.Jur. (Oxford), Eng.; RV composite ext.-int., showing pallial line, etc. (not retouched), $\times 1$ (Cox, n).—Fig. F21,1c. P. uniformis, U.Jur. (Corallian Beds), Eng.; LV hinge tilted slightly toward observer, showing protuberance just anterior to beak, $\times 2$ (Cox, n).—FIG. F21,1d. P. marginata AGASSIZ, M.Jur.(Bathon.), France; diagram showing relation between protuberances of hinge margins of valves, LV on left, enl. (Douvillé, 1907) .---- Fig. F21,1e,f. P. uniformis, M.Jur.(Inf. Oolite), Eng.; 1e,f, transverse sections through dorsal region of slightly separated valves, on left, le just behind, lf just in front of beaks, $\times 2$ (Cox, n).

Superfamily PANDORACEA Rafinesque, 1815

[nom. transl. STEWART, 1930 (ex Pandoridae RAFINESQUE, 1815)] [Materials for this superfamily prepared by MYRA KEEN with additions as recorded]

Sedentary to burrowing forms, shell material nacreous, at least inner layer; mostly thin, somewhat elongate or gaping, inequivalve; hinge without regular heterodont dentition but hinge margin variously reinforced by buttresses or denticles; ligament and resilium sheathed with a calcareous layer or lithodesma in many forms. U.Trias.-Rec.

Family PANDORIDAE Rafinesque, 1815

[nom. correct. GRAY, 1840 (pro family Pandoracia RAFINES-QUE, 1815)] [Materials for this family prepared by MYRA KEEN]

Compressed, inequivalve, dorsal border of one valve overlapping other; ligament wanting, resilium internal, reinforced in some by elongate lithodesma; dorsal margin edentulous but with laminar buttresses beside the resilium; pallial line entire. Oligo.-Rec.

Pandora BRUGIÈRE, 1797 (genus without species)
[*Solen inequivalvis LINNÉ, 1758; SM LAMARCK, 1799] [=Calopodium Röding, 1798 (obj.); Trutina BROWN, 1827 (type, T. solenoidea, =Solen pinna MONTAGU, 1803; M)]. Of medium size, flat, thin, RV flatter than LV, dorsal border convex; anterior end rounded, posterior rostrate. Oligo.-Rec., N. Am.-S. Am.-C.Am.-Eu.-Pac.-Ind.O.
P. (Pandora). Sculpture of RV feebly concentric; without lithodesma. Oligo.-Rec., W.N.Am.-Eu.-



FIG. F22. Pandoridae (1,3-7); Cleidothaeridae (2) (p. N843-N844).

- W.Pac.—FIG. F22,3. *P. (P.) inaequivalvis (LINNÉ), Rec., Eu.; 3a-c, LV int., ext., RV hinge, $\times 1$ (7c).
- P. (Clidiophora) CARPENTER, 1864 [*P. claviculata CARPENTER, 1856; OD]. With 3 laminae in either valve; lithodesma present. Mio.-Rec., E.N. Am.-W.N.Am.-C.Am.—FIG. F22,5. *P. (C.) claviculata CARPENTER, Rec., W.Mex.; 5a,b, RV ext., LV int., ×0.7 (Stanford Univ. specimen).

- P. (Foveadens) DALL, 1915 [*F. panamensis; OD]. Hinge with 2 diverging laminae in RV, posterior longer and higher; LV with 2 short laminae close together; sheet of shelly material bridging bases of laminae, forming cavities between them. Rec., W.C.Am.—FIG. F22,4. *P. (F.) panamensis (DALL),; 4a,b, holotype, RV ext., LV int., $\times 2$ (U.S. National Museum).
- P. (Frenamya) IREDALE, 1930 [*Coelodon patulus TATE, 1889; OD] [=Coelodon CARPENTER, 1865 (non AUDINET-SERVILLE, 1882) (type, P. ceylanica SowERBY, 1835; SD STOLICZKA, 1871)]. Sculpture of concentric wrinkles; LV with laminae united by transverse plate; no lithodesma. Rec., W.C.Am.-S.Pac.-W.Pac.-Ind.O.—FIG. F22,6. *P. (F.) patula (TATE), S.Australia, 6a,b, RV int, LV hinge, ×2 (Cotton, 1938).
- P. (Heteroclidus) DALL, 1903 [*P. punctata CON-RAD, 1837; OD]. With 1 laminar buttress in LV, 3 in RV; lithodesma present. Plio.-Rec., W.N.Am.-C.Am.——FIG. F22,7. *P. (H.) punctata CONRAD, Rec., USA(Calif.); 7a,b, LV ext., int., ×1 (Stanford Univ. specimen).
- P. (Pandorella) CONRAD, 1863 [*P. arenosa CON-RAD, 1834; M] [=Kennerlia CARPENTER, 1864 (type, K. bicarinata; SD STOLICZKA, 1870) (Kennerleya, Kennerleyia, Kennerlyia, spelling errors)]. With radial ribbing in RV; lithodesma wanting. Mio.-Rec., E.N.Am.-W.N.Am.-S.Am. —FIG. F22,1. *P. (P.) arenosa CONRAD, Mio., USA(Va.); 1a,b, LV ext., int., ×1 (Conrad, 1838).

Family CLEIDOTHAERIDAE Hedley, 1918

[=Chamostreidae FISCHER, 1887] [Materials for this family prepared by MYRA KEEN]

Shell attached by right valve; one cardinal tooth in LV; ligament wanting but resilium present, submerged, with lithodesma. *Mio.-Rec.*

Cleidothaerus STUTCHEURY, 1830 [*C. chamoides (=*Chama albida LAMARCK, 1819; M] [=Chamostrea HERRMANNSEN, 1846 (latinization of "Camostrée" DE BLAINVILLE, 1825, ex ROISSY MS); OD (obj.); "Chamostraea ROISSY, 1805, AUCTT." (fictitious reference)]. Inequivalve, fixed on anterior slope; hinge of RV with large pit; lithodesma long, curved. Mio.-Rec., Australasia.-----FIG. F22,2. *C. albidus (LAMARCK), Rec., S. Australia; 2a,b, LV int., RV int., ×0.5 (307).

Family LATERNULIDAE Hedley, 1918

[=Anatinidae GRAY, 1840 (invalid, based on junior homonym); Cercomyacidae Скіскмач, 1936] [Materials for this family prepared by Мука Кеем and L.R. Cox]

Subequivalve, elongate, gaping posteriorly; umbones not at all or only slightly protruding, with transverse external slit, or with internal plate represented by slit on internal molds; hinge edentulous; ligament (where known) on two projecting spoonshaped chondrophores, each supported by thin oblique buttress (or clavicle); pallial sinus broad; shell thin, subnacreous internally (526). U.Trias.-Rec.

- Laternula Röding, 1798, p. 155 [*L. anatina (=Solen anatinus Linné, 1758, p. 673); SD GRAY, 1847, p. 190] [=Auriscalpium Megerle von MÜHLFELD, 1811 (obj.; M); Anatina LAMARCK, 1818 (non SCHUMACHER, 1817) (obj.; T); Butor GISTEL, 1848 (non FORSTER, 1827) (pro Anatina LAMARCK); Butorella STRAND, 1928 (pro Butor GISTEL)]. Thin subcylindrical, posterior end roundly gaping. U.Cret.-Rec., N.Am.-Eu.-Pac.-Ind.O.
- L. (Laternula). Surface nearly smooth; posterior gape wide. U.Cret.-Rec., N.Am.-Eu.-S.Pac.-Ind.O. —-FIG. F23,1. *L. (L.) anatina RÖDING, Rec., E.Indies; 1a,b, LV int., with RV hinge, LV ext., $\times 0.7$ (307).
- L. (Laternulina) HABE, 1952, p. 266 [*Anatina japonica LISCHKE, 1872, p. 107 (=A. flexuosa REEVE, 1863, sp. 5); OD]. Surface with wrinkled undulations; gape narrower than in L. (Laternula). Rec., W.Pac.—FIG. F23,2. *L. (L.) flexuosa (REEVE), Japan; LV view of shell, $\times 1$ (Habe, 1952).
- Anatimya CONRAD, 1860, p. 276 [*Pholadomya (A.) anteradiata; SD SHIMER & SHROCK, 1944, p. 414]. Oblong, subequilateral, with concentric furrows anteriorly and radiating lines posteriorly; hinge unknown. U.Cret., E.N.Am.—FIG. F23,3. *A. anteradiata (CONRAD), USA(N.J.); LV view, $\times 0.7$ (Whitfield, 1907).
- Cercomya AGASSIZ, 1843, p. 143 [*C. pinguis; OD] [=?Kercomya GRESSLY, 1838 (nom. nud.)]. Elongate, subequilateral to distinctly inequilateral, compressed, with tapering posterior end, upcurved in some species; umbones level with posterodorsal margin or almost so; posterior umbonal ridges well defined; umbonal slit or impression of internal umbonal plate observed in some species; hinge and pallial line unknown; surface bearing minute, radially aligned pustules. U.Trias.-Cret., cosmop. C. (Cercomya). Flanks with concentric folds, posterodorsal area smooth. U.Trias.-Cret., cosmop. -Fig. F23,7a,b. *C. (C.) pinguis Agassiz, M.Jur. (Bajoc.), Switz.; 7a,b, LV ext., and dorsal views, ×1 (Agassiz, 1843).—FIG. F23,7c,d. C. (C.) sp. aff. C. (C.) gurgitis (PICTET & CAM-PICHE), L. Cret.(Alb.), Eng.;7c,d, RV ext., and dorsal view, $\times 0.7$ (Woods, 1909).
- C. (Capillimya) CRICKMAY, 1936, p. 558 [*Capillimya capillifera; OD]. With punctate radial striae on posteroventral sector and concentric

folds on rest of surface. Jur., Eu.-N.Am.—Fig. F23,6. C. (C.) striata AGASSIZ, U.Jur.(L. Kimmeridg.), France; 6a,b, RV ext. and dorsal views, $\times 1$ (de Loriol, 1872).

- Clistoconcha SMITH, 1910, p. 217 [*C. insignis; M]. Small, irregularly oblique-ovate; chondrophores small, buttress large; valves united in adult except for siphonal gape. *Rec.*, S.Afr.—FiG. F23,5. *C. insignis; 5a,b, LV ext., RV int., ×4 (Kuehnelt, 1958).
- Periplomya CONRAD, 1870 (July 7), p. 76 [nom. subst. pro Leptomya CONRAD, 1867, p. 15 (non ADAMS, 1864)] [*Periploma applicata CONRAD, 1858, p. 324; SD GARDNER, 1916, p. 633] [=Plicomya STOLICZKA, 1870 (Sept. 1) (pro Leptomya CONRAD)]. Like Laternula, but with chondrophores tapering and attached to buttress; slit anterior, oblique, long; surface with concentric ribbing. U.Cret., E.N.Am.—Fig. F23,4. *P. applicata (CONRAD), USA (Tenn.); RV ext., ×1 (951).
- Platymyoidea Cox, 1964, p. 42 [nom. subst. pro Platymya AGASSIZ, 1843, p. 180 (non ROBINEAU-DESVOIDY, 1830)] [*Platymya dilatata AGASSIZ; OD]. Ovate-oblong, not tapering posteriorly, compressed, with broad, scarcely protruding umbones between middle and anterior third of length; internal umbonal plate well developed; hinge unknown; ornament of irregular concentric folds strongest at anterior end of shell. L.Jur.-L.Cret., Eu.(Switz.-France-Eng.).—Fig. F23,8. P. rostrata (AGASSIZ), L.Cret.(Neocom.), France; 8a,b, LV ext. and dorsal views, $\times 0.7$ (696).
- Plectomya DE LORIOL, 1868, p. 525 [*Tellina rugosa Römer, 1836, p. 120 (non Pennant, 1777) (=Anatina subrugosa d'Orbigny, 1850, p. 49)] [=?Rhynchomya Agassiz, 1843, p. 152 (type, Cercomya gibbosa AGASSIZ, possibly founded on imperfect specimens of A. subrugosa)]. Oblong, compressed, some specimens with trigonal tendency; umbones near mid-length; oblique internal umbonal plate present; hinge and pallial line unknown; ornament consisting of folds which follow or are slightly oblique to growth lines and are best developed at ends of shell; minute, radially aligned granules are also present. U.Jur.(U.Kimmeridg.) - L.Cret.(Apt.), Eu.(Ger.-Switz.-France-Eng.)-Afr.(Congo).-FIG. F23,9. *P. subrugosa (D'ORBIGNY), U.Jur. (Portland.), France: 9a,b, LV ext. and both valves showing variability, $\times 1$ (de Loriol, 1868, 1872).

Family LYONSIIDAE Fischer, 1887

[Materials for this family prepared by MYRA KEEN]

Thin, subnacreous, inequivalve, beaks not slit; hinge edentulous; ligament sunken or submarginal, lithodesma present, median; pallial sinus distinct (508, 522). Eoc.-Rec. Lyonsia TURTON, 1822 [*Mya striata MONTAGU, 1815 (=*M. norwegica GMELIN, 1791); M] [==Hiatella BROWN, 1827 (non Bosc, 1801) (obj.); Magdala BROWN, 1827 (obj.; M); Osteodesma DE-SHAYES, 1830, AUCTT. (non DE BLAINVILLE, 1825); Myatella BROWN, 1833 (obj.; M); Pandorina SCACCHI, 1833 (non BORY ST. VINCENT, 1827) (obj.; M)]. Sculpture of radial lines. Eoc.-Rec., W.N.Am.-Eu.

L. (Lyonsia). Elongate, posterior end attenuate,



Fig. F23. Laternulidae (p. N845).

© 2009 University of Kansas Paleontological Institute

slightly gaping; sculpture of radial striations and raised threads. *Eoc.-Rec.*, N.Am.-Eu.——Fig. F24,1. *L. (L.) norwegica (GMELIN), Rec., Eng.; 1a,b, LV ext., int., 1c, RV hinge, ×1 (7c).

- L. (Bentholyonsia) HABE, 1952 [*Allogramma (B.) teramachii HABE, 1952; OD]. Sculpture of radial granules but not ribs; lithodesma large; posterior end short, gaping. Rec., W.Pac.——FiG. F24,3. *L. (B.) teramachii (HABE), Japan; 3a-d, RV ext., int., LV and RV hinges, ×1 (Habe, 1952).
- L. (Endomargarus) COSSMANN, 1887 [*L. heberti DESHAYES, 1857; OD]. Shape irregular because of nestling habit; sculpture of radial punctuations. *Eoc.*, Eu.—FIG. F24,2. *L. (E.) heberti DES-HAYES, France; 2a,b, LV, RV int., ×3 (160).
- Allogramma DALL, 1903 [*Lyonsia formosa JEF-FREYS, 1881; OD]. Valves with radial and vertical undulations; posterior end gaping. Rec., Eu.-N.Am.-NW.Afr.-Pac.—FIG. F24,6. *A. formosum (JEFFREYS), NW.Afr.; 6a-c, LV ext., int., dorsal view of both valves, ×2 (852).
- Entodesma PHILIPPI, 1845 [*E. chilensis; M] [=Tetragonostea HERRMANNSEN, 1849 (ex DE-SHAYES, VETAC.) (type, Mya solemyalis LAMARCK, 1818; M); Philippina DALL & SIMPSON, 1901 (type, Lyonsia beana D'ORBIGNY, 1853; OD)]. Periostracum thickened; shell irregularly rhomboidal, deformed by nestling; resilifer in each valve relatively small. Rec., N.Am.-S.Pac.
- E. (Entodesma). Small to medium-sized, not gaping; periostracum adherent; commensal with sponges and tunicates. *Rec.*, W.Indies-W.S.Am., N.Am.-S.Pac.—Fig. F24,4. *E. (E.) chilense PHILIPPI, W.S.Am.; LV ext., $\times 1$ (124b).
- E. (Agriodesma) DALL, 1909 [*Lyonia saxicola BAIRD, 1863; M]. Large, gaping ventrally; periostracum conspicuously thick, leathery, friable; ligament large. *Rec.*, W.N.Am.—FIG. F24,7. *E. (A.) saxicola (BAIRD), USA(NW. coast); 7a,b, LV ext., RV int., ×0.3 (Reeve, 1875).
- E. (Phlycticoncha) BARTSCH & REHDER, 1940 [nom. subst. pro Phlyctiderma BARTSCH & REH-DER, 1939 (non DALL, 1899)] [*Lyonsia lucasana BARTSCH & REHDER, 1939; OD]. Narrowed anteriorly, periostracum thin; surface with radial rows of pustules obsolete near margins. Rec., W.C.Am.-W.S.Am.—FIG. F24,10. *E. (P.) lucasanum (BARTSCH & REHDER), W.Mexico; 10a,b, LV ext., RV int., ×1 (Stanford Univ. specimen).
- Mytilimeria CONRAD, 1837 [*M. nuttallii; M]. Thin, fragile, ventricose, with thin, adherent periostracum; beaks subspiral; hinge edentulous but with one or more ligamental pits; muscle scars small, pallial sinus inconspicuous. *Rec.*, W.N.Am.— FIG. F24,8. *M. nuttallii, USA(Calif.); 8a,b, RV int., ext., X1 (7c).
- Ostomya Conrad, 1874 [*O. papyria; M] [=Hi-

mella H.ADAMS, 1860 (non DALLAS, 1852) (type, H. fluviatilis; M); Anticorbula DALL, 1898 (pro Himella); Guianadesma MORRISON, 1943 (type, G. sinuosum; OD)]. Thin, concentrically plicate; hinge with spoon-shaped process and small tooth near apex in LV; RV with oblique chondrophore. [Estuarine.] U.Oligo.-Rec., S.Am.——FIG. F24,5. *O. papyria, Plio., Peru; RV ext., $\times 2$ (Conrad).

Family MARGARITARIIDAE Vokes, 1964

[Materials for this family prepared by MYRA KEEN]

Shell moderately large, subcylindrical, gaping, nearly smooth except for some widely spaced radial ribs and surface irregularities; inner layer nacreous; hinge area wide but without teeth, beaks low; adductor muscle scars unequal in size, posterior elongate, anterior rounded; pallial line entire or only slightly sinuate. *Mio*.

Margaritaria CONRAD, 1849 [*Pholadomya abrupta CONRAD, 1832; M] [=Actinomya MAYER, 1870 (obj.; OD)]. Differing from Panopea, which it resembles, by edentulous hinge, radial ribbing, and nacreous shell material. Mio., E.N.Am.— FIG. F24,9. *M. abrupta (CONRAD), USA(Md.); 9a,b, LV ext., RV int., ×0.5 (Glenn, 1904).

Family MYOCHAMIDAE Bronn, 1862

[Materials for this family prepared by MYRA KEEN]

Inequivalve, free or sessile, subnacreous; hinge edentulous, dorsal margins overlapping; ligament external or wanting, resilium internal; pallial sinus small. *Mio.-Rec.*

- Myochama STUTCHBURY, 1830 [*M. anomioides; M]. Sessile, attached by RV and modified in form by surface of attachment. *Mio.-Rec.*, Australasia. —FIG. F25,1. *M. anomioides; 1a,b, LV ext., RV int., ×1 (305).
- Myadora GRAY, 1840 [*Pandora brevis SOWERBY, 1829; M] [=Myodora, spelling error]. Free, resembling Pandora, with flattened cardinal area on either side of beaks. Mio.-Rec., Australasia-W.Pac.
- M. (Myadora). Surface irregular but not squamose; RV convex, LV flat; hinge with triangular resilifer; pallial sinus rather shallow. Mio.-Rec., Australasia-W.Pac.—Fig. F25,3. *M. (M.) brevis (Sowerby), Rec., Australia; 3a-c, RV int., LV ext., RV int., ×1 (124b, 305).
- M. (Hunkydora) FLEMING, 1948 [*Thracia transenna SUTER, 1913 (=*T. australica novozelandica REEVE, 1859); OD]. Surface squamose or granular, with low concentric folds; hinge with bladelike resilifer obliquely directed backward;

pallial sinus broader, deeper, and more open than in *M. (Myadora). U.Plio.-Rec.*, N.Z.—FiG. F25,4. **M. (H.) novozelandica* (REEVE), Rec.; 4a, LV hinge, $\times 4$; 4b,c, LV ext., int., $\times 1.3$ (Fleming, 1948).

M. (Myadoropsis) HABE, 1960 [*Thracia trans-

montana YOKOYAMA, 1922; OD]. Somewhat inflated; hinge with 2 distinct toothlike knobs below umbo in RV; pallial sinus deep. *Pleist.-Rec.*, W.Pac.-Australasia.—FIG. F25,2. *M. (M.) *transmontana* (YOKOYAMA), Rec., Japan; 2a,b, RV int., ext., $\times 2.5$ (Habe, 1960).



FIG. F24. Lyonsiidae (1-8,10); Margaritariidae (9) (p. N846-N847).

© 2009 University of Kansas Paleontological Institute



FIG. F25. Myochamidae (p. N847-N848).

Family PERIPLOMATIDAE Dall, 1895

[nom. correct. Dall, 1900 (pro Periplomidae Dall, 1895)] [Materials for this family prepared by MYRA KEEN]

Subnacreous, strongly inequivalve; beaks with a slit; hinge edentulous, resilium in two spoon-shaped chondrophores directed anteriorly or downward; pallial sinus mostly wide but shallow (524). U.Cret.-Rec.

- Periploma SCHUMACHER, 1817 [*P. inaequivalvis (=*Corbula margaritacea LAMARCK, 1801); M]. Thin, RV more convex than LV and overlapping it, surface granular, beaks opisthogyrate; chondrophores supported by clavicle in most forms. U.Cret.-Rec., cosmop.
- P. (Periploma). Ovate-quadrate, smooth; anterior muscle scar long and narrow, posterior small and crescentic; pallial sinus short, rounded. U.Cret.-Rec., N.Am.-S.Am.-E.Asia-Eu.—Fig. F26,1.
 *P. (P.) margaritaceum (LAMARCK), Rec., W.Indies; 1a-c, LV int., LV view of both valves, RV hinge, ×1 (H. Adams & A. Adams).
- P. (Aelga) SLODKEVICH, 1935 [*Tellina besshoensis YOKOYAMA, 1924; OD]. Large, ovate-quadrate, with undulating concentric sculpture; chondrophores massive and shallow, clavicle long, curved. Oligo.-Mio., NE.Asia.—FIG. F26,7. *P. (A.) besshoense (YOKOYAMA), Mio., Japan; 7a,b, RV ext., dorsal view of both valves, $\times 0.5$ (Makiyama, 1957).

P. (Albimanus) PILSBRY & OLSSON, 1935 [*P. (A.) pentadactylus; OD]. Strongly inequilateral, longer than high, with 5 grooved ribs projecting

1cCochlodesma 3a la 3Ь Albimanus 4Ь 1Ь Periploma 4a 5d Offadesma 5c 5b Halistrepta 50 Pendaloma 8c 8Ь 7a Aelga 8a Bontaea 7b

FIG. F26. Periplomatidae (p. N849-N850).

at margins; inequivalve, LV smaller. Rec., W.C.Am.—FIG. F26, 3. *P. (A.) pentadactylus, W. Panama; 3a,b, RV ext., int., $\times 1$ (Pilsbry & Olsson, 1935).

- P. (Halistrepta) DALL, 1904 [*P. sulcata; M]. Sculpture of irregular concentric ribs. Rec., W.N. Am.-W.Pac.—FIG. F26,6. *P. (H.) sulcatum, USA(Calif.); RV ext., $\times 0.8$ (Dall).
- P. (Offadesma) IREDALE, 1930 [*P. angasi CROSSE & FISCHER, 1864; OD[. Large, thin, oblique, chondrophore directed downward; pallial sinus triangular, deep, narrow. Rec., S.Pac.-W.Pac.----FIG. F26,4. *P. (O.) angasi CROSSE & FISCHER, S.Australia; 4a,b, LV ext., post. view of both valves, $\times 0.5$ (Cotton, 1938).
- P. (Pendaloma) IREDALE, 1930 [*P. micans HED-LEY, 1901; OD]. Posterior area rostrate, set off by rib; periostracum thin, obliquely ridged; shell with concentric undulations and 1 or 2 radial furrows; chondrophore small, directed downward. *Rec.*, S.Pac.—FIG. F26,5. *P. (P.) micans HED-LEY, E.Australia; 5a-c, RV ext., dorsal, int., ×1.5 (396); 5d, RV hinge, ×7 (Hedley).
- Cochlodesma Couthouy, 1839 [*Anatina leana CONRAD, 1831; SD HERRMANNSEN, 1847 (Mar.)] [=Aperiploma HABE, 1952 (OD, obj.)]. Lenticular, subequilateral; lithodesma present; chondrophore buttressed. Mio.-Rec., Eu.-Atl.-Pac.
- C. (Cochlodesma). Slightly inflated, surface not granulose; lithodesma cartilaginous. *Mio.-Rec.*, Eu.-W.Atl.-S.Pac.-NW.Pac.—FIG F26,2. *C. (C.) leanum (CONRAD), Rec., USA(Mass.); RV ext., ×1 (Gould & Binney, 1870).
- C. (Bontaea) BROWN, 1844 (ex LEACH MS) (in synonymy of Ligula praetenuis [*Chama praetenuis PULTENEY, 1799; M] [=Galaxura GRAY, 1852 (ex LEACH MS) (M, obj.); Calcaraea RécLUZ, 1868 (M, obj.)]. Less rounded than C. (Cochlodesma), flatter, posterior somewhat attenuated; surface granulose; lithodesma small. Plio.-Rec., N.Eu.-S.Eu.—FIG. F26,8. *C. (B.) praetenue (PULTENEY); Rec., Eng., 8a, LV ext., ×1 (Jeffreys, 1869); Rec., Norway, 8b,c, LV and RV hinges, ×2 (857).

Family THRACIIDAE Stoliczka, 1870

[nom. transl. DALL, 1903 (ex Thraciinae Stoliczka, 1870)] [=Osteodesmacea Desnaves, 1839 (invalid family-group name, Code Art. 11, e); Osteodesmidae Hörnes, 1859 (invalid family-group name, Code Art. 11, e)] [Materials for this family prepared by Myrak KEEN]

Smooth, nonnacreous, inequivalve (RV larger), surface granular in most; hinge edentulous; chondrophore directed obliquely toward posterior end; pallial line with sinus (510). Jur.-Rec.

Thracia Sowerby, 1823 (ex Leach MS) [*"T. pubescens Lam." (=*Mya pubescens Pulteney, 1799); SD Anton, 1839] [=Throna Carpenter, 1859 (nom. null); Osteodesma de Blainville, 1825 (OD, obj.); Odoncineta Costa, 1829 (type, O. papyracea; M); Odontocineta, Cinetodonta (nom. van. pro Odoncineta); Corymya Agassiz, 1843 (type, Mya depressa Sowerby, 1823, non DONOVAN, 1802, =Corimya pinguis AGASSIZ, 1845; M; Jur., Eu.); Corimya, Coromya (nom. null.); Homoeodesma Fischer, 1887 (type, T. conradi COUTHOUY, 1839; M); Eximiothracia IREDALE, 1924 (type, T. speciosa ANGAS, 1869; OD); Cetothrax IREDALE, 1949 (type, T. alciope Angas, 1872, =Anatina imperfecta LAMARCK, 1818; OD)]. Oblong, somewhat inflated, nearly equilateral, posterior end broadly truncate and set off by low ridge; periostracum present in some. Jur.-Rec., Eu.-N.Am.-Pac.-Atl.-Afr.-Arctic.

- T. (Thracia). Concentrically striate; surface granulate; beaks touching and perforate; ligament external; cardinal plate with fissure occupied by lithodesma; chondrophore moderately long. Jur.-Rec., Eu.-N.Am.-Pac.—Fig. F27,11. *T. (T.) pubescens (PULTENEY), Rec., Eng.; 11a-c, LV int., RV hinge, LV view both valves, $\times 1$ (H. Adams & A. Adams, 1858).
- T. (Crassithracia) SOOT-RYEN, 1941 [*T. crassa BECHER (=*T. septentrionalis JEFFREYS, 1872); OD]. Solid, smooth, periostracum present, thin, shining, except on posterior truncation; chondrophore very narrow, horizontal. Rec., N.Atl.,— FIG. F27,2. *T. (C.) septentrionalis JEFFREYS, Norway; 2a, RV ext., $\times 0.5$; 2b,c, RV and LV hinges, enl. (857).
- T. (Ixartia) GRAY, 1852 (ex LEACH MS) [*Mya distorta MONTAGU, 1803; M] [=Rupicola FLEU-RIAU, 1802 (non BRISSON, 1760) (obj.); Pelopia H.ADAMS, 1868 (non MEIGEN, 1800) (type, P. brevifrons; M); Rupicilla SCHAUFUSS, 1869 (pro Rupicola)]. Distorted by nestling habit, inequilateral; chondrophore free from hinge plate posteriorly; pallial sinus large. Rec., Eu.-W.N.Am.-S.Afr.—FIG. F27,3. *T. (1.) distorta (MON-TAGU); Eng.; 3a, LV ext., $\times 1$ (Jeffreys, 1869); Norway, 3b,c, hinge, lat. and ventral views, $\times 2$ (857).
- T. (Lampeia) MACGINITIE, 1959 [*T. (L.) adamsi; OD]. Chondrophore buttressed, forming depression under beaks. Rec., Arctic.—FiG. F27,8. *T. (L.) adamsi, USA(Alaska); 8a,b, LV ext., RV ext., ×1; 8c,d, RV and LV hinges, ×3 (MacGinitie, 1959).
- T. (Trigonothracia) YAMAMOTO & HABE, 1959 [*T. (T.) nomurai; OD]. Small, thin, chondrophore small, trigonal, directed downward. Rec., W.Pac.—FIG. F27,5. *T. (T.) nomurai, Japan; 5a,b, LV ext., int., $\times 2$ (Yamamoto & Habe, 1959).
- Asthenothaerus CARPENTER, 1864 [*A. villosior; M]. Edentulous, surface somewhat granular; cartilage below umbones, not in chondrophore; pallial sinus large. Rec., E.C.Am.-W.N.Am.—Fig.

F27,10. *A villosior, W.Mex.; 10a-c, LV ext., int., RV int., $\times 2.5$ (specimen, U.S.Natl.Mus.). Bushia DALL, 1886 [*B. elegans; M]. Resembling Asthenothaerus but surface without granulations; ligament external; apices solid within, supporting resilium. *Rec.*, W.Indies-C.Am.-S.Am.—FiG. F27,12a. *B. elegans, W.Indies; LV ext., X3 (Dall, 1889).—FiG. F27,12b,c. B. panamensis



FIG. F27. Thraciidae (p. N850-N852).

DALL, Panama; 12b,c, RV int., LV oblique view inside apex, $\times 2$ (specimen, U.S.Natl.Mus.).

- Cyathodonta CONRAD, 1849 [*C. undulata; M]. With strong undulating and somewhat oblique folds; beaks nonperforate; resilium small, chondrophore short, rounded, prominent, lithodesma thin, semicircular, vertical. *Pleist.-Rec.*, N.Am.-C.Am.-S.Am.—FIG. F27,7. *C. undulata, Rec., W.Mex.; 7a,b, RV ext., LV int., $\times 0.5$ (Stanford Univ. specimen).
- Parvithracia FINLAY, 1927 [*P. suteri (pro Montacuta triquetra SUTER, 1913) (non VERRILL & BUSH, 1898); OD]. Small, like miniature Thracia with deep pallial sinus. Mio.-Rec., S.Pac.—FIG. F27,1. *P. suteri, Rec., N.Z.; 1a,b, LV ext., RV int., ×10 (modified from Suter, 1913).
- Phragmorisma TATE, 1894 [*Thracia watsoni SMITH, 1885; SD LAMY, 1931]. Inequivalve, RV larger, resembling Thracia but with large subumbonal plate in each valve hanging from umbo; pallial sinus broad. Oligo.-Rec., Australasia.— FIG. F27,9. *P. watsoni (SMITH), Rec., N.Australia; 9a,b, RV ext., int., $\times 0.5$ (852).
- Thracidora IREDALE, 1924 [*Thraciopsis arenosa HEDLEY, 1904; OD]. Oblong, equilateral, ventricose, gaping behind; ligament external; shell surface radially granular. Rec., S.Pac.—FIG. F27,6. *T. arenosa (HEDLEY), Australia; 6a,b, RV ext., hinge, $\times 6$ (Hedley, 1904).
- Thraciopsis TATE & MAY, 1900 [pro Alicia ANGAS, 1867 (non JOHNSON, 1861)] [*Alicia angustata ANGAS, 1867; SD STOLICZKA, 1871] [=?Thracidentula GARRARD, 1961 (type, T. perulae; OD)]. Inequivalve, quadrate, very inequilateral, posterior end short and truncate; beaks not fissured; interior subnacreous; hinge with posterior callosity in RV and a socket in LV, with marginal plate anteriorly; resilium below beaks under large triangular lithodesma; pallial sinus large. Rec., S.Pac.——Fig. F27,4. *T. angustata (ANGAS), Australia; 4a-c, LV ext., RV int, LV hinge, ×2 (Angas, 1867).

Superfamily POROMYACEA Dall, 1886

[nom. transl. DALL, 1895 (ex Poromyidae DALL, 1886)] [Materials for this superfamily prepared by MYRA KEEN]

Rounded to elongate, generally not gaping; hinge with somewhat developed cardinal and lateral teeth; resilium reinforced by lithodesma; pallial sinus small. Gills scantily reticulate or even absent; mantle lobes united. *Cret.-Rec.*

Family POROMYIDAE Dall, 1886

Rounded-quadrate; shell surface granulate in most, tending toward radial ribbing; interior subnacreous to nacreous; ligament external; hinge with cardinal tooth in one valve. Cret.-Rec.

- Poromya Forbes, 1844 [*P. anatinoides (=*Corbula granulata NYST & WESTENDORP, 1839); M] [=Embla LOVÉN, 1847 (type, E. korenii; M, =Corbula granulata NYST & WESTENDORP, 1839); Ectorisma TATE, 1892 (type, E. granulata; OD; =P. laevis SMITH, 1885); Questimya IREDALE, 1930 (type, P. undosa HEDLEY & PETTERD, 1906; OD)]. Nacreous, thin, posterior slope set off by angle; surface granular. Cret.-Rec., cosmop.
- P. (Poromya). Hinge with strong cardinal in RV, socket in LV, and ridgelike PII. Cret.-Rec., Eu.-E.N.Am.-W.N.Am.-worldwide (deep water).— FIG. F28,1. *P. (P.) granulata (NYST & WESTEN-DORP), Rec., Atl.; 1a,b, RV ext., LV hinge, $\times 3$ (124b).
- P. (Cetomya) DALL, 1889 [*P. elongata DALL, 1886; SD GLIBERT, 1936]. Hinge teeth obsolete in adult; pallial sinus wanting. *Rec.*, Atl.— FIG. F28,4. *P. (C.) elongata DALL; LV ext., X1 (Dall, 1889).
- P. (Dermatomya) DALL, 1889 [*P. (D.) mactroides; M]. Surface not granular; hinge strong; pallial sinus developed. Rec., W.N.Am.-S.Am.-S.Afr. (deep water).——FIG. F28,5. *P. (D.) mactroides, Chile; LV ext., ×1.5 (Dall, 1890).
- P. (Mioporomya) SACCO, 1901 [*M. taurinensis; OD]. Larger than P. (Poromya), with heavier hinge and strong radial sulci. Mio., Eu.——FiG. F28,10. *P. (M.) taurinensis (SACCO), Italy; 10a-d, RV ext., int., LV int., ext., ×1 (Sacco, 1901).
- Cetoconcha DALL, 1886 [*Lyonsia bulla DALL, 1878; OD] [= Silenia SMITH, 1885 (non RYE, 1873) (type, S. sarsii; M)]. Differing from Poromya in having fossettes smaller and upturned, resilium almost external, ligament obsolescent; hinge teeth weak or absent except cardinal in RV, present in young, weaker in adult. Rec., Atl.-S.Pac. (deep water).—-FIG. F28,8. *C. bulla (DALL), Atl.; 8a,b, LV int., ext., $\times 2$ (Dall, 1889).
- Cymella MEEK, 1864 [*Pholadomya undata MEEK & HAYDEN, 1856; OD]. Small, ovate, with many regular concentric undulations, crossed midway by some radial lines impressed on crests of waves. U.Cret., N.Am.—FIG. F28,7a. *C. undata (MEEK & HAYDEN), USA(Mont.); LV ext., $\times 1$ (Meek, 1876).—FIG. F28,7b,c. C. bella CON-RAD, USA(N.J.); 7b,c, RV int., LV int., $\times 1$ (Meek, 1876).
- Liopistha MEEK, 1864 [*Cardium elegantulum ROEMER, 1852 (non BECK, 1842) (=*L. elegantulata VOKES, 1956); OD]. Thin, ovate, posterior end somewhat attenuate; hinge with 2 cardinal teeth, no laterals; ligament external; pallial area indistinct. U.Cret., N.Am.-Afr.-Asia.
- L. (Liopistha). Sculpture of fine radial ribs except on dorsal part of posterior slope. U.Cret.,

N.Am.-Afr.——FIG. F28,2. *L. elegantulata VOKES, USA(Tex.); 2a, RV ext., $\times 1$; 2b, sculpture, ext. (Roemer, 1852).

- L. (Psilomya) WHITE, 1874 (ex MEEK MS) [*L. (P.) meekii; M]. Radial ribs present as rows of granules or spines. U.Cret., N.Am.-Asia.——FiG. F28,3. *L. (P.) meekii, USA(Utah); RV ext., ×1 (White, 1874).
- Neaeroporomya COSSMANN, 1887 [*Corbula argentea LAMARCK, 1807; OD]. Shell subnacreous, without surface punctations; posterior slope with concentric folds; single tooth in each valve, no in-

ternal fossette or posterior lamella; pallial line sinuous. *Eoc.*, Eu.—FIG. F28,6. **N. argentea* (LAMARCK), France; *6a*, LV ext., X3 (Vincent, 1898); *6b,c*, RV, LV hinges, X3 (Cossmann, 1914).

Pseudocuspidaria EAMES, 1951 [*Cuspidaria lakiensis Cox, 1938; OD]. Resembling Cuspidaria in outline but larger; subequivalve; sculpture of strong concentric folds; shell very thin, nacreous within. Eoc., Asia.—FIG. F28,9. *P. lakiensis (Cox), NW.India; 9a,b, both valves dorsal, RV ext., ×1 (Cox, 1938).



FIG. F28. Poromyidae (p. N852-N853).

Family CUSPIDARIIDAE Dall, 1886

Small to medium-sized, thin, ovate, mostly strongly rostrate; hinge with external ligament; resilium on small resilifer; hinge teeth present or absent. Carnivorous pelecypods, gill lamellae forming muscular partition across mantle cavity. U.Cret.-Rec.

- Cuspidaria NARDO, 1840 [*C. typus (*=Tellina cuspidata OLIVI, 1792); M] [==Neaera GRIFFITH, 1834 (non ROBINEAU-DESVOIDY, 1830) (type, N. chinensis; M); Aulacophora [EFFREYS, 1882 (non CHEVROLAT, 1842) (type, N. lamellosa SARS, 1858; SD KEEN, herein); Vulcanomya DALL, 1886 (type, V. smithii, nom. dub.; M)]. Inequivalve, LV more convex; hinge with resilifer and one or more teeth; posterior end of shell strongly rostrate. U.Cret.-Rec., Eu.-N.Am.-Atl.-Pac.-Medit.-IndoPac.
- C. (Cuspidaria). Hinge with single posterior lateral tooth in RV; exterior of shell feebly sculptured; resilium in chondrophore or fossette that is inclined and attached by posterior edge. U.Cret.-Rec., Eu.-N.Am.—FIG. F29,5. *C. (C.) cuspidata (OLIVI), Rec., Medit.; Sa-c, LV int., ext., RV hinge, $\times 1$ (H. Adams & A. Adams, 1858).
- C. (Halonympha) DALL, 1886 [*Neaera claviculata DALL, 1881; OD]. Smooth or concentrically striate; hinge with single tooth, acute cardinal in RV; fossette small, central; posterior clavicular rib in each valve. Rec., Atl.——FIG. F29,6. *C. (H.) claviculata (DALL), Carib.; 6a,b, RV ext., int., $\times 2$ (216).
- C. (Leiomya) A. ADAMS, 1864 [*Neaera adunca GOULD, 1861; M]. Smooth, hinge with anterior cardinal in each valve; RV with anterior and posterior laterals, LV without laterals. *Rec.*, Pac.
- C. (Pseudoneaera) STURANY, 1902 [*P. thaumasia; M] [=Bendoneaera Cossmann, 1904 (nom. van.)]. Rostrum short, pointed; hinge with shallow fossette, anterior and posterior laminae in RV and denticle in LV in front of fossette. Rec., IndoPac.—FIG. F29,12. *C. (P.) thaumasia (STURANY), Red Sea; 12a-c, LV ext., LV and RV hinges, \times 5 (Sturany, 1902).
- C. (Rhinoclama) DALL, 1886 [pro Rhinomya A. ADAMS, 1864 (non ROBINEAU-DESVOIDY, 1830)] [*Neaera philippinensis HINDS, 1843; SD STO-LICZKA, 1871] [=Luzonia DALL, 1890 (obj.; OD)]. Surface concentrically striate, not granulate; hinge without cardinal teeth. Rec., Pac.— FIG. F29,13. *C. (R.) philippinensis (HINDS), Philip.Is.; 13a-c, RV ext., int., LV int., X7.5 (type specimens, British Museum).
- C. (Tergulina) Noszky, 1939 [*Neaera (T.) sulcosa; M]. Surface with fine concentric ribs. Oligo., Eu.—FIG. F29,4. *C. (T.) sulcosa

(Noszky), Hung.; RV ext., ×1.3 (Noszky, 1939).

- C. (Tropidomya) DALL, 1886 [pro Tropidophora JEFFREYS, 1882 (non TROSCHEL, 1847)] [*Neaera abbreviata FORBES, 1843; SD DALL, 1886] [=Goniophora JEFFREYS, 1883 (non PHILLIPS, 1848) (pro Tropidophora JEFFREYS, 1882, non TROSCHEL, 1847)]. With anterior cardinal in each valve, no lateral teeth. Rec., Atl.-Medit.-FIG. F29,3. *C. (T.) abbreviata (FORBES), Medit.; RV ext., ×3 (Forbes & Hanley, 1848).
- Austroneaera PowELL, 1937 [**A. brevirostris;* OD]. Thin, smooth, rostrum poorly developed; LV edentulous, RV with laterals; sinus broad, rounded. *Rec.*, S.Pac.—FIG. F29,7. **A. brevirostris,* N.Z.; 7*a-c,* RV ext., int., LV int., $\times 5$ (Powell, 1937).
- Boriesia DONCIEUX, 1911 [*B. cossmanni; OD]. Shape and sculpture somewhat as in *Cardiomya*; hinge unknown. *Paleoc.*, Eu.—Fig. F29,10. *B. cossmanni, Ypres., France; 10a,b, RV ext., both valves dorsal, ×2 (Doncieux, 1911).
- Cardiomya A. ADAMS, 1864 [*Neaera gouldiana HINDS, 1843; M] [=Spathophora JEFFREYS, 1882 (non AMYOT & SERVILLE, 1843) (type, Neaera curta JEFFREYS, 1876; SD KEEN herein)]. Surface radially ribbed. U.Cret.-Rec., N.Am.-C.Am.-Pac.
- C. (Cardiomya). RV with prominent posterior lateral tooth. U. Cret.-Rec., N.Am.-Pac.—FIG. F29,2. *C. (C.) gouldiana (HINDS), Rec., E.Indies; RV ext., ×1.5 (124b).
- C. (Bowdenia) DALL, 1903 [*Cuspidaria distira; OD]. Without laterals; margin of RV grooved. Mio., E.C.Am.—FIG. F29,1. *C. (B.) distira (DALL), Jamaica; 1a, LV ext., $\times 6$ (Dall, 1903); 1b,c, LV int., RV int., $\times 6$ (1005).
- **?Fabagella** COSSMANN, 1887 [*Corbula faba De-SHAYES, 1824; OD]. Carinate, umbones acute, lunule deep; hinge edentulous, fossette triangular. *Eoc.*, Eu.—FIG. F29,9. *F. faba (DESHAYES), France; 9a,b, LV int., RV hinge, $\times 3$ (160).
- Myonera DALL, 1886 [*Neaera paucistriata DALL, 1885; OD]. Sculpture radiating or concentric; hinge without teeth; fossette vertical or posteriorly directed. Rec., Atl.-Pac.—FIG. F29,8. *M. paucistriata (DALL), Atl.; LV ext., $\times 2$ (Dall, 1890).

Family VERTICORDIIDAE Stoliczka, 1871

[=Euciroidae DALL, 1894]

Small (few more than 25 mm. in diameter), cordate, nacreous within, more or less strongly ribbed radially; hinge mostly weak or with one or two low teeth. *Paleoc.-Rec.*

Verticordia SOWERBY, 1844 (ex WOOD MS) [*Hippagus? cardiiformis SOWERBY, 1844; M] [=Trigonulina D'DORBIGNY, 1846 (type, T. ornata; M) Iphigenia COSTA, 1850 (non SCHUMACHER, 1817) (type, Hippagus acuticostatus PHILIPPI, 1844; OD); Hippella, AUCTT. (non Mörch, 1861)]. Small to minute, ligament external; ribs well developed. Paleoc.-Rec., Eu.-Carib.-N.Am.-C.Am.-Pac.

- V. (Verticordia). Ribs raised, well spaced; lunule deep in LV, shallower in RV; hinge with cardinal in RV, lateral behind beaks in LV. *Paleoc.-Rec.*, Eu.-Carib.-W.N.Am.-C.Am.-W.Pac.——FIG. F30, 2. *V. (V.) cardiiformis (SQWERBY), Plio., Eng.; 2a,b, LV ext., int., ×2 (1004).
- V. (Spinosipella) IREDALE, 1930 [*V. ericia HED-LEY, 1911; OD]. Borders of ribs prickly; lunule wanting. *Rec.*, Pac.—FIG. F30,5. *V. (S.) ericia HEDLEY, S.Australia; 5a,b, RV ext., hinge, X4; 5c, surface detail, ext. (Cotton, 1938).

V. (Vertambitus) IREDALE, 1930 [*V. vadosa



FIG. F29. Cuspidariidae (p. N854).

HEDLEY, 1907; OD]. Minute, solid, granose, hinge heavy. Rec., S.Pac.—FIG. F30,7. *V. (V.) vadosa HEDLEY, Australia; 7a-d, LV ext., dorsal, LV and RV hinges, ×10 (Hedley, 1907).
V. (Vertisphaera) IREDALE, 1930 [*V. cambrica; OD]. Thin, nearly smooth, ribs as fine radial threads; hinge narrow. Rec., S.Pac.—FIG.

F30,6. *V. (V.) cambrica IREDALE, Australia; 6a,b, LV dorsal, int., ×2.5 (Hedley, 1907). Euciroa DALL, 1881 (in synon.) [*Verticordia elegantissima DALL, 1881; M]. Relatively large, with numerous granular ribs; lunule and escutcheon present; resiliary ossicle triangular, wider behind. Rec., Atl.-Pac.



FIG. F30. Verticordiidae (p. N854-N857).

© 2009 University of Kansas Paleontological Institute

- E. (Euciroa). Valves subequal, hinge well developed. *Rec.*, Atl.-Pac.—FIG. F30,3. *E. (E.) elegantissima (DALL), Carib.; 3a,b, LV ext., int., $\times 2$ (216).
- E. (Acreuciroa) THIELE & JAECKEL, 1931 [*E. (A.) rostrata; M]. Hinge weak; LV broadened. Rec., Pac.—FIG. F30,4. *E. (A.) rostrata, Japan; 4a-c-, RV ext., RV and LV hinges, $\times 0.6$ (Thiele & Jaeckel, 1931).
- Halicardia DALL, 1895 [*Mytilimeria flexuosa VER-RILL, 1881; OD] [=Haloconcha, AUCTT., spelling error]. Dorsal margin flaring at ends; surface of shell granular; hinge obsolete, lunule in RV larger; lithodesma asymmetrical, right limb longer; shell slightly inequivalve. *Rec.*, Atl., Pac.—FIG. F30,11. *H. flexuosa (VERRILL), N.Atl.; RV ext., ×1 (Verrill, 1881).
- Halicardissa DALL, 1913 [*Verticordia perplicata DALL, 1890; OD]. Resembling Halicardia in form, few-ribbed; soft parts as in Verticordia. Rec., Pac.—FIG. F30,10. *H. perplicata (DALL), Galapagos Is.; RV ext., ×1 (Dall, 1890).
- Haliris DALL, 1886 [*Verticordia fischeriana DALL, 1881; OD]. Globose, lunule shallow; hinge of RV as in Verticordia, LV with single small cardinal and short stout lateral behind beak; resiliary ossicle short, quadrate. Rec., Atl.-Pac.
- H. (Haliris). Ventral margin even, shell rounded. Rec., Atl.-Pac.——FiG. F30,9. *H. (H.) fischeriana (DALL), W.Atl.; 9a,b, RV hinge, ext., $\times 3$ (216).
- H. (Setaliris) IREDALE, 1930 [*Verticordia setosa HEDLEY, 1907; OD]. Smaller than H. (Haliris), more quadrate, ventral margin sinuous. Rec., S.Pac.—FIG. F30,8. *H. (S.) setosa (HEDLEY), N.Z.; 8a,b, RV ext., dorsal, $\times 5$ (Hedley, 1904).
- Kurinuia MARWICK, 1942 [*Trigonia areolata MARshall, 1919; OD]. Ribless area on posterior slope, crossed only by low concentric ridges. Eoc., N.Z.—FIG. F30,12. *K. areolata (MARSHALL); 12a,b, RV int., ext., ×1.3 (Marwick, 1942).
- Lyonsiella G. SARS, 1872 (ex M. SARS MS) (in synon.) [*Pecchiolia abyssicola SARS, 1872; M]. Quadrate, thin, ligament internal, with lithodesma; hinge weak to edentulous; pallial line entire. Rec., Atl.-Pac.
- L. (Lyonsiella). Surface ribbed, ribs granular in some. Rec., Atl.-Pac.—Fig. F30,1. *L. (L.) abyssicola (SARS), N.Atl.; 1a-c, LV ext., both valves dorsal, RV int., ×4 (829).
- L. (Proagorina) IREDALE, 1930 [*L. quadrata HEDLEY, 1907; OD]. Surface granular, with some radial furrows, granules prickly; hinge edentulous. Rec., S.Pac.—FIG. F30,13. *L. (P.) quadrata HEDLEY, Australia; 13a,b, RV ext., int., $\times 6$ (Hedley, 1907).
- Laevicordia SEGUENZA, 1876 [*Verticordia (L.) orbiculata SEGUENZA, 1876; SD SOOT-RYEN, 1966]. Resembling Policordia but more rounded, with fine surface granulation. Plio.-Rec., Eu.-Atl.-Pac.



FIG. F31. Verticordiidae (p. N857).

- Pecchiolia SAVI & MENEGHINI in MURCHISON, 1850 [*P. argentea (=Chama arietina BROCCHI, 1814);
 M]. Resembling Verticordia but larger, ribs lower, beaks higher, spirally twisted; hinge tooth larger, more solid. Eoc.-Plio., Eu.—-FIG. F31,2. *P. arietina (BROCCH), Plio., Italy; 2a-c, LV ext., int., RV int., ×1 (Hörnes, 1870).
- Policordia DALL, BARTSCH, & REHDER, 1939 [*P. diomedea; OD] [=Laevicordia, AUCTT. (non SEGUENZA, 1876)]. Small, ovate, nearly smooth, with fine radial ribs; ligament in groove, with lithodesma below it; hinge edentulous; pallial sinus small, not deep. Rec., Atl.-Pac.—FiG. F31,1. *P. diomedea, Hawaii; Ia-c, RV int., LV ext., int., ×2.5 (Dall, Bartsch, & Rehder, 1939).

Superfamily CLAVAGELLACEA d'Orbigny, 1844

[nom. transl. THIELE, 1934 (ex Clavagellidae D'ORBIGNY, 1843] [Materials for this superfamily prepared by MYRA KEEN and L. A. SMITH]

Shell nacreous, free when young, degenerate in adult; with one or both valves at least partially embedded in elongate calcareous tube, an adaptation for burrowing; hinge-

N857

plate wanting; ligament external. U.Cret. (Turon.)-Rec.

Family CLAVAGELLIDAE d'Orbigny, 1843

[=Aspergillidae GRAY, 1858]

Tube anteriorly rounded or discoid and smooth or fringed with simple or branching tubules, or partially closed by calcareous disc having several pedal foramina. U.Cret. (Turon.)-Rec.

- Clavagella LAMARCK, 1818 [*C. echinata; SD CHILDREN, 1823] [=Bacilia GRAY, 1858 (ex VALENCIENNES MS) (obj.); Clavigella, spelling error]. One valve never merging with tube and both adductors persistent in adult. U.Cret. (Turon.)-Rec., cosmop.
- C. (Bryopa) GRAY, 1847 [*C. aperta SOWERBY, 1823; OD] [=Tiria DE GREGORIO, 1886 (obj.; SD SMITH, 1962)]. Siphonal end of tube periodically expanded, anterior end smooth; with small very short tubules through tube around valves. U.Oligo.-(Aquitanian)-Rec., Medit. - Ind.O. - Pac. —-FIG. F32,8. *C. (B.) aperta SOWERBY, Rec., Malta; ×0.3 (124b).
- C. (Dacosta) GRAY, 1858 [*C. australis SOWERBY, 1829; M]. Siphonal end of tube not expanded, anterior end smooth, rounded; with small very short tubules through tube around valves. *Rec.*, W.Pac.—FIG. F32,9. *C. (D.) australis SOW-ERBY, Australia; ×0.6 (Sowerby in Reeve, 1872, mod.).
- C. (Stirpulina) STOLICZKA, 1870 [*C. coronata DESHAYES, 1824; OD] [=Styrpulina, spelling error; may prove to be synonym of Tubolana BIVONA-BERNARDI, 1832 (type, T. digitata, =Aspergillum bacillaris DESHAYES, 1830, M); Tubulana (nom. null.)]. Siphonal end of tube periodically expanded, anterior end with tubules formed only in terminal corona; tube long and with more or less distinct anterior slit. U.Cret.(Turon.)-Rec., N.Am.-Eu.-Asia.---FIO. F32,2. *C. (S.) coronata DESHAYES, U.Eoc.(Barton.), Paris Basin; ×0.67 (124b).
- Humphreyia GRAY, 1858 [*Aspergillum strangei A. ADAMS, 1854; M] [=Humphreysia, spelling error]. Tube twisted and irregularly square in cross section; both valves united into single plate forming most of anterior baglike cavity. Rec., W.Pac.—FIG. F32,7. *H. strangei (A. ADAMS), Australia; $\times 0.8$ (124b).

Penicillus Bruguière, 1789 [*P. javanus (=Serpula penis LINNÉ, 1758); SD HABE, 1952] [=Brechites Guettard, 1770 (nonbinom.); Penecilli daCosta, 1776 (vernacular) (Penecillus, Peni-



FIG. F32. Clavagellidae (p. N858-N859).

cellus, nom. null.); Verpa Röding, 1798 (obj.); Aquaria PERRY, 1811 (type, A. radiata; SD SMITH, 1962, obj.); Arytene OKEN, 1815 (obj.; rejected ICZN, 1956); Bunodus DE BLAINVILLE, 1817 (nom. nud.) (ex GUETTARD, nonbinom.); Arytaena OKEN, 1817 (obj.) (Arythaena, Arytene, spelling errors); Aspergillum LAMARCK, 1818 (obj.) (Adspergillum, Aspergillium, Aspergillus, spelling errors); Clepsydra SCHUMACHER, 1817 (obj.) (Clepydra, spelling error]]. Both valves merging with tube; tube circular in cross section; anterior adductor degenerate, posterior adductor absent in adult. U.Oligo.(Aquitan.)-Rec., IndoPac.-Australia-Pac.-Japan-Eu.

- P. (Penicillus). Siphonal end of tube simple; anterior end fringed with single row of distinct simple tubules; anterior disc with slit. U.Oligo. (Aquitan.) - Rec., IndoPac. - Australia.——FIG. F32,3. *P. (P.) penis (LINNÉ), Rec., Singapore; ×0.3 (Haas, 1935).
- P. (Focgia) GRAY, 1847 ["Aspergillum novaezelandiae" (=*P. novaezelandiae BRUGUIÈRE, 1789); OD]. Umbo almost covered with swollen prominence; fringe indistinct, of short thick tubules, formed like hole in disc. U.Oligo.(Aquitan.)-Rec., IndoPac.-W.Pac.-FIG. F32,6. *P. (F.) novaezelandiae BRUGUIÈRE, Rec., Australasia; ×0.8 (Reeve, 1860).
- P. (Pseudobrechites) MAGNE, 1941 [*Aspergillum leognanum HOENINGHAUS, 1827; OD]. Similar to P. (Penicillus), but fringe tubules shorter, less distinct, and anterior disc without central slit. U.Oligo.(Aquitan.), Eu.—FIG. F32,5. *P. (P.) leognanus (HOENINGHAUS); ×0.67 (Peyrot, 1920).
- P. (Warnea) GRAY, 1858 [*Aspergillum australe CHENU, 1843; SD STOLICZKA, 1871]. Tube cylindrical, siphonal end with series of plaited ruffles; fringe distinct, of single series of thick simple tubules. *Plio.-Rec.*, Red Sea-Australasia-Japan.—FIG. F32,4. *P. (W.) australis (CHENU), Rec., Australasia; ×0.55 (305).

Subclass UNCERTAIN

Order CONOCARDIOIDA Neumayr, 1891

[nom. correct Newell, 1965 (ex order Conocardiiden Neu-MAYR, 1891)] [Materials for this order prepared by C. C. BRANSON, AURÈLE LAROCQUE, and N. D. NEWELL]

Characters of genus Conocardium. M. Ord.-U.Perm., ?U.Trias.

Superfamily CONOCARDIACEA Miller, 1889

[nom. transl. Newell, 1965 (ex Conocardiidae MILLER, 1889)]

Characters of genus Conocardium. M. Ord.-U.Perm., ?U.Trias.

Family CONOCARDIIDAE Miller, 1889

Characters of genus Conocardium. M. Ord.-U.Perm., ?U.Trias.

Only *Conocardium* is recognized currently within this poorly understood group. Hence, the family, superfamily, and ordinal traits are identical with those of the genus.

Conocardium BRONN, 1835, p. 92 [*Cardium elongatum Sowerby, 1812 (=Conchiolithus rostratus MARTIN, 1809); M] [=Pleurorhynchus PHILLIPS, 1836, p. 210 (type, Cardium hibernicum Sowerby, 1812; SD Branson, LaRocque & New-ELL, herein); Lichas STEININGER, 1837, p. 231 (type, L. antiquus; M); Hippocardia BROWN, 1843, p. 97 (type, Cardium hibernicum Sowerby, 1812; M); Rhipidocardium FISCHER, 1887, p. 1036 (type, Conocardium amygdala BARRANDE, 1881; M)]. Equivalve, alate anteriorly, produced posteriorly in elongate, tubular rostrum; shell surface minutely ornamented; shell material thick, inlaid by vertically set partitions which form more or less submerged radial ribs appearing as external ribs in some species, or weathering in relief by exfoliation of smooth outer prismatic layer and terminating as alternating denticulations at ventral margin; 1 or more ridges or septa in each valve curve upward and inward along hinge to form conical, forward directed receptacles of unknown function; hinge ankylosed in mature individuals, edentulous; some species distinctly carinate behind beaks and at least in some species carinae serving as attachment for collar of prismatic texture (Schleppe, éventail, fringe, flange, Kragen, hood); ventral anterior margin gaping, denticulate. M.Ord. (Chazyan)-U.Perm. (Capitan.), ?U.Trias., cosmop.—FIG. G1,1. *C. rostratum (MARTIN), L.Carb., Eng.; 1a-c, hinge, ventral and LV views of holotype, $\times 1$ (Hind, 1900); 1d, RV ext., ×1 (Hind, 1900).——Fig. G1,2. C. herculeum (DEKONINCK), L.Carb., Belg.(Tournai); 2a,b, LV ext., LV int., ×1 (Hind, 1900); 2c, hinge view of another individual, $\times 1$ (a, ligament furrow?; b, muscle scar? and septum; x, ligament furrow) (Hind, 1900).-Fig. G1,3. C. ventricosum (HALL), M.Dev., USA(Iowa); 3a,b, restoration seen from ventral side; both approx. $\times 1$ (Branson, n).

BIVALVE GENERA UNCERTAINLY ASSIGNED TO FAMILIES

Families, and likewise genera tentatively assigned to them, are arranged alphabetically. All are considered to be nomenclaturally sound but some may be *nomina oblita*.

Bivalvia



FIG. G1. Conocardiidae (p. N859).

ANTHRACOSIIDAE (p. N406)

Amnigeniella BETEKHTINA, 1966 (?1967) [*Anthraconauta kumsassiana RAGOZIN, 1960; OD]. U.Carb.-L.Perm., USSR(W.Sib.). [Not an anthracosiid, but may be near Procopievskia (nonmarine Myalinidae).] [WEIR]

ARCIDAE (p. N250)

Arclites SCHLOEPFER, 1821.

Calliarca CONRAD, 1866.

Cucullea MICHELIN, 1838.

- Cyphoxis RAFINESQUE, 1818.
- Hataiarca Noda, 1966, p. 114 (as subgenus of Anadara) [*H. kakchataensis HATAI & NISIYAMA, 1949; OD]. Mio.-Rec., Japan.

Kikaiarca Noda, 1966, p. 127 [*Anadara (Kikiarca) Kikaizimana Nonura & Zinbo, 1934; OD]. Pleist.(Ryukyu Ls.), Japan. Pectinarca Sacco, 1898. Polyodonta Megerle, 1811.

Scaphura GRAY, 1842.

Thyas GRAY, 1857.

Tosarca NODA, 1965, p. 120 [*Anadara (Tosarca) tosaensis NODA, 1965; OD]. Plio., Japan.

ARCTICIDAE (p. N645)

Ambonicardia Whitfield, 1885. Bradicardia Loriol, 1891. Bruntrutia Cossmann, 1902. Kobya Loriol, 1901.

AVICULOPECTINIDAE (p. N335)

Schizopecten KOBAYASHI, 1936.

CAPRINIDAE (p. N789)

Caprinus Montfort, 1810.

CARDIIDAE (p. N583)

Avardaria Andrussov, 1923. Callicardia Conrad, 1873. Cardiarlus Dumeril, 1806. Cartissa Hermannsen, 1848.

CHAMIDAE (p. N518)

Camostraea Deshayes, 1830.

CORBICULIDAE (p. *N*665)

Limnocyrena Martinson, 1961. Mesoz.

ETHERIIDAE (p. N466)

Caillaudiana Bourguignat, 1880. Chambardiana Bourguignat, 1880. Niloticiana Bourguignat, 1880.

GRAMMYSIIDAE (p. N819)

Goldfussia Castelnau, 1843. Rhombocardia Meek & Worthen, 1866.

HIPPURITIDAE (p. N799)

Campiloceratites Fortis, 1778.

LIMOPSIDAE (p. N264)

Feliciella LAMY, 1934.

LUCINIDAE (p. N492)

Loripoderma Poli, 1795.

LYMNOCARDIIDAE (p. N590)

Suchumca Seninski, 1905.

MACTRIDAE (p. N595)

Cycladina Berthold, 1827. Villarita Dunker, 1846.

MACTROMYIDAE (p. N511)

Ferrata ROEDER, 1882 (subj. syn. of Unicardium, according to Cox).

MARGARITIFERIDAE (p. N414)

Damaris Swainson, 1823.

MODIOMORPHACEA FAMILY UNCERTAIN (p. N393)

Coxiconcha BABIN, 1966, p. 281 [*Lyonsia britannica ROUAULT, 1851; OD]. Tert.(Dandeil.), Eu. (France).

MODIMORPHIDAE (p. N393)

Taimyria LUTKEVICH, 1951 [*T. taimyrensis; OD]. L.Perm., USSR(W.Sib.). [WEIR]

MUTELIDAE (p. N463)

Berpolis LEACH, 1825. Dentina MEGERLE, 1841.

MYALINIDAE (p. N289)

Hoplomytilus Sandberger, 1856. Myalinoptera Frech, 1891.

MYTILIDAE (p. N271)

Callitriche Poli, 1791. Callitricoderma Poli, 1798. Ciboticola Iredale, 1939. Dactylus Mörch, 1861. Pisima Mörch, 1884. Pseudomodiolus Betekhtina, 1966 (?1967) [*? (First included species, Anthraconauta vulgaris KHALFIN; first fully described species, P. ella Betekhtina, 1967)]. [Weir] Septiola Bittner, 1895. Sinomytilus Thiele, 1934. Stenolema Dall, Bartsch & Rehder, 1939.

PARALLELODONTIDAE (p. N256)

Areocuculla Cossmann, 1923.

PECTINACEA FAMILY UNCERTAIN (p. N332)

Protopalliolum SADYKOV, 1962, p. 66 [*P. kazanli; OD]. Dev., USSR(Kazakhstan).

PTERIIDAE (p. N302)

Unionum Dall, 1890 (new name for Unionium LINK, 1807).

PTERINEIDAE (p. N298)

Stainieria MAILLIEUX, 1930.

RADIOLITIDAE (p. N803)

Enargetes Fischer de Waldheim, 1830.

REQUIENIIDAE (p. N779)

Arietina Conrad, 1853.

TEREDINIDAE (p. N722)

Teredarius DUMERIL, 1806.

TRIDACNIDAE (p. N594)

Tridacnoides KRUEGER, 1823.

UNIONIDAE (p. N415)

Abakaniella BETEKHTINA, 1966(?1967) [*Anthracomya magna CHERNYSHEV; OD]. M.Carb., USSR (W.Sib.). [WEIR]
Brussiella BETEKHTINA, 1966(?1967) [*B. curta; OD]. U.Perm., USSR (Sib.). [WEIR]
Sinomya POGOREVICH, 1951 [*S. kriegeri; OD]. USSR (W.Sib.). [WEIR]

UNIONACEA FAMILY UNCERTAIN (p. N411)

N862

Abbreviatiana BOURGUIGNAT, 1881. Acalliana BOURGUIGNAT, 1881. Adamiana Bourguignat, 1881. Acgericiana LOCARD, 1889. Alpecanusiana LOCARD, 1889. Amnicusiana Locard, 1889. Anatiniana Bourguignat, 1881. Arealiana BOURGUIGNAT, 1881. Arnouldiana LOCARD, 1890. Arrosiana Locard, 1890. Asticusiana Locard, 1889. Ateriana Locard, 1889. Avoniana Bourguignat, 1881. Aximedia RAFINESQUE, 1820. Barvana Locard, 1889. Batavusiana Locard, 1889. Beccariana LOCARD, 1890. Berenguieriana LOCARD, 1889. Brebissoniana LOCARD, 1889. Briandiana BOURGUIGNAT, 1881. Brotiana BOURGUIGNAT, 1881. Camuriana Locard, 1890. Carvalhoiana LOCARD, 1890. Coelatura Conrad, 1853. Collobiana Locard, 1890. Complanatiana Locard, 1890. Courquiniana LOCARD, 1889. Crassiana Locard, 1889. Cygnaeana Bourguignat, 1881. Cyrtusiana Locard, 1889. Depressiana Bourguignat, 1881. Despontainiana LOCARD, 1889. Diplasma RAFINESQUE, 1831. Ellipsaria RAFINESQUE, 1820. Ellipsopsiana Bourguignat, 1881. Ellipsopsiana Locard, 1889. Elongatiana Locard, 1890. Embiana Locard, 1890. Eydyusiana Locard, 1889. Falsusiana Locard, 1889. Fusculusiana LOCARD, 1889. Gallandriana Bourguignat, 1881. Gallicusiana LOCARD, 1889. Gastrodiana Bourguignat, 1881. Gestrouana Locard, 1890. Glyciana Bourguignat, 1881. Granigeriana LOCARD, 1889. Gravidiana Locard, 1890. Heckingiana LOCARD, 1889. Hemisolasma RAFINESQUE, 1831. Hispaniana Locard, 1889. Holandriana LOCARD, 1889. Humbertiana LOCARD, 1890. Idriniana LOCARD, 1890. Illuviosiana FAGOT, 1885. Incrassatiana Locard, 1890. Jacqueminiana LOCARD, 1889. Joannisiana Locard, 1889.

Iourdheuiliana Bourguignat, 1881. Jousseaumeana Locard, 1889. Lacanniciana LOCARD, 1880. Lapidosus SIMPSON, 1900. Lemotheuxiana Locard, 1889. Letourneuxiana Locard, 1890. Leucosilla RAFINESQUE, 1831. Limnoica GRAY, 1857. Locardiana LOCARD, 1889. Lusitaniana BOURGUIGNAT, 1881. Machadoiana Locard, 1890. Macilentiana Bourguignat, 1881. Macrosteniana Locard, 1890. Mancusiana Locard, 1889. Mariana Locard, 1889. Mariolana Locard, 1890. Melasiana LOCARD, 1889. Meretricisiana LOCARD, 1889. Meretrixiana Locard, 1890. Metaptera RAFINESQUE, 1820. Milletiana BOURGUIGNAT, 1881. Moquiniana Locard, 1889. Moreletiana Locard, 1889. Mucidusiana LOCARD, 1889. Nanusiana Locard, 1889. Nemrodia PALLARY, 1939. Notopala COTTON, 1935. Notopalena IREDALE, 1943. Nubilusiana Locard, 1889. Ogerieniana LOCARD, 1890. Ovuliana Locard, 1890. Pammegaliana BOURGUIGNAT, 1881. Parreyssiana Bourguignat, 1884. Penchinatiana LOCARD, 1889. Perniana Locard, 1889. Picardiana BOURGUIGNAT, 1881. Pisaniana Locard, 1889. Piscimaliana BOURGUIGNAT, 1881. Platteniciana BOURGUIGNAT, 1881. Platyrhynchoidiana LOCARD, 1889. Ponderosiana Bourguignat, 1881. Pseudocaelatura GERMAIN, 1921. Pseudoglyciana Locard, 1890. Rayana Locard, 1890. Requieniana LOCARD, 1889. Rhombeidiana Locard, 1889. Rockanaia de Morretes, 1941. Rossmassleriana Bourguignat, 1881. Rossmassleriana LOCARD, 1890. Rostratiana Bourguignat, 1881. Rostratiana Locard, 1889. Rumanicana Locard, 1890. Sandriana LOCARD, 1889. Schizostoma Schlueter, 1838. Scrupeana Locard, 1890. Securilla DROUET, 1855. Simonisiana Locard, 1889. Socardiana LOCARD, 1889. Spengleriana BOURGUIGNAT, 1881. Sperchinusiana LOCARD, 1889.

Spondaeana Locard, 1890. Sturmiana Locard, 1890. Tricassiniana Locard, 1890. Tumidusiana Locard, 1889. Turtoniana Locard, 1889. Unioniformiana Locard, 1890. Ventricosiana Bourguignat, 1881. Vietuliana Locard, 1890. Viliaeana Locard, 1889. Vilianana Fugot, 1889. Willanana Fugot, 1882.

VENERIDAE (p. N670)

Radiocrista DALL, 1901 [*Venus pulcherrima DESHAYES, 1860; OD]. DALL assigned this genus to Veneracea, but the age and locality of the type was unknown at the time of description. It could be a Protocardia or a Trigonia. [KEEN]

CLASS, ORDER, AND FAMILY UNCERTAIN

Allocardium HALL, 1883.

Anomianella DE RYCKHOLT, 1847, p. 45 [*A. proteus; M]. L.Carb.(Tournais.), Eu.(Belg.). [New-ELL]

Arnoldia MAYER, 1887 [*A. consecta; M].

- Aviculomya HOLZAPFEL, 1889 [*A. peralata; OD]. Shell thin, much swollen; beaks pointed, spirally enrolled, small; anterior wing rather large, continuing as ridge on dorsal margin behind beaks; posterior wing very large, not distinctly separated from main body of shell. Dentition and pallial line unknown. Ligament probably external, lying between shell surface and ridgelike prolongation of anterior wing. L.Carb., Eu. (Ger.).—Fig. H1, 10. *A. peralata, Liebstein (near Herborn); RV ext., X1 (Holzapfel, 1889). [LAROCQUE]
- Barcoona FINLAY, 1926, p. 526 [pro Pachydomella ETHERIDGE, JR., 1907, p. 325 (non ULRICH, 1891)] [*Pachydomella chutus ETHERIDGE; M]. Small (length 8 mm. or less), subtrigonal, subequilateral, longer than high, equivalve, compressed, relatively thick-shelled; umbones obtusely angular, scarcely incurved; hinge supposedly edentulous; muscle scars and pallial line unknown; surface unornamented except for well-marked growth rugae. L.Cret., Australia(Queensl.).—FIG. H1, 2. *B. chutus (ETHERIDGE); LV, X3 (Etheridge, 1907). [Cox]

Binghami BROWN, 1827 [*B. paradoxus; M].

Bitubulites BLUMENBACH, 1803.

Blainvilla CHIAJE, 1829.

- Bleta DE GREGORIO, 1930, p. 17 [*B. elegans; M]. Genus founded on strongly convex, acutely triangular, subequilateral valve about 25 mm. high with strong growth rings; internal characters unknown. U.Trias., Sicily. [Cox]
- Carnidia BITTNER, 1901, p. 6 [*C. pannonica; SD DIENER, 1923, p. 223]. Small smooth, very gib-

bose, trigonally subquadrate, only slightly inequilateral, with well-marked posterodorsal angle and diagonal ridge delimiting narrow posterior area; posterior margins with broad gape; internal characters unknown. U.Trias., Eu.(Hung.-Austria). — FIG. H1,3. *C. pannonica, Veszprém, Hung.; 3a, RV lat.; 3b, dorsal view; 3c, posterior end showing gape, all ×3 (Bittner, 1901). [Cox] Ceratoconcha KRAMBERGER-GORJAHOVIC, 1889. Conchites SCHLAEPFER, 1821.

Costulopteria PAUL, 1941.

- Cruciella Koken, 1913, p. 35 [*Nucula inflata WISSMANN in MÜNSTER, 1841, p. 20 (non J. DE C. Sowerby, 1827) (=Megalodon klipsteini BITT-NER, 1895, p. 22; OD]. Small to medium-sized, gibbose, ovately cuneiform, inequilateral, slightly inequivalve; umbones at anterior 0.25 or 0.3 of length, that of LV higher than RV; lunule wide, cordiform; escutcheon deep, with well-defined bordering ridges; weak diagonal ridge commonly present; ligament apparently external, opisthodetic; hinge margin thickened below beak in RV, forming toothlike process received in recess of LV, hinge otherwise edentulous; pallial line entire; shell wall rather thin; exterior smooth or with weak concentric folds. U.Trias.(Carn.), Austria(S.Tyrol).-Fig. H1,1. *C. klipsteini (BITTNER), Heiligenkreuz; 1a, LV lat.; 1b, ant. view showing greater prominence of LV umbo, both $\times 2$ (Bittner, 1895). [Cox]
- Cyclostrea Gentil, 1902.
- Cyrenolimopsis HABE, 1953.
- Delia DE LORIOL, 1891, p. 246 [*D. amaena; M]. Medium-sized, equivalve, moderately and evenly inflated, suboval, slightly longer than high; umbones moderately prominent, just posterior to midlength; lunule present but no bordered escutcheon; ligament external, opisthodetic; internal characters unknown; surface smooth except for growth lines. U.Jur.(Oxford.), Eu.(Switz.).—Fig. H1, 12. *D. amaena; 12a, RV lat.; 12b, dorsal view, both $\times 1$ (de Loriol, 1891). [Cox]
- Diptyxis Oppenheim, 1889.
- Donacites GMELIN, 1793.
- Dorsomya de Ryckholt, 1847, pl. 10, fig. 20 [*D. dorsata; M]. [Newell]
- Ectenoptera Ulrich, 1894, p. 485 (nom. nud.). [Newell]
- Elasmatium CLARKE, 1904, p. 293 [*E. gowandense; OD]. U.Dev.(Naples), USA(N.Y.). [New-ELL]
- Elliptoidea TASCH, 1961 [*E. vulgaris; OD]. Similar to stunted Palaeanodonta. Perm.(Leonard.), USA(Kans.). [WEIR]
- Ensia DE GREGORIO, 1930, p. 21 [*Pleuromya? (Ensia) pumila; M]. Genus founded on small, sublunate, smooth shell with moderately prominent, almost terminal umbo; internal characters unknown. Trias., Eu.(Sicily). [Cox]
- Gibboconcha de GREGORIO, 1930, p. 30 [*G. sicula;

N864



FIG. H1. Class, Order and Family Uncertain (p. N864).

M]. Genus founded on fragment of small, concentrically ribbed, subtrigonal, strongly inequilateral shell; internal characters unknown. Possibly young *Cardinia* or *Astarte*. *L.Jur.(Lias.)*, Sicily. [Cox]

- Gingillum DE GREGORIO, 1930, p. 27 [*G. lindum; M]. Medium-sized, smooth, obliquely oval, higher than long, with narrow submedian umbo and short, arcuate dorsal margin; internal characters unknown. L.Jur.(Lias.), Italy(Sicily). [Cox]
- Guebhardia Cossmann, 1905, p. 841 [*G. veneriformis; M]. Small, oblong-oval, subequilateral, moderately inflated, with broad, slightly protruding umbo and posterior umbonal ridge bordering narrow, radially costulate posterior area; surface otherwise smooth; anterior end with shallow radial sulcus forming lower border of slightly swollen anterodorsal region; ligament external, opisthodetic; 1 strong cardinal tooth in each valve. in LV posterior to that of RV, which occupies median position below beak; 1 short, thick posterior lateral in each valve; adductor scars & pallial line unknown. M.Jur.(Bathon.), Eu.(S. France).-Fig. H1,4. *G. veneriformis, Courmes, Alpes-Maritîmes; 4a,b, LV lat., ext., int., both ×1.3 (Cossmann, 1905). [Cox]

Hadrodon Yen, 1952.

- Ischyrinia BILLINGS, 1866, p. 52 [*1. winchelli; SD S. A. MILLER, 1889] [=?Technophorus MILLER, 1889, p. 541 (type, T. faberi; M)]. Equivalve, inequilateral; 2 strong ridges radiating from beak to extended posteroventral extremity; hinge and musculature unknown. M.Ord.-U.Ord., E.N.Am. —-FIG. H1,5. *1. winchelli, U.Ord., Can.(Anticosti I.); RV ext., ×1 (Billings, 1866). [NEWELL] Laevipinna PAUL, 1941.
- Laubeia BITTNER, 1895, p. 116 [*Cardita strigilata KLIPSTEIN, 1845, p. 255; M]. Small, slightly inequivalve, LV larger than RV; oval, strongly inequilateral; umbones prosogyrate, presence of diagonal ridge variable, deep escutcheon bordered by sharp ridge present in each valve; LV with 2 teeth, more dorsal of which is bifid, consisting of short posterior limb directed radially from beak and larger, longitudinally directed anterior limb, 2nd tooth below and parallel to this anterior limb; RV with single bifid tooth consisting of short radial posterior limb and longer longitudinal anterior limb; lateral teeth absent; pallial line and adductor scars unknown; surface smooth. U.Trias. (Carn.), Austria(S. Tyrol).-FIG. H1,7. *L. strigilata (KLIPSTEIN), St. Cassian; 7a, LV ext.; 7b, dorsal view; 7c, hinge teeth of LV; 7d, hinge teeth of RV; all ×1.3 (Bittner, 1895). [Cox]
- Libyaconchus HASSAN, 1957, p. 135 [*L. parvus; OD]. Small (<5 mm. long), suborbicular, gibbose, slightly inequivalve; umbones broadly rounded, that of RV more prominent; beaks prosogyrous; RV with strong cardial tooth, recurved in socket of LV; pallial line obscure; pedal retractor scars conspicuous, paired, on posterodorsal side of

anterior adductor; ornament of strong radial ribs, some specimens also with radial sulcus posterior to mid-length in each valve, sulcus of RV with median rib. U.Cret. or Paleoc.(Dan.), Esna Shales, Egypt.——Fic. H1,6. *L. parvus; 6a, RV, int. mold; 6b, dorsal view of bivalve int. mold, showing pedal retrack scars; both ×5 (Hassan, 1957). [Cox]

- Liocardia AGASSIZ, 1842, p. 26 [Virtual nom. nud. without included nominal species.] Said to be close to "Ceromya" [Ceratomya] in external characters, but closer to Isocardia in other respects [Cox]
- Macrodonta Costa, 1845.
- Mcgagrypha Spreistersbach, 1922, p. 419 [*M. dahmeri; OD]. L.Dev., Eu.(Ger.). [LaRocque] Mallaca Mapur, 1800
- Mellaca MABILE, 1899.
- Modioptera Schindewolf, 1924, p. 275 (nom. nud.). [Newell]
- Nothamusium HIND, 1904, p. 159 [*N. radiatum; SD NEWELL, herein]. Equivalve, very inequilateral, obliquely ovate, prosogyre with beaks about 0.3 distance behind anterior extremity of hinge; posteroanterior margin subquadrate; free border ornamented by bifurcating flattened costae; hinge unknown. L.Cam., Eu.(Ire.-Eng.-Scot.).—Fig. H1,8. *N. radiatum, Eng.(Staffords.); RV ext., $\times 1$ (Hind, 1904). [NEWEL]
- Omalia de Ryckholt, 1847 (nom. oblit.), L.Carb., Eu.(Belg.). [Newell]
- Onkogrypha Spriestersbach, 1925, p. 418 [*Megogrypha (Onkogrypha) cullmanni; M]. L.Dev., Eu.(Ger.). [Newell]
- Opisenia Etallon, 1862.
- Osteophorus Philippi, 1893.
- Ostreavicula Blanckenhorn, 1934, p. 179 [*O. dayi; M]. Large, quadrate, oysterlike, LV feebly convex, RV slightly concave; no clearly demarcated posterior wing; RV with anterior auricle bordered posteriorly by narrow incision running from beak toward anterior margin; hinge structure and musculature unknown; surface bearing narrow dichotomous ribs. U.Cret.(Turon.), Syria. [Cox] Paradoxia KRUMBECK, 1923, p. 101 [*P. timorensis; M]. Known only by single valve, possibly LV; with attachment area at tip; large, very thickshelled, oval, higher than long, with large, down curved, hooklike ?posterior wing with median external crest; broad, dorsoventrally elongated cardinal area, without median depression, occupying posterior half of inner side and curved in posterior direction of dorsal end; visceral cavity shallow, single adductor scar occupying position
- dorsal to median; surface with uncertain rugae and a few wartlike protuberances. L.Jur.(mid. Lias., Pliensbach.), E.Indies(Timor).——Fig. H1, 11. *P. timorensis; 11a,b, ?LV ext., int., ×0.7 (Krumbeck, 1923). [Cox]
- Patogocardia DOELLO-JURADO, 1946.
- Planktomya SIMROTH, 1896 [*P. henseni; OD]. Rec., Atl.



FIG. H2. Class, Order and Family Uncertain (p. N866).

Plicatostylus Lupher & Packard, 1930, p. 204 [*P. gregarius; OD]. Known mainly or solely from attached valve (AV) (=?LV, ?RV) which is large, greatly elongated, acutely conical or columnar, straight or slightly curved, attached at apex; cross section almost semicircular, one side with broad, flat, or slightly concave area (interpreted as ligamental area) extending whole length of AV between 2 riblike projections and bearing numerous low, flat-topped longitudinal ridges varying in width and separated by narrow intervals; convex (probably ventral) side, bearing coarse, upward-arched undulations at distant intervals and growth lines curved in conformity with them, indicating that commissure of valves was very oblique, sloping upward from hinge margin, which presumably was located at upper end of ligamental area; body chamber greatly elongated, subelliptical in cross section, with one side close to ligamental area, other side separated from outer surface of AV by thick wall, which has compact outer layer formed of rather coarse calcite prisms normal to surface, and thick, probably originally vesicular, inner layer of uncertain structure; hinge edentulous, its margin thin; 2 adductor scars present, one located on thick projecting buttress in upper part of body chamber on one side, other limited by low ridge; free valve (FV) imperfectly known or unknown, probably a flat, relatively thin structure. [This colonial reef-building bivalve, with largest illustrated specimen 48 cm. (19 in.) in height, was assigned by LUPHER & PACKARD (1930) to their monotypic Plicatostylidae. By other authors it has been referred to the Caprinidae and with small doubt seems to be a rudist.] L.Jur.(low. Pleiensbach.), N.Am.(Ore.)-S.Am.(Peru).-Fig. H2,4. *P. gregarius, Robertson Formation, USA(Ore.); 4a, presumed dorsal side of AV showing ?ligamental area, $\times 0.4$; 4b, opposite (?ventral) side of same specimen showing uparched undulations. $\times 0.4$; 4c, assemblage of AVs indicating colonial mode of life, $\times 0.3$ (Cox, n). [Cox]

[In the original description of the genus it was stated that the upper valve was curved and cap-shaped, with a prominent umbo and broad ligamental area like that of the lower valve. Dr. R. L. LUPHER has informed me that the specimens originally thought to be upper valves probably are small deformed lower valves and that the upper valve (not yet found complete) seems to have been as here stated.]

Praecardiomya AwAD, 1952, p. 7 [*P. sinaitica; M]. Rather small, elongate-ovate, beaks at anterior third of length, escutcheon lanceolate; posterior area defined by faint diagonal groove with corresponding internal ridge; integripalliate; LV with triangular chondrophore, RV with corresponding pit; 5 irregular transverse teeth in each valve, forming protuberances from hinge margin on posterior side of beaks. U.Cret.(Cenoman.), Sinai. [Cox]

Preroderma Kuroda, 1945.

- Productea TASCH, nom. subst. herein [pro Productae TASCH, 1961 (nom. vet.)] [*P. dunbari TASCH, herein (nom. subst. pro Productae dunbaris TASCH, 1961, nom. vet.); OD]. L.Perm.(Leonard.), USA (Kans.). [TASCH]
- Psammoconcha TOMMASI, 1896, p. 61 [*P. servini; M]. Medium-sized, elongate-oval, anterior margin more abruptly curved than posterior; subequilateral, with broad, scarcely projecting umbones; obscure diagonal ridge present in some specimens; internal characters unknown. L.Trias., Eu.(S.Alps). [Cox]
- **Pseudomya** ROEDER, 1882, p. 103 [*P. rarissima; OD]. Founded on single imperfect elongate, oval, inequilateral LV; muscle scars and pallial line unknown; prominent spoon-shaped chondrophore, extending upwards, and with groove behind it, situated just anterior to beak. U.Jur.(Oxford.), Eu. (Alsace). [Cox]

Ptychodes FISCHER DE WALDHEIM, 1848.

- Rebusum DE GREGORIO, 1930, p. 27 [*R. drepanense; M]. Small to medium-sized, smooth, obliquely oval, higher than long, subalate, compressed, recalling some Limidae in outline but apparently lacking cardinal area; internal characters unknown. L. Jur. (Lias.), Eu. (Sicily). [Cox].
- Rhenanomya LAROCQUE, nom. subst. herein [pro Rhenania FUCHS, 1915, p. 53 (non WAAGEN, 1907)] [*Rhenania tumida FUCHS, 1915; OD]. Shell ventricose, elongate oval; umbones near anterior end, prosogyrous, strongly incurved; lunule small; hinge curved, prolonged posteriorly; LV with 3, RV with 2 to 3 cardinal teeth; lateral teeth lacking; ligament opisthodetic and external. L. Dev., Eu.(Ger.).—FIG. H1,9. *R. tumida (FUCHS), Coblenz.; 9a, LV ext. showing outline and position of beaks, $\times 0.7$; 9b, RV dentition, $\times 0.7$ (Fuchs, 1915). [LAROCQUE]
- Rhinchotropis MEEK, 1872.
- Rostrotortus TASCH, 1961 [*R. dissimilis; OD]. ?Estheriid or possibly pathologic bivalve. Perm. (Leonard.), USA(Kans.). [Newell]

Sanoarca Stephenson, 1952.

Sollea DAHMER, 1949.

Spinarcullaea CHAVAN, 1952.

Sponditolites REICHENBACH, 1828.

- Stagnestesta TASCH, 1961 [*S. solitaria; OD]. ?Possibly estheriid. Perm.(Leonard.), USA(Kans.). Stunted bivalves from deposits of temporary, variable saline pools. [NEWELL]
- Stalagmina DENCKMANN, 1887, p. 89 [*S. koeneni; M]. Small (8 mm.), obliquely suborbicular, inequilateral; umbones prosogyrate but scarcely protruding; small lunule present; dentition consisting in each valve of elongate posterior lateral and about 3 small teeth of taxodont appearance close to beak; surface smooth. L.Jur.(up.Lias.-Toarc.), Eu.(Goslar, Ger.).—Fig. H2,3. *S. koeneni; 3a, LV ext., X1; 3b, RV showing impression of teeth, X1 (Denckmann, 1887). [Cox]
- Taeniodon DUNKER, 1848, p. 179 [*T. ellipticus; M]. Small (20 mm.) equivalve, oval, smooth, moderately inequilateral; LV with curved, upwardly concave, lamellar tooth just posterior to beak, with recess between it and margin for reception of thickened margin of RV; ligament external; muscle scars and pallial line unknown. L.Jur.(Hettang.), Eu.(Ger.).—F16. H2,2. *T. ellipticus; 2a,b, LV ext., int., ×1 (Dunker, 1848).
- Tatella ETHERIDGE, 1901, p. 27 [*Corbicella? maranoana ETHERIDGE, 1892, p. 471; OD]. Medium-sized, elongate, subrectangular or ovate, subequilateral, compressed, gaping slightly at both ends; RV with 2 short subumbonal teeth, LV with 1 blunt tooth recurved between them; no lateral teeth; anterior adductor scars elongate pyriform, oblique, posterior ones rounded; pallial line with small sinus; no ornament except concentric rugae. L.Cret., Australia.—FIG. H2,1. *T. maranoana, Maranoa River, Queensl.; 1a,b, LV, ext., hinge, $\times 1$ (Jack & Etheridge, 1892). [Cox]

Taxocardia Olsson & Harbison, 1953.

- Verticipronus HEDLEY, 1904 [*V. mytilus; OD]. Although assigned to Philobryidae by some authors, it was provisionally assigned to Carditidae and is so listed by POWELL and other Australasian workers. [KEEN]
- Zoreia BRUSINA, 1907 [*Z. sanguinea; M]. ?Pleist., Yugosl. Unfigured, minute (2 mm. long); description follows that of a species of Tapes in Veneridae, but it is so vague that one cannot be sure the author intended it in that family. [KEEN]

GENERA OF DOUBTFULLY MOLLUSCAN AFFINITIES

(With cross references to Treatise Part R)

Anatifopsis BARRANDE, 1872 (see p. R329).

- Aptychopsis Woodward, 1872 (see p. R329).
- Discinocaris Woodward, 1866 (see p. R329).
- Eoischyrina Kobayashi, 1933.
- Euchasmella Kobayashi, 1933.

Euclusaea GRAY, 1852. Brachiopod?

Bivalvia

- Fordilla BARRANDE, 1881.
- Lebescontia Jones & Woodward, 1899 (see p. R326).
- Lingulocaris SALTER, 1866 (see p. R330).
- Modioloides WALCOTT, 1889.
- Myocaris SALTER, 1864 (see p. R331).
- Ozomia Walcott, 1924.
- Paleodora FLEMING, 1957.
- Pinnocaris Etheridge, 1878 (see p. R331).
- Pseudoeuchasma Kobayashi, 1933.
- Pseudotechnophorus KOBAYASHI, 1933.
- Ribeirella Schubert & WAAGEN, 1903.
- Ribeiria Sharpe, 1853.
- Spirodomus BEECHER, 1886, p. 162 [*S. insignis; OD, M]. Miss. (Waverly), USA (Pa., Warren Co.). Probably not a mollusk. [NEWELL]
- Wanwania Kobayashi, 1933.
- Wanwanella Kobayashi, 1933.
- Wanwanoidea Kobayashi, 1933.

UNRECOGNIZABLE GENERA

- Aegilops HALL, 1850, p. 179 [*A. subcarinata; M]. M.Ord.(Trenton), USA(N.Y.). [Possibly a cyrtodontid (p. N248).]
- Burriera LASERON, 1910 [*B. dunii; OD]. L.Perm. (U. Marine, Wandrawan.), Australia(N.S.Wales). [NEWELL]
- Dolabra M'Cox, 1844. Carb. [May belong to Myophoridae.]
- Hemisterias RAFINESQUE, 1832, p. 142 [*H. quadriloba; M]. ?Penn., Sherman Cr., Allegheny Mts., USA(Pa.). [NEWELL]
- Mactrula Risso, 1826.
- Pleureterites RAFINESQUE, 1832, p. 142 [*P. lateristria; SD NEWELL, herein]. ?Penn., Sherman Cr., Allegheny Mts., USA(Pa.). [NEWELL]

- Preavicula Williams & Breger, 1916, p. 205 [*Megambonia oblonga Hall, 1895; OD]. L.Dev., USA(N.Y.). [NEWELL]
- Protopecten HIND, 1910 [*P. vimineus, *P. crenulatus]. Probably a brachiopod. Sil.(Llandov.), Eu.(Eng.). [NEWELL]
- Sarka BARRANDE, 1881, p. 150 [*S. infelix; M]. Possibly a brachiopod. M.Dev., Eu.(Boh.). [New-ELL]
- Telistrophis RAFINESQUE, 1832, p. 142 [*T. torsala; OD, M]. ?Penn., Sherman Cr., Allegheny Mts., USA(Pa.). [NEWELL]

Family UNCERTAIN

Paramonopleura Korobkov in Korobkov & Makar-ENKO, 1967 [addition by B. F. PERKINS (see p. N783)]. Anterior muscle insertion of AV on shell wall, posterior insertion on prolongation of cardinal platform and separated from 3' by low ridge; muscle insertions of FV on thickened areas of shell wall. [Note.-If the conclusions of KOROBKOV & MAKARENKO are correct, this genus would be the only known Tertiary rudist. It was assigned to the Monopleuridae by KOROBKOV, but without data on larger, more mature shells, such placement is doubtful. The size of the type specimens and their occurrence in "glauconitic sandy-argillaceous deposits with intercalations of shelly detritus" suggest that they may be juveniles reworked from older deposits.] [Ref.-Korobkov, I. A., & MAKARENKO, D. YE., 1967, Paramonopleura gen. nov. (Rudistae) iz verkhnego Paleotsena Ukrainy: Paleont. Zhurnal, no. 4, p. 135-138, 1 fig. [Paramonopleura gen. nov. (Rudistae) from the upper Paleocene of the Ukraine: Paleont. Jour., 1968 (July), no. 4, p. 109-112, 1 fig. (transl. Am. Geol. Inst.).]